RESEARCH ARTICLE

Life at the top: Lake ecotype influences the foraging pattern, metabolic costs and life history of an apex fish predator

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Abstract

1. We used acoustic telemetry and acceleration sensors to compare population-specific measures of the metabolic costs of an apex fish predator living in four separate lakes. We chose our study species and populations to provide a strong test of recent theoretical predictions that optimal foraging by an apex fish predator in a typical aquatic environment would be consistent with feeding to satiation rather than continuous feeding. We chose four populations where the primary prey type differed along a body size gradient (from small invertebrates to large planktivorous fish) and along a thermal accessibility gradient (from easily accessible cold-water pelagic prey to less accessible warm-water epilimnetic and littoral prey). We expected that these gradients in prey type would evoke distinctly different activity gradients depending on whether predators fed to satiation (e.g., less frequent "rest" detections where primary prey are smaller/less accessible) or fed continuously (e.g., fixed level of "rest" detections under all prey conditions).

2. Our study organism was a fall spawning, cold-water visual apex predator (lake trout). Therefore, we focused our study on diel (early night, dawn, day, dusk, late night) changes in metabolic costs associated with summer feeding behaviour. The duration (~20 days) and fine temporal scale (~30 min) of our behavioural data provided a uniquely detailed picture of intra- and inter-population differences in activity patterns over a critical period in the annual growing season.

3. In all populations, diel shifts in activity were qualitatively consistent with that expected of a visual predator (e.g., resting state detections were most frequent at night).

4. Between-lake differences in daytime thermal experience were qualitatively consistent with between-lake differences in the location of primary prey (e.g., excursions to warm habitats were common in lakes with epilimnetic/littoral fish as primary prey and relatively rare in lakes with pelagic cold-water invertebrates/fish as primary prey).

5. Daytime activity patterns were more consistent with the feeding pattern expected from feeding to satiation rather than continuous feeding: (a) individuals in all four populations exhibited clearly delineated bouts of resting behaviour and active behaviour; (b) the frequency of resting bouts and the resultant overall cost

of daily activity were strongly associated with the size and accessibility of prey—in lakes with smaller and/or less accessible prey, predators rested less frequently, exhibited marginally higher costs when active and had higher overall daytime activity costs. Within each lake, similar changes in activity occurred concurrently with diel changes in prey accessibility/relative density.

KEYWORDS

acceleration telemetry, activity costs, metabolism in wild animals, predator bioenergetics, prey and predator

1 | INTRODUCTION

Foraging is a primary activity for all animals: it provides the energy needed for all other biological processes (e.g., basal and active metabolism, tissue production—Brett & Groves, 1979; Brown, Gillooly, Allen, Savage, & West, 2004). Fitness increases when an organism can reduce the energy it uses for necessary metabolic processes and invests the resultant surplus in the production of tissues (Jobling, 1994; Quince, Abrams, Shuter, & Lester, 2008) that support improved survivorship and/or reproductive success (e.g., Kozłowski, Czarnołęski, & Dańko, 2004; Lester, Shuter, & Abrams, 2004). Foraging activity refers to the time and energy spent searching for food: the greater the time spent in foraging, the greater the activity cost (Boisclair & Leggett, 1989; Kerr, 1982) and the less energy is available for other processes. For fish, foraging can be a costly metabolic process (Fish, 2010; Jobling, 1994), taking up to 40% of total energy expenditure in some situations (Boisclair & Leggett, 1989; Jobling, 1994), and these costs can escalate if fish have to forage outside their environmental tolerance, for example in anoxic, turbid or thermally unfavourable waters.

Theoretical studies (e.g., Giacomini, Shuter, & Lester, 2013; Kerr, 1971) suggest that the prey size of particulate feeding fish predators must increase with predator size if growth efficiency is to be maintained. In pelagic environments, individual productivity is much more sensitive to changes in prey size than to changes in prey density (Appendix S1) and, given the slow decline in biomass density with prey size that is typical of freshwater pelagic environments (Sprules & Barth, 2016), particulate feeding on smaller prey leads to higher foraging costs per calorie consumed, with a consequent decline in growth efficiency and net growth overall (Appendix S1). These higher activity costs can modify optimal life-history trajectories, leading to smaller adult body sizes (Giacomini et al., 2013; Quince et al., 2008). These arguments can be extended to include additional metabolic costs associated with feeding in thermally unfavourable environments (Appendix S1). The qualitative effect on net energy gain of this sort of reduction in prey accessibility matches the effect of a reduction in prey size.

Many studies of marine and freshwater fish species have revealed correlations that are consistent with this theory: size of preferred prey increases with predator size (Fuji, Kasai, Ueno, &

Yamashita, 2016; Graeb, Mangan, Jolley, Wahl, & Dettmers, 2006); predator growth rate and/or condition increase when accessibility of larger prey increases (Golet et al., 2015; Kaufman, Morgan, & Gunn, 2009); size at maturity and maximum adult size change in concert with changes in typical prey size (Kennedy, Bartley, Gillis, McCann, & Rennie, 2018; Shuter, Giacomini, de Kerckhove, & Vascotto, 2016). In addition, physiological measures of activity on top predators (e.g., respiratory enzyme concentrations—Sherwood, Pazzia, Moeser, Hontela, & Rasmussen, 2002; Kaufman, Gunn, Morgan, & Couture, 2006; indices based on bioenergetic models of contaminant accumulation—Henderson, Morgan, & Vaillancourt, 2004; Pazzia, Trudel, Ridgway, & Rasmussen, 2002) are also consistent with this theory.

In a recent extension of these ideas (Giacomini et al., 2013), the performance of two different foraging strategies ("constant activity" and "constant satiation") was evaluated in environments where prey size varies and predator life histories are shaped by size-dependent allometric relationships for both metabolic rate and fecundity. In typical aquatic environments, optimal foraging through "constant satiation" was superior to optimal foraging through "constant activity." Under the constant activity hypothesis evaluated by Giacomini et al. (2013), (a) a visual predator is expected to forage consistently throughout its diel feeding period with a feeding pattern (i.e., the combination of time "at rest" and energy expenditure when actively foraging) that is independent of prey size/accessibility/density; (b) consequently, foraging cost is independent of prey size/accessibility/density and both ingestion rate and net energy gain vary directly with prey density. Under the constant satiation hypothesis, (a) a visual predator is expected to become satiated within its diel feeding period and hence exhibit a feeding pattern that depends primarily on prey size/accessibility; (b) consequently, ingestion is independent of prey density and both foraging cost and net energy gain depend primarily on prey size/accessibility.

Physiological constraints and theory lead to a clear set of expected behavioural changes for a top predator whose feeding behaviour is shaped by "constant satiation": smaller, less accessible prey should be associated with a feeding pattern characterized by a shorter "rest" period, a longer period of active foraging and a relatively constant level of energy expenditure while actively foraging. Four arguments support this set of expectations: (a) since active foraging typically ceases post-satiation (Fu et al., 2009; Gill, 2003;

Nie, Cao, & Fu, 2017; Nie & Fu, 2017), and since small prey typically require shorter digestion times due to higher surface area-to-volume ratios (Andersen & Beyer, 2005; Legler, Johnson, Heath, & Ludsin, 2010; Sun, Liu, Liu, & Tang, 2010), therefore the post-feeding digestive "rest" period of a predator should be shorter when feeding to satiation on small prey; (b) since more small prey are needed to reach satiation (Deslauriers, Chipps, Breck, Rice, & Madenjian, 2017; Gill, 2003), and since the search distance required to capture sufficient prey for satiation is longer for small prey in typical pelagic environments (Appendix S1), therefore the foraging cost needed to reach satiation should be greater for a predator feeding on small prey; (c) since foraging cost is an increasing function of both time spent foraging and swimming speed while foraging, and since the cost of swimming increases with the square of swimming speed (e.g., Weihs, 1973), therefore the net energy gain when feeding to satiation will be greater if the higher foraging distance required when feeding on small prey can be covered by increasing foraging time rather than foraging speed (Werner & Anholt, 1993); (d) in the absence of predation risk (Nie et al., 2017), "fitness" (e.g., net energy gain, reproductive value) is maximized by minimizing the foraging cost required to reach satiation (Abrams, 1982, 1991; Houston & McNamara, 2014).

