

# Behavioral responses to annual temperature variation alter the dominant energy pathway, growth, and condition of a cold-water predator

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There is a pressing need to understand how ecosystems will respond to climate change. To date, no long-term empirical studies have confirmed that fish populations exhibit adaptive foraging behavior in response to temperature variation and the potential implications this has on fitness. Here, we use an unparalleled 11-y acoustic telemetry, stable isotope, and mark-recapture dataset to test if a population of lake trout (*Salvelinus namaycush*), a cold-water stenotherm, adjusted its use of habitat and energy sources in response to annual variations in lake temperatures during the open-water season and how these changes translated to the growth and condition of individual fish. We found that climate influenced access to littoral regions in spring (data from telemetry), which in turn influenced energy acquisition (data from isotopes), and growth (mark-recapture data). In more stressful years, those with shorter springs and longer summers, lake trout had reduced access to littoral habitat and assimilated less littoral energy, resulting in reduced growth and condition. Annual variation in prey abundance influenced lake trout foraging tactics (i.e., the balance of the number and duration of forays) but not the overall time spent in littoral regions. Lake trout greatly reduced their use of littoral habitat and occupied deep pelagic waters during the summer. Together, our results provide clear evidence that climate-mediated behavior can influence the dominant energy pathways of top predators, with implications ranging from individual fitness to food web stability.

food web | climate change | habitat coupling | lake trout | north-temperate lake

There is growing urgency to understand how ecosystems are responding to climate change (1, 2). Recent work, using latitudinal gradients as proxies to warming, has argued that the behavioral responses of mobile top predators to changing temperatures can drive fundamental shifts in aquatic food webs by altering the coupling of major energy pathways (3, 4). Although this work is intriguing, no one has yet examined long-term empirical data that have explicitly tested if populations of top predators can shift their foraging behavior in response to annual changes in temperature or has evaluated what implications this might have for individual fitness. Temporal studies are critically important in this context because they control for the ecosystem-specific adaptations that can confound latitudinal studies and instead focus on the active responses to changing conditions that are highly relevant to understanding the impacts of climate change.

Mobile top predators display adaptive foraging behavior by moving across spatially disparate habitats in response to changing conditions, most notably prey densities. For example, birds feed on both terrestrial and aquatic prey, effectively coupling these ecosystems (5). Habitat coupling can also occur within ecosystems and has been well described in freshwater lakes, where predatory fish feed upon prey supported by dissimilar energy sources, such as offshore pelagic phytoplankton and nearshore littoral benthic algae (6). These adaptive foraging shifts between littoral and pelagic food

chains (i.e., littoral–pelagic coupling) in response to changes in prey densities can be a stabilizing force in aquatic food webs (7–9).

As ectotherms, the body temperatures of fish closely follow that of their ambient environment, and they must occupy species-specific temperature ranges to optimize physiological performance (10–12). Adaptive foraging behavior therefore should be particularly important in north-temperate lakes, because these systems undergo annual cycles in water temperatures and stratify thermally in summer. During thermal stratification, surface waters often exceed the temperature preferences of cold-water fish, substantially increasing the metabolic costs associated with occupying littoral habitats (10–12). In response, cold-water predators exhibit seasonality in their foraging, feeding in the littoral zone in the spring and fall when surface waters are cool and relying on pelagic energy when surface waters are warm in summer (13, 14). Therefore, variations in both prey density and seasonality should be important factors in directing the foraging behavior of fish in north-temperate lakes.

Recent studies have shown that lake-surface temperatures have risen globally over the past 30 y (15), with north-temperate lakes also having longer open-water seasons and undergoing shifts in the phenology of seasonal water temperatures (16). These observed changes in lake temperatures suggest that future warming may alter littoral–pelagic coupling by mobile predatory

## Significance

Climate