These expectations are particularly well suited to testing in the wild with acceleration telemetry (e.g., Cooke et al., 2016; Cruz-Font, Shuter, & Blanchfield, 2016), and our objective in this study was to carry out such a test by: (a) generating extended (~20 days), temporally fine scale (~10 min) direct measures (i.e., the frequency of resting periods and the intensity of activity during active periods) of the feeding activity of an apex visual predator during a critical period in its annual growing season; (b) comparing those measures across populations that differ greatly in both the size and accessibility of available prey. Acceleration telemetry has been used in much recent work to assess the short-term impact on fish behaviour of various anthropogenic manipulations (e.g., fisheries capture—Gutowsky et al., 2017; light pollution—Foster, Algera, Brownscombe, Zolderdo, & Cooke, 2016). Our study is one of only a few so far reported (e.g., Brownscombe, Cooke, & Danylchuk, 2017) that uses acceleration telemetry to generate cross-population comparative data designed to address a question of fundamental ecological interest.

2 | MATERIALS AND METHODS

2.1 | Testing the theory

2.1.1 | Choosing the test organism

We focused our work on lake trout *Salvelinus namaycush*, an apex visual predator that lives in many lakes across Canada and the northern United States. Lake trout is a fall spawning, cold-water fish (preferred temperature ~12°C—Hasnain, Shuter, & Minns, 2013; frequented temperature range of 4–18°C—Plumb & Blanchfield, 2009). Lake trout prey communities can differ widely in size, species composition, energetic value (Vander Zanden & Rasmussen, 1996) and thermal accessibility (Guzzo, Blanchfield, & Rennie, 2017;

Morbey, Addison, Shuter, & Vascotto, 2006). Plasticity in both the growth and life history of this species has long been recognized (Martin, 1966, 1970), and empirical links with prey size, lake size and climate are well documented (Matuszek, Shuter, & Casselman, 1990; McDermid, Shuter, & Lester, 2010; Shuter, Jones, Korver, & Lester, 1998). This empirical work inspired some of the first theoretical studies (Kerr, 1971; Kerr & Martin, 1968) on the links between prey size, growth and life history, and lake trout has served as a model organism in several more recent theoretical treatments (Giacomini et al., 2013; Quince et al., 2008; Shuter et al., 2016). In addition, lake trout has also been the focus of several recent empirical tests of that theory (e.g., Pazzia et al., 2002; Shuter et al., 2016) and is particularly suited to behavioural studies using acoustic telemetry (Cruz-Font et al., 2016; Guzzo et al., 2017; Morbey et al., 2006).

2.1.2 | Choosing the test populations

Lake trout populations generally fall along a continuum of prey size/adult size combinations, ranging from small prey/small adults to large prey/large adults (Quince et al., 2008). Under "constant satiation," we would expect to see the lowest frequency of resting behaviour in small prey/small adult populations, the highest frequency in large prey/large adult populations and intermediate levels in populations falling in the middle of this continuum. We used the extensive data available on existing lake trout populations (e.g., McDermid et al., 2010; Vander Zanden & Rasmussen, 1996) to select four lake populations that would cover the full range of expected behaviour (Figure 1) and thus provide a strong test of the hypothesis that foraging patterns in the wild are dominated by behaviours consistent with "constant satiation" rather than "constant activity."

All four study lakes contained littoral minnows and small-bodied pelagic zooplankton as potential lake trout prey (Figure 1). Either of these prey types may dominate lake trout diets when preferred prey is absent (e.g., Konkle & Sprules, 1986; Morbey et al., 2006), or access to other prey is limited by adverse environmental conditions (e.g., high water temperatures—Tunney, McCann, Lester, & Shuter, 2014). Each study lake contains a different prey community (Figure 1, Appendix S2): (a) Lake 373 has abundant (~13 per m^3, Paterson, Podemski, Wesson, & Dupuis, 2011), cold-water invertebrate prey *Mysis diluviana*, or *Mysis* hereafter; (b) Lake 626 has yellow perch *Perca flavescens* (introduced ca. 2005—Wall & Blanchfield, 2012), a forage fish of moderate size, with a preferred temperature (~18°C—Hasnain et al., 2013) that exceeds the preferred temperature for lake trout by an amount sufficient to ensure that it is typically found in epilimnetic and/or littoral habitats that are thermally hostile to lake trout in summer; (c) Lake Louisa has no alternate prey; consequently, lake trout diet is dominated by zooplankton and littoral minnows (Konkle & Sprules, 1986; Morbey et al., 2006); and (d) Lake Opeongo has abundant (~0.03 per m^3—Moryk, 2010) cisco *Coregonus artedi*, a large pelagic, cold-water planktivore which is a preferred prey for lake trout—Matuszek et al., 1990; Shuter et al., 2016), along with yellow perch. Prey resources in Lakes 626 and Louisa are similar in that larger vertebrate prey (perch, minnows) are
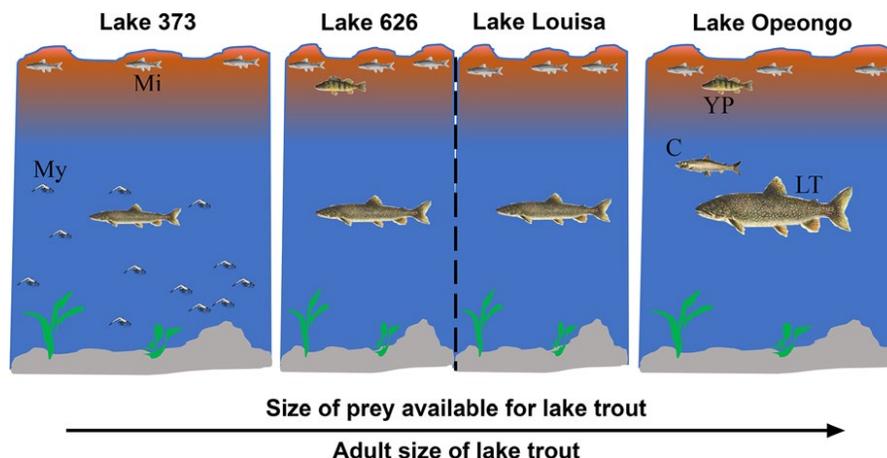
FIGURE 1 Representation of the four ecotypes studied where lake trout (LT) is the apex predator in each of the lakes and feeds on the prey it has available: *Mysis* (My), minnows (Mi), yellow perch (YP) and/or cisco (C). The lakes are ordered along a size continuum for adult lake trout and for its prey (prey and predator smallest in Lake 373, and largest in Lake Opeongo). Lakes 373 and Opeongo represent lakes where prey types are readily available (pelagic) and share the same thermal habitat with LT (cold and cool); therefore, foraging costs are expected to be lower and lake trout adult sizes higher in Lake Opeongo compared to Lake 373. Lakes 626 and Louisa are similar in terms of lack of available prey in the preferred habitat of LT (prey is more abundant in the warm littoral areas), with typical prey sizes lying between the extremes established by Lakes 373 and Opeongo. The black dotted line between Lake 626 and Lake Louisa is meant to represent the similarities in prey availability. This figure does not accurately represent the depth of each lake

found in epilimnetic/littoral environments that were thermally hostile to lake trout during the study period (Figure 1).

Life-history characteristics of each population (Table 1) are well documented (see Appendix S3 for methods) and follow the expected pattern of small adults in lakes with small and/or less accessible prey and large adults in the lake with large and accessible prey. Lake trout in Lake 373 have the smallest maximum size, Lake Opeongo fish have the largest, and values for the other lakes lie between these extremes. Lake Louisa fish mature at the smallest size, Lake 373 and 626 fish are somewhat larger at maturity and Lake Opeongo fish are largest. In contrast, adult mortality rates in 373/626 are similar and ~ 50% lower than in Louisa and Opeongo—a result consistent with the fact that the Algonquin lakes are subjected to moderate levels of angler harvest (e.g., Shuter, Matuszek, & Regier, 1987) while the ELA lakes are unexploited. Although overall angling effort on Opeongo is higher than on Louisa, many Opeongo anglers have little experience fishing on the lake (Shuter et al., 1987) and hence the similarity in their total mortality rates is not surprising.

In all four lakes, usable lake trout habitat was known to be sufficiently constrained spatially (i.e., the overall lake surface area is small in Lakes 626 and 373, and the usable lake trout habitat space has been mapped in previous studies in Lakes Louisa and Opeongo) that temporally fine scale (~10 min) telemetry data could be generated with an affordable network of receivers.

2.1.3 | Choosing the test period

We chose midsummer as our study period in all lakes: this covers a significant portion of the intense feeding period that supports the gonadal development (Morbey & Shuter, 2013; Plumb, Blanchfield, & Abrahams, 2014) essential for successful reproduction, but is sufficiently separated from the October spawning period (Weatherley, Kaseloo, Gare, Gunndr, & Llpicnik, 1996) so that the observed behaviour should only reflect foraging. To compare lakes under relatively similar environmental conditions, we focused our analysis on data collected during the 20-day period in each lake when (a) average epilimnetic water temperatures reached their seasonal maximum, (b) all lakes were fully stratified, and (c) the temperature difference between epilimnion and hypolimnion always exceeded 10°C (Appendix S4). ELA lake trout were tracked from July to August of 2010, and Algonquin lake trout from July to August of 2011. Offshore water temperatures were sampled in each lake with a single string of temperature thermistors (Onset HOBO Data Loggers, Cape Cod, MA, USA) deployed at regular depths (every 1 m in ELA lakes; every 1.5 m in Algonquin lakes) down to the top of the hypolimnion and every 5 m thereafter. The temperature sampling interval was 30 min in ELA lakes and 15 min in Algonquin lakes.

2.2 | Activity transmitter implantation and data collection

The activity of 36 adult lake trout was studied using internally implanted acceleration–depth telemetry transmitters (V9AP, VEMCO, Nova Scotia, Canada; Table 2). Transmitters were implanted in the posterior of the body cavity, following recommended procedures for fish (Harms, 2005), adapted to this type of transmitter (see Cruz-Font et al., 2016 and Appendix S5.1 for details). Transmitter depth sensors were calibrated prior to implantation in fish.

TABLE 1 Population life-history characteristics for lake trout across the study lakes

Lake	L_{mat} [SE] (mm) (n; CI)	L_{max} [SE] (mm) (n; CI)	$L_{max\ vb}$ [SE] (mm) (n; R^2)	Z [SE] (age range; R^2)
373	379.6 [2.7] (179, 374–384)	425 [2.56] (179; 418.4–428)	409 [1.72] (176; 0.78)	0.183 [0.01] (7–25; 0.95)
626	392 [2.6] (505; 386–395)	452 [2.11] (505; 448.6–455.6)	428 [1.76] (468; 0.50)	0.173 [0.01] (5–28; 0.91)
Louisa	348 [1.1] (2,090; 346–350)	417 [2.29] (2,090; 414–422)	471 [10.4] (347; 0.73)	0.375 [0.03] (6–15; 0.96)
Opeongo	440 [2.44] (1,310; 434–445)	603 [4.55] (1,310; 595–610)	752 [7.5] (2,455; 0.69)	0.364 [0.02] (7–20; 0.98)

Note. Maturation traits (size at first maturity—L_{mat}) and maximum size (L_{max}) were estimated from pooled information from males and females. This is acceptable given the typically low sexual dimorphism observed in lake trout (McDermid et al., 2010). Bootstrap methods were applied to the 20% and 90% quantiles for the fork length distribution of mature fish to generate both mean and standard error (SE) values for L_{mat} and L_{max}, respectively. Von Bertalanffy fits to fork length-at-age data were used to generate a second set of L_{max} estimates ($L_{max\ vb}$). Regression analysis of relative abundance at age data was used to estimate adult mortality (Z). Sample size (n) and R^2 values are given where relevant (see Appendix S3 for details).

TABLE 2 Information for the fish studied in each of the lakes

Lake	Year	No. of fish	Mean size [range] (mm)	Mean mass [range] (g)
373	2010	10	401 [354–454]	665 [499–785]
626	2010	10	421 [356–540]	839 [487–1,848]
Louisa	2011	9	387 [327–455]	663 [500–1,100]
Opeongo	2011	7	463 [361–566]	1,223 [520–1,920]

Note. All sampled fish were adults and were implanted with acceleration–depth transmitters.

The transmitters alternately measured and reported estimates of (a) depth (in m.) and (b) acceleration (A in arbitrary units—a.u.). Acceleration was measured on just the lateral and dorso-ventral axes of the transmitter, in order to capture the acceleration of the fish's tail when engaged in the lateral, undulating movements associated with swimming (Cruz-Font et al., 2016). The two-axis values from each measurement were summed to yield a single sample value. Acceleration was reported as the root mean square of ~450 sample values, recorded over a 45-s time period. Depth was sampled instantaneously, and the following acceleration sampling interval was initiated immediately after reporting the depth. The reporting interval between successive sensor estimates (depth then acceleration) was approximately 2 min (i.e., the time interval between each report varied randomly between 100 and 140 s). In practice, the reporting interval between successive estimates from the same sensor (depth–depth or acceleration–acceleration) was ~5 min. The raw acceleration data (values ranging from 1 to 255 a.u.) represent measures of the frequency of fish tailbeats in the lateral and dorso-ventral axes of the fish. Consequently, they do not directly translate to forward acceleration of tagged fish, but can be used to estimate swimming speed and the metabolic cost of swimming (M_{swim}), using the results from laboratory calibration studies (Cruz-Font et al., 2016 and Appendix S5.2). The temperature that each fish experienced was estimated over each 30-min period for each day by coupling the mean depth occupied by each individual fish over each 30-min period with the lake-specific water temperature-at-depth profile for that same 30-min period. Standard metabolism (M_{std}) for each fish at each point in time was estimated from its weight and temperature using well-founded, laboratory-derived relationships (Evans, 2007). This M_{std} value,

along with the concurrent value for M_{swim}, was used to estimate an activity cost index ACI = M_{swim}/M_{std}.

Underwater omni-directional receivers (a mix of VR2s and VR2Ws, Vemco, Nova Scotia, Canada) were used to detect the transmitter signals. The receivers were deployed at fixed positions (Figure 2), selected to maximize the acoustic coverage of the lakes and improve fish detection probability. The acoustic arrays in the small ELA lakes provided almost complete coverage, and consequently, ELA fish were detected with a higher average frequency (~every 5 min across all fish) compared to Algonquin fish (~15 min on average, with frequencies reaching ~5 min for some detection strings).

2.3 | Analysis of telemetry data

2.3.1 | Data screening and diel data partitioning

False detections (caused by signals too close in time or fish exhibiting apparent swimming speeds faster than their physiological capacity) were identified and removed. Throughout the study period, mortality checks were run on the location and depth data from each fish included in our analyses: all fish exhibited some level of movement and activity throughout the study period and hence were judged to be alive and exhibiting "typical" behaviour.

As a visual predator (Vogel & Beauchamp, 1999), time of day (a proxy for illumination intensity) is an important determinant of lake trout foraging behaviour (Hrabik, Jensen, Martell, Walters, & Kitchell, 2006; Jensen, Hrabik, Martell, Walters, & Kitchell, 2006). Therefore, we assigned each acceleration-detection to one of five periods of the day according to the level of illumination existing
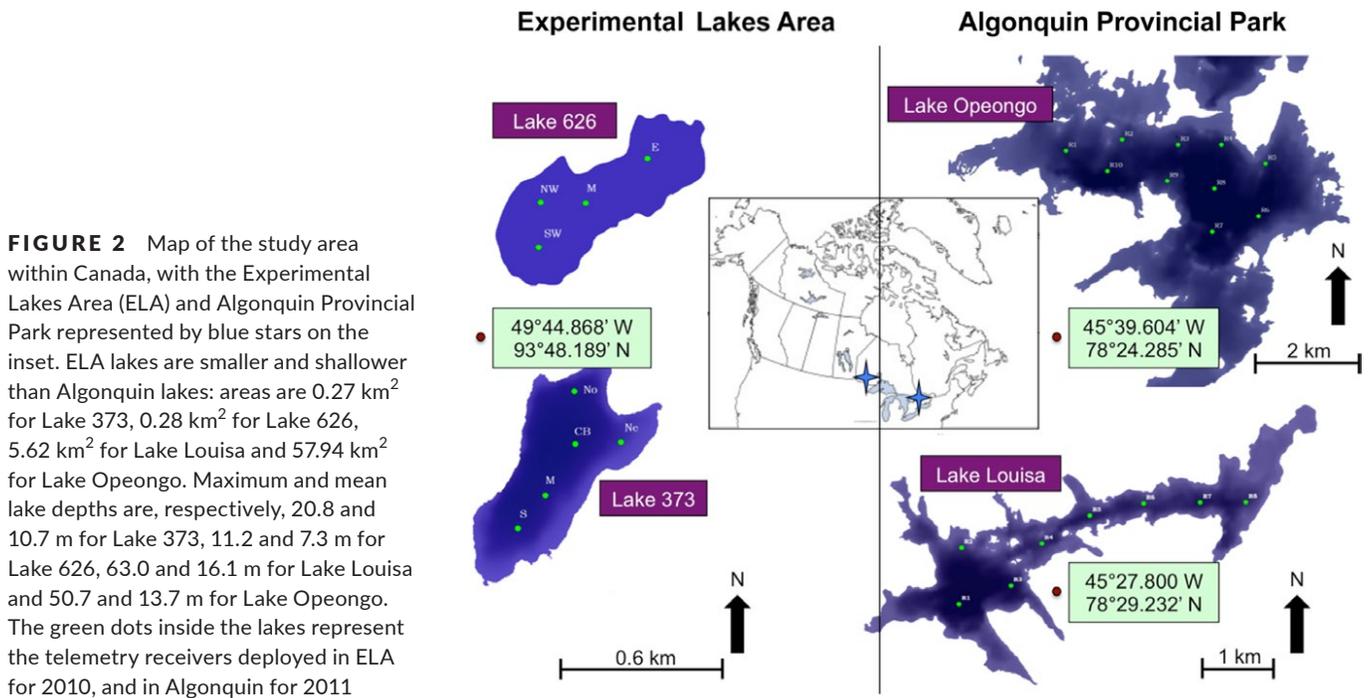
FIGURE 2 Map of the study area within Canada, with the Experimental Lakes Area (ELA) and Algonquin Provincial Park represented by blue stars on the inset. ELA lakes are smaller and shallower than Algonquin lakes: areas are 0.27 km^2 for Lake 373, 0.28 km^2 for Lake 626, 5.62 km^2 for Lake Louisa and 57.94 km^2 for Lake Opeongo. Maximum and mean lake depths are, respectively, 20.8 and 10.7 m for Lake 373, 11.2 and 7.3 m for Lake 626, 63.0 and 16.1 m for Lake Louisa and 50.7 and 13.7 m for Lake Opeongo. The green dots inside the lakes represent the telemetry receivers deployed in ELA for 2010, and in Algonquin for 2011

at the time the detection was reported. The periods were defined by sunlight data obtained from the National Research Council of Canada (https://www.nrc-cnrc.gc.ca/eng/services/sunrise/index.html) and were as follows: (a) N1 early night: the period from midnight to the beginning of morning nautical twilight; (b) T1 dawn: the period from the start of morning nautical twilight until sunrise; (c) D day: the period from sunrise until sunset; (d) T2 dusk: the period from sunset until the end of evening nautical twilight; and (e) N2 late night: the period from the end of evening nautical twilight to midnight.

2.3.2 | Defining active and "resting" states

In the laboratory, lake trout were observed to be inactive (motionless or with slow movements of pectoral fins only) at values of acceleration <8 a.u. with levels of oxygen consumption typical of fish "at rest" (Cruz-Font et al., 2016). For these situations, total metabolism (M_{tot}) was assumed equal to standard metabolism (M_{std}) and therefore both swimming metabolism (M_{swim}) and our index of activity cost (ACI = M_{swim}/M_{std}) were set to 0. After applying this filter to the field-based acceleration data, we found that $\log_{10}$-transformed values for all the ACI data from each lake were strongly bimodal (Appendix S6). The first mode represented ACI values corresponding to acceleration ≤ ~ 8 a.u., the level characteristic of "resting" behaviour in the laboratory. Since this bimodal pattern in ACI values is consistent with the hypothesis that fish can exhibit two quite different modes of behaviour (i.e., resting and active), we analysed the data accordingly by: (a) splitting the data into two subsets: resting (A ≤ 8 a.u.) and active (A > 8 a.u.); (b) assessing how the frequency of occurrence for the resting state varied over time of day, both within and between lakes; and (c) assessing how the level of activity

exhibited during active periods varied over time of day both within and between lakes.

2.4 | Statistical analyses

The autocorrelation pattern in the activity data for each individual in each time period was assessed over lags 1–9. Across lakes and time periods, values were low: for lag 1, typical autocorrelation values ranged from −0.13 to +0.25 with a median of 0.08. Values for longer lags had narrower ranges, all with medians close to 0. This result is consistent with the assumption that individual activity measures are relatively independent of each other and hence permits our use of the standard statistical fitting procedures outlined below.

2.4.1 | Resting states

For the "resting" dataset, we compared the proportion of detections that represented resting behaviour (i.e., A ≤ 8 a.u.) across lakes and times of day. The proportions were calculated for each individual fish within each lake and for each time period of the day. We used generalized linear mixed-effects models (GLMM), specifically logistic regression, because they are appropriate for analysing proportional data (Warton & Hui, 2011). The predicted variable (the logit function of the ratio of "resting detections" to the total number of detections within a time period) was modelled with lake and time of day as fixed effects and individual fish as random effects within lakes. This model was fitted using the "lme4" package (Bates, Maechler, Bolker, & Walker, 2015) within the R environment (R Core Team 2017). The structure (random and fixed effects) of the "best" (based on AIC) GLMM was used in a likelihood ratio test performed using the type II ANOVA option from the "car" package in R (Fox & Weisberg, 2011; Langsrud,

2003), which compares the significance of covariates (lakes, period of day) and interactions, when present, and reports a chi-squared (χ^2) statistic. Pairwise comparisons of the proportion of resting behaviour observed among lakes at different times of day were performed with two tests: Tukey's pairwise comparisons (Tukey's) and Fisher's least significant difference test (Fisher's LSD) (Sokal & Rohlf, 1995). We used both tests because each was best suited to particular characteristics of the data: the a priori Fisher's LSD test was appropriate given our basic study design of pre-selecting study lakes to make pre-planned comparisons of the effect of prey size on the relative occurrence of resting vs. active states; however, we supplemented this with the more conservative Tukey's test for pairwise comparisons to account for the unbalanced aspects (e.g., unequal sample size across lakes) of the final dataset. These tests were performed using the "multcomp" package in R (Hothorn, Bretz, & Westfall, 2008), which permits the use of mixed model structures in multiple comparisons.

2.4.2 | Active states

For the active dataset (A > 8 a.u. and ACI > 0), the ACI values were $\log_{10}$-transformed to achieve normality. Since the data consisted of repeated measures on random individual fishes grouped into four different lakes, we used linear mixed models (LMM—Zuur, Ieno, Walker, Saveliev, & Smith, 2009) to compare the mean values of ACI across lakes and time periods of the day as fixed effects, and individual fish as random effects within lakes. Because these data were unbalanced, we used the mixed model structure in a likelihood ratio test performed by the type II ANOVA option within the "car" package (Fox & Weisberg, 2011) in R (R Core Team 2017), which uses a Wald test to evaluate the ANOVA results, and reports a chi-squared (χ^2) statistic. Similar to the resting state dataset, we performed multiple comparisons of mean ACI across lakes using the best LMM structure (random and fixed effects) and applied Tukey's and Fisher's LSD (Sokal & Rohlf, 1995).

3 | RESULTS

3.1 | Overall patterns in lake trout metabolic rates, depths and temperatures

Among-lake differences in raw metabolic rate and ACI values were often significant but not particularly large. The largest among-lake

differences were observed for M_{std} (Appendix S7), and these were the product of among-lake differences in body size and experienced temperature, as defined in Evans' (2007) equation.

Low median acceleration values were common across all lakes (Table 3; Appendix S8). Lake-to-lake differences in resting state occurrence frequency were consistent across time: for each of the 20 days of the study, the daily resting state frequency was typically <20% in Lake 373 and was almost always between 25 and 50% in Lake Opeongo. These lake-to-lake differences were also consistent across individual fish: for all individuals in Lake 373, the resting state occurrence frequency was always < 25% and was always between 25 and 50% for all individuals in Lake Opeongo (Appendix S9). Visual inspection of the raw acceleration data from these two lakes reveals some individual variation between fish within lakes; however, it is clearly smaller than the overall difference between these two lakes.

Peaks of high activity (A ≥ 130 a.u., laboratory swimming speeds of ~ 80 cm/s) were observed in all lakes, and the maximum values reported by the activity transmitters (250–255 a.u., representing burst movements with laboratory swimming speeds ≥110 cm/s) were most frequent in Lakes Louisa (0.7%) and Opeongo (2%).

The depths of lake trout throughout the study period were around or below the thermocline (Appendix S9). Variability in depth among fish was greater in 373 and 626, with some fish visiting depths as shallow as 1–2 m, but this was not common (< ~ 2% of detection overall); in addition, the range of depth visited by each individual fish across all lakes was on average within 1–2 m, except for two fish in Lake Louisa that on average changed depth within a range of 5–10 m. In Louisa and Opeongo, most fish stayed near the thermocline during the study period, with occasional forays to both deeper and shallower waters. Lake Louisa fish experienced the warmest temperatures (Appendix S9) while Lake 373 fish exhibited the coldest; however, across all lakes and fish, the estimated median temperature experienced by lake trout was below 15°C (Table 3).

3.2 | Differences in the occurrence frequency for resting states

Across lakes and daily time periods, Opeongo fish exhibited the highest frequency of resting state detections (mean ± SE = 0.6 ± 0.02), reaching values as high as 0.9 (Figure 3, Appendix S10a). In contrast, Lake 373 fish exhibited the lowest occurrence frequency

TABLE 3 Values reported by depth–acceleration transmitters implanted in fish

Lake	Year	No. of fish	Median No of detections per individual	Depth (m)	Acceleration (a.u.)	Temperature occupancy (°C)
373	2010	10	4,529	7.8–9.9–13.0	13–23–38	5.8–7.1–10.0
626	2010	10	4,469	6.5–7.1–8.3	7–14–29	8.2–9.6–11.0
Louisa	2011	9	1,811	6.6–7.5–8.7	4–20–40	11.0–14.7–17.3
Opeongo	2011	7	671	10.0–12.0–17.1	5–9–23	6.5–8.9–10.0

Note. The information for the number of detections, fish depth, acceleration and temperature occupancy, corresponds to the 20 warmest days studied in each lake. Fish depth, acceleration and temperature occupancy are presented within the interquartile range (1st quartile–median–3rd quartile).

(0.26 ± 0.02). GLMM analyses revealed significant effects of both lake and time of day (χ^2 = 2,485, df = 12, p < 0.001) on resting state occurrence: across all lakes, the frequency peaked at night, with lower frequencies during daylight periods. Opeongo fish exhibited higher frequencies than all other fish during night, dawn and dusk.

Pairwise comparisons of differences in the occurrence frequency of resting states (Figure 3) were consistent with the following observations: (a) across all lakes, the night periods (N1 and N2) exhibited the highest resting state occurrence frequencies; (b) across all lakes and periods, Lake 373 fish exhibited the lowest resting state occurrence frequencies; (c) the greatest lake-to-lake differences in resting state occurrence took place in the twilight periods of the day, with Opeongo fish consistently exhibiting the highest frequency during both dawn and dusk; and (d) for the daylight period, no significant differences were found between 626, Louisa and Opeongo fish, suggesting a similar resting state frequency across these three lakes.

3.3 | Differences in the intensity of activity

To assess differences among lakes in diel variation in active metabolic rate, we plotted ACI distributions for each daily period across all four lakes (Figure 4, see also Appendix S10b). In each lake, lowest median ACI values occurred at night, with higher values during periods with some level of light (dawn, day and dusk). In Lake 373, the highest ACI values were observed during dawn, although day and dusk also exhibited higher ACI values compared to night. In Lakes 626, Louisa and Opeongo, the highest ACI values occurred during the day. LMM indicated that the interaction between lake

and the daily time period was significant. ANOVA of the best mixed model (ΔAIC = 13,923 between "best" model and next "best") showed that the variation in ACI across lakes was best explained by the significant interaction (F = 111.4, df = 12, p < 0.001, marginal R-squared = 0.20, and conditional R-squared = 0.32) between lake and daily period. Given the possibility that the variability within individuals could influence the overall response of ACI, we evaluated the possible improvement of a model where this variability was included. This could be the result of unique influential fish behaviours affecting the overall variance of the model. The amount of variation within groups was smaller than among groups (within-group variances were on average more than 50% smaller—d-hat^2 = 0.007—compared to the among-group variances—d-hat^2 = 0.2). The "best model" assumed that the main source of variation in the ACI data occurred around the population response (among lakes and time periods) rather than among individual fish behaviours. Multiple comparisons among groups (Figure 4) revealed dawn and dusk with the highest significant differences in median ACI among lakes. The general trend for both periods was characterized by decreasing values of ACI from Lake 373, with the highest values, to Opeongo with the lowest. During the day, median ACI values were similar across lakes, with significant differences only between Lakes 373 and 626. Finally, during the nighttime periods (N1 and N2), the median ACI value was highest in Lake 373 and then decreased in order from Lake 626 through Opeongo to Louisa. When we compared the means of the two nighttime periods across lakes, we found a significant lake–period interaction (F = 33.5, p < 0.0001) indicating that the two nighttime periods have statistically different behaviours with respect to the ACI across lakes.

Fisher's LSD pairwise comparisons

(a) N1

	373	626	LO	OP
373			***	***
626			*	*
LO				
OP				

(b) T1

	373	626	LO	OP
373		**	***	***
626				***
LO				*
OP				

(c) D

	373	626	LO	OP
373		***	*	*
626				
LO				
OP				

(d) T2

	373	626	LO	OP
373			**	***
626			.	***
LO				*
OP				

(e) N2

	373	626	LO	OP
373			**	**
626			*	**
LO				
OP				

Tukey's pairwise comparisons

(a) N1

	373	626	LO	OP
373			**	***
626				.
LO				
OP				

(b) T1

	373	626	LO	OP
373		*	**	***
626				**
LO				.
OP				

(c) D

	373	626	LO	OP
373		**		.
626				
LO				
OP				

(d) T2

	373	626	LO	OP
373			*	***
626				**
LO				
OP				

(e) N2

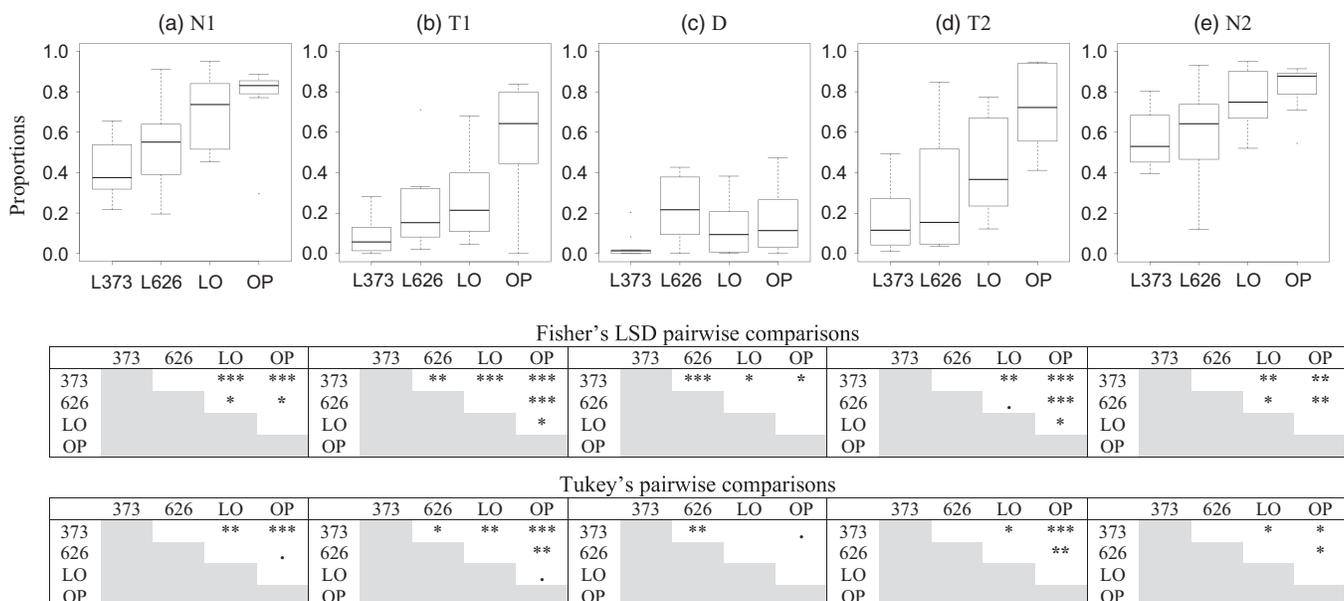|	373	626	LO	OP
373			*	*
626				*
LO				
OP				

FIGURE 3 The resting state contained the proportion of time that fish were detected with low acceleration (<8 a.u.) across five time periods of the day (early night—N1, dawn—T1, day—D, dusk—T2 and late night—N2). The boxplots represent the actual proportion of inactivity. However, the multiple comparison tests refer to the logistic models that used log odds ratio for the number of inactive detections. Tukey's and Fisher's LSD test results are presented for each period. The asterisks (*) indicate the level of significance as reported by R software: (***) for p < 0.001, (**) for p < 0.01, (*) for p < 0.05, (.) for p < 0.1 and () for p < 1
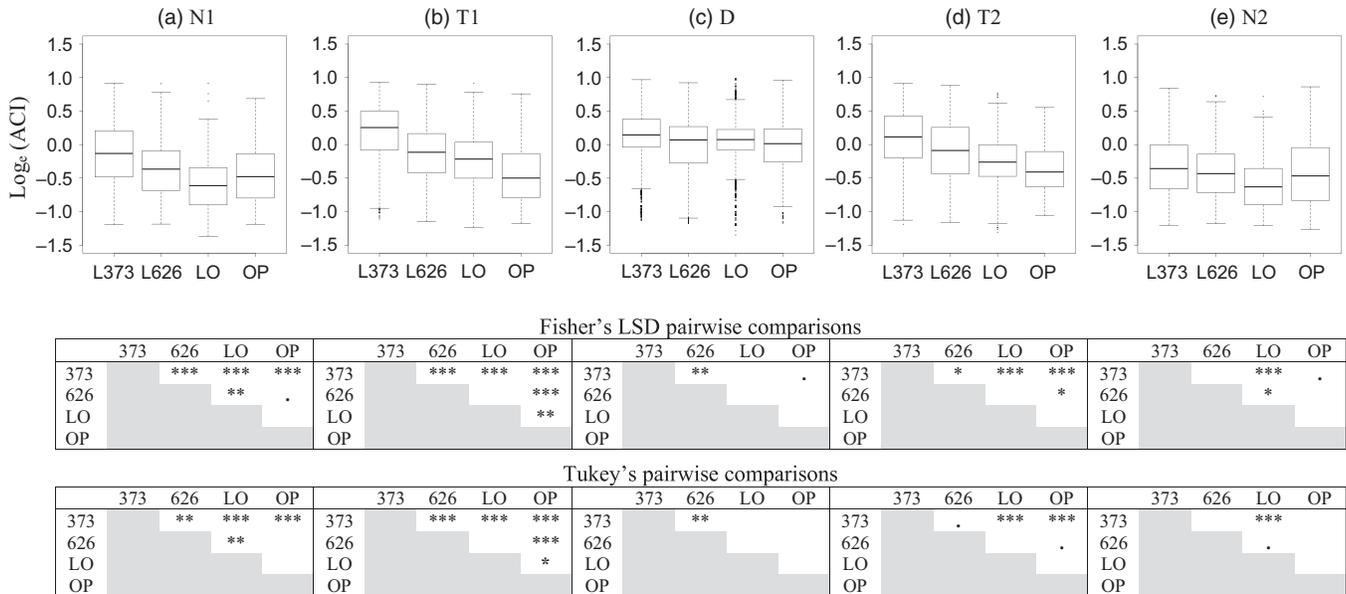
FIGURE 4 Pairwise multiple comparisons among lakes to characterize the differences in fish activity rate (measured by the cost index—ACI = M_{swim}/M_{std}) for the active dataset across five periods of the day (early night—N1, dawn—T1, day—D, dusk—T2 and late night—N2). Tukey's and Fisher's LSD test results are presented for each period. The asterisks (*) indicate the level of significance as reported by R software: (***) for $p < 0.001$, (**) for $p < 0.01$, (*) for $p < 0.05$, (.) for $p < 0.1$ and () for $p < 1$

4 | DISCUSSION

4.1 | Cross-lake differences in foraging patterns are consistent with "constant satiation"

Many models of fish growth (e.g., Deslauriers et al., 2017) and predation dynamics assume activity costs are invariant and that food ingestion rate is the major component of the energy budget affected by prey size/accessibility/density—the "constant activity" hypothesis (e.g., Casas & McCauley, 2012). However, some authors (Andersen & Beyer, 2006; Breck, 1993) have suggested an alternative view: that ingestion over a typical feeding period is relatively constant at near satiation levels and that it is active metabolism that varies in response to changes in prey size/accessibility/density—the "constant satiation" hypothesis. Our results are consistent with the "constant satiation" hypothesis: in all populations, a considerable fraction of potential foraging time was spent in a resting state, that fraction decreased with decreases in the size/accessibility of prey and this change was accompanied by moderate increases in ACI values. Lake trout from Lakes Louisa and 626 exhibited activity levels typically midway between fish from Lakes 373 and Opeongo, which is consistent with the fact that prey in these lakes were typically midway between Lake 373 and Opeongo in size and energy content, and were associated with habitats that were thermally unfavourable to lake trout and hence energetically costly to exploit. Our study adds to the growing body of empirical evidence that active metabolism does vary under natural foraging conditions (Boisclair & Leggett, 1989; Rennie, Johnson, & Sprules, 2012) and that top predators are often satiated.

Jeschke (2007) and Jeschke, Kopp, and Tollrian (2002) have argued that top predators in the wild are typically satiated and have supported this contention by comparing consumption in the wild with maximum expected consumption. Armstrong and Schindler (2013) have argued that fish exhibit maximum consumption rates that are rarely met under natural conditions. However, their empirical support for this contention hinges on a meta-analysis of fish growth models, most of which were fitted assuming constant activity. The cost of excess digestive capacity is high, and the ability to plastically adjust digestive capacity to average feeding conditions is widespread (Allen, Rosenfeld, & Richards, 2016; Piersma & van Gils, 2011). Hence, fitness should be enhanced by plastic adjustments of the satiation feeding level to what is typically achievable under natural conditions. This conclusion should hold except possibly in situations where prey accessibility varies widely on a time-scale sufficiently short that there is a selective advantage in maintaining excess digestive capacity to take advantage of brief "feast" intervals in a "feast or famine" environment (Armstrong & Schindler, 2013). However, Giacomini et al.'s (2013) analysis shows that this incentive would be opposed by additional selective pressures in favour of satiation foraging that operate at longer, life-history-level time-scales.

Our results also suggest that predator foraging activity varies adaptively within lakes, in response to diel changes in prey availability/density. In each lake, over the lake trout foraging window (T1 + D+T2) set by the diel light cycle (Vogel & Beauchamp, 1999), typical values for both foraging time and ACI increased from T1 to D, and then decreased from D to T2. The changes in foraging time are typically larger than the changes in ACI. These shifts parallel the

decrease in prey availability/effective density that occurs in each lake from T1 to D and the increase in prey availability/effective density that occurs from D to T2, as summarized below:

1. Lake 373: Mysis undertake a diel migration where individuals swim up into the water column at dusk and return to oxygen-poor sediments at dawn (Paterson et al., 2011); hence, their accessibility to lake trout is greatest during T1/T2 when they are visually exposed in a high oxygen environment and lowest during D, when they are resident in a low light/low oxygen refuge;

2. Lakes 626 and Louisa: the epilimnetic/littoral prey in these lakes inhabit thermal refuges whose accessibility varies daily as water temperatures warm during T1 and cool during T2; Louisa lake trout make frequent forays into high-temperature littoral habitats to feed on littoral minnows over the foraging window, but these are more frequent (Morbey et al., 2006), and our results suggest less costly, during T1 and T2;

3. Lake Opeongo: cisco respond to well-defined light level thresholds by aggregating into schools at dawn and disaggregating at dusk (De Kerckhove, Milne, & Shuter, 2015; Milne, Shuter, & Sprules, 2005); this insures that the density of cisco foraging targets (individuals vs. schools) decreases from T1 to D and then increases from D to T2.

In all four lakes, high (3rd-quartile values ~2 for all populations) and similar ACI values were observed during D. This suggests that, when ample light ensures both high predator search efficiency and effective prey defence measures in all four prey environments, active foraging costs approach the bounds set by the scope for activity (~ the difference between maximum achievable metabolic rate and standard metabolism) for lake trout (ACI~3.5 for temperatures 10–15°C as summarized in Evans, 2007). Our overall observation that foraging effort increases with decreases in prey accessibility/relative density, and that foraging time plays a larger part than ACI in driving changes in foraging effort are both consistent with the optimal foraging analyses of Abrams (1982, 1991) and Werner and Anholt (1993).

The apparent confirmation of the "constant satiation hypothesis" in our study is contingent on the assumption that our daytime observations of activity are dominated by foraging behaviours. Several lines of evidence support this assumption: (a) lake trout are the apex predator in our study systems and hence should not exhibit predator avoidance behaviours; (b) our observations were temporally well separated from the known spawning season and hence should not be confounded with reproductive behaviours; (c) our observations were focused on the final foraging period prior to spawning, when energy acquisition through foraging is a primary determinant of future reproductive success; hence, foraging should be a priority activity; (d) the shift in activity patterns from night to day is consistent with that expected when a visual predator resumes foraging in daylight (i.e., in all lakes, the proportion of resting state detections was higher at night and the median activity level was lower); (e) lake-to-lake differences in water temperatures selected by lake trout varied in concert with temperature preferences of primary prey: colder temperatures were selected in lakes (Lakes 373 and Opeongo) with pelagic cold-water prey, while warmer temperatures were selected in lakes with warm-water epilimnetic/littoral prey (e.g., Lake Louisa); and (f) in the active dataset, the distribution of daytime values for a typical individual is skewed left with a heavy right-hand tail; this is consistent with the feeding behaviour typical of a predatory feeder like lake trout where foraging activity is dominated by "low"-intensity prey search behaviours, interrupted by short-term bursts of high intensity associated with attempts at prey capture; (e.g., Dunlop, Milne, Ridway, Condiotty, & Higginbottom, 2010—a study of lake trout predation on cisco in Lake Opeongo).

4.2 | Characterizing the overall cost of foraging behaviour

Our activity cost index (ACI) is directly related to the "multiplier" (ACT = ACI+1, first defined by Winberg, 1956) that has been used in the Wisconsin bioenergetics model (Deslauriers et al., 2017; Kitchell, Stewart, & Weininger, 1977) to estimate the foraging requirements of fish living in natural freshwater and marine environments around the world. Winberg (1956) suggested that the metabolic cost of activity was ~ $(ACT–1)·M_{std}$, where ACT is a constant with a value of ~ 2. Many studies have generated estimates of ACT in natural environments. Values ($n = 104$) in a recent summary (Deslauriers et al., 2017) covered the range from 1 to 10. ACI values in our study ranged from 0 to 9 (=1 to 10 for ACT) over the course of a day, with typical daily values (accounting for the proportion of time spent "resting") in the range from 1 (ACT = 2, Lake 373) to 0.2 (ACT = 1.2, Lake Opeongo). Many authors (e.g., Boisclair & Leggett, 1989; Casas & McCauley, 2012) have argued that a "realistic" and consistent representation of both daily and seasonal variation in the cost of activity is essential to generating an informative picture of feeding costs and consumption in the wild. Our study illustrates one approach to providing these kinds of data.

Differences in predicted costs of foraging (based on reliable estimates of prey caloric content and prey density) for the two lakes at the extreme ends of our observed prey size gradient (Lakes 373 and Opeongo) were qualitatively consistent with our observed differences in activity costs. Consider a 420-cm lake trout living in each lake at the mean temperature observed for fish in that lake (Table 3): (a) Evans' (2007) equation provides M_{std} estimates for Lake 373 (44 mg O_2/hr) and Opeongo (48 mg O_2/hr) lake trout that are equivalent to 614 and 681 Joules/hr, respectively (Brey, Müller-Wiegmann, Zittier, & Hagen, 2010); (b) from prey-specific energy content data (Appendix S2), and assuming 17% energy loss during digestion (Stewart, Weininger, Rottiers, & Edsall, 1983), we estimated the ration size (number of prey items) needed to satisfy M_{std} as 21.3 Mysis/hr in Lake 373 and 0.0024 cisco/hr in Lake Opeongo; (c) given summer prey densities in Lake 373 (~13 Mysis/m^3, from the range of 8.9 to 22 individuals/m^3 reported in Paterson et al., 2011) and Lake Opeongo (~0.03 cisco/m^3, from the range 0.01 to 0.05 cisco/m^3 reported by Moryk, 2010), we

estimated that the search volume needed to acquire a ration sufficient to satisfy M_{std} in Lake 373 was ~20 times (~1.6 m^3 vs. 0.08 m^3) that needed in Lake Opeongo; (d) we also used nearest neighbour distances for prey (Appendix S1) to compare the minimum travel distance needed to contact the number of prey in the M_{std} ration for each lake: Lake 373 lake trout require ~9000 more successful prey captures and must travel a distance at least ~700 times longer (given by [9,000·(0.01/22)$^{0.333}$]— Appendix S1, equation for distance between successive prey captures) than Lake Opeongo lake trout. These values provide some direct measures of the impact that prey size has on the essential foraging costs that lake trout must bear over the range of natural environments that support them.

4.3 | Adaptive foraging links prey size structure to predator life-history trajectories

The associations observed between prey characteristics and predator life histories in our study lakes (Figure 5) are consistent with the following: (a) in Lake 373, the smallest prey type with the lowest caloric content supports adult lake trout that grow to a smaller size and exhibit both higher ACI values and less frequent resting "events" than are observed in other lakes; (b) in Lake Opeongo, the largest prey type supports adult lake trout that grow to the largest sizes observed among these populations and exhibit both lower ACI values and more frequent "resting" events than are observed in other lakes; and (c) in Lakes 626 and Louisa, prey of intermediate-size concentrated in thermally unfavourable habitats (for lake trout) support adult lake trout that are intermediate in size and exhibit intermediate activity indices compared to those observed in other lakes. These differences in adult size hold even though mortality rates are higher for the populations with larger adult sizes. This suggests that the energetic advantages offered by larger adult sizes in Opeongo and Louisa more than compensate for the selective pressure towards younger smaller adults imposed by higher mortality (Conover, Munch, & Arnott, 2009).

The observed association between prey characteristics and lake trout adult size is consistent with energy budget theory. In lakes where the primary prey type is small and energetically unrewarding, lake trout would need to forage for longer periods of time to reach satiation (Giacomini et al., 2013), therefore reducing the relative amount of time at rest. Consequently, as they grow older and larger and their absolute ration demand increases, subsequent increases in activity costs would begin to offset the advantages (e.g., higher fecundity) of larger adult size and selection would favour increased investment in reproduction at smaller sizes. This, in turn, would lead to smaller sizes at first maturity and smaller maximum sizes (Giacomini
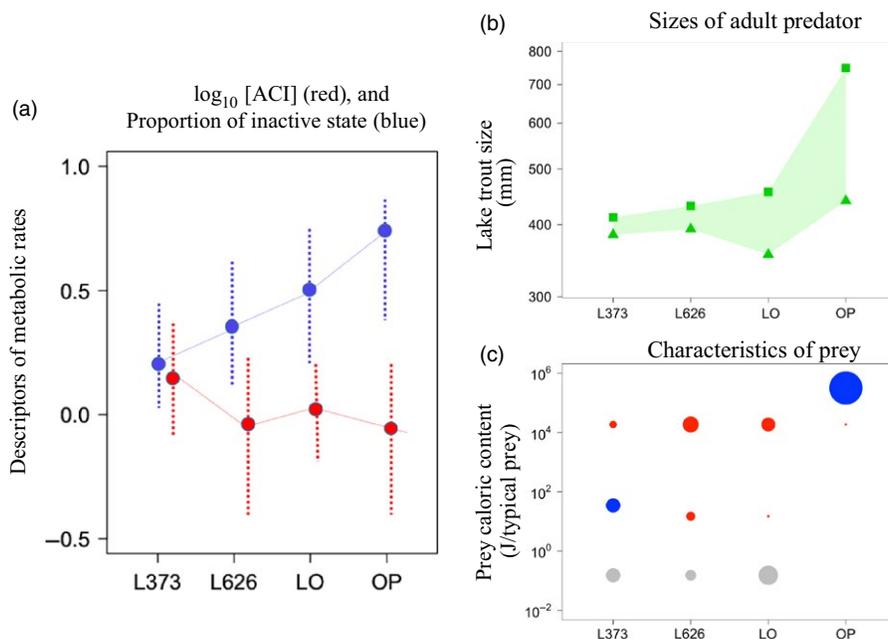

FIGURE 5 Graphic comparison of lake trout (a) metabolic rates, (b) adult body sizes and (c) prey characteristics across the four study lakes: 373 (L373), 626 (L626), Louisa (LO) and Opeongo (OP). (a) Activity measures for each lake: the cost index (ACI = M_{swim}/M_{std}) for active detections is in red and the fraction of inactive detections is in blue (circles represent median values, whiskers give the interquartile range); (b) adult predator size for each lake: the range is defined by the maximum adult size (upper curve delimited by solid squares) calculated from the von Bertalanffy fits and the size at maturity (lower curve delimited by solid triangles); (c) caloric content per individual primary prey type for lake trout in each lake. The primary prey types were categorized based on their "size," expressed as caloric content (in J/individual). Therefore, from least to highest energy content: pelagic zooplankton [~10^{-1}], large zooplankton and crustaceans [~10], for which the mega-zooplankton *Mysis* [~30, present in L373 only] is a special case, small forage fish [~ 10^4] and large forage fish [~3 × 10^5]). The size (radius) of the circles in panel c reflects the relative frequency of occurrence of each prey item in the diet. The colour represents the thermal habitat where each prey is typically found: blue, grey and red indicate cold, cool and warm habitats, respectively; this order parallels habitat accessibility (high to low) for lake trout

et al., 2013; Quince et al., 2008). The opposite would be expected for lakes with larger and more rewarding prey. Shuter et al. (2016) demonstrated this effect over historical (~70 years) changes in prey size in Lake Opeongo: lake trout grew to smaller sizes and matured earlier when they fed on prey of smaller sizes. A similar real-life situation for lean and siscowet lake trout in Lake Superior has been reported by Hrabik et al. (2006) and Jensen et al. (2006).

Plastic responses to these adaptive pressures on life-history characteristics are possible. Shuter et al. (2016) demonstrated that the changes in size at first maturity and maximum adult size that accompanied shifts in prey size for Opeongo lake trout occurred at a rate that was consistent with a plastic response and likely too fast to be a genetic response. Recent work (Allen et al., 2016; Hooker, Van Leeuwen, & Adams, 2017) has shown that the digestive structures of individual fish can adjust to prolonged changes in diet. Hooker et al. (2017), working with a close relative of lake trout (Arctic Charr *Salvelinus alpinus*), have shown that the plastic adaptations of physiology to diet differences experienced in early life impose costs on diet switching that can promote prolonged diet specialization. They argue that these persistent adaptations to early life diet differences can lead to lifetime diet specializations that are strong enough to drive sympatric speciation. This proposal is consistent with the common observation of sympatric, diet-based morphological diversity among adult lake trout in large lakes (e.g., Great Bear Lake—Chavarie, Howland, & Tonn, 2013; Great Slave Lake—Zimmerman, Krueger, & Eshenroder, 2006). Plastic responses of life history to this type of plastic diet specialization would add to, and reinforce, the efficacy of these processes in driving sympatric speciation in fish, particularly in environments where habitat diversity supports diversity in potential prey. In such environments, spatial separation of prey types, high cost of prey switching and divergence in adult sizes would promote both spatial separation of adult feeding territories and size-based preferences for mating within adult diet types.

5 | CONCLUSIONS

We used accelerometer telemetry to document diel patterns of foraging activity in four lake trout populations supported by four quite different prey communities. Foraging patterns were consistent with "constant satiation" foraging and not with "constant activity" foraging, as predicted by recent theory (Giacomini et al., 2013). Our results demonstrate how adult size can depend on the costs and benefits of feeding on prey of different size/quality. Fish that feed on large accessible prey (Lake Opeongo lake trout) can grow to a larger size before the constraints imposed by the energy expenditures associated with feeding reach a point where diversion of energy from somatic growth to reproduction becomes optimal. Fish from these populations are able to reach larger adult sizes, compared to other populations of fish that are forced to rely on smaller (Lake 373 lake trout) and/or less accessible (Lakes 626/Louisa lake trout) prey. These findings demonstrate the value of accelerometer data to bioenergetic field studies and provide a starting point for tackling such topics such as how intra-population variation in individual activity patterns and prey resource partitioning influences overall population dynamics and as well as promoting the development of subpopulation structures that may serve as precursors to sympatric speciation.

AUTHORS' CONTRIBUTIONS

L.C.-F., B.J.S., P.J.B. and C.K.M. conceived the ideas and designed the methodologies used in different parts of the manuscript; L.C.-F., P.J.B. and M.D.R. collected the data; L.C.-F., B.J.S. and M.D.R. analysed the data; B.J.S. and L.C.-F. led the writing of the manuscript. L.C.-F., B.J.S., P.J.B., C.K.M. and M.D.R. contributed critically to the drafts and gave final approval for publication.

DATA ACCESSIBILITY

Data associated with this manuscript are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.55c84q7 (Cruz-Font, Shuter, Blanchfield, Minns, & Rennie, 2018).

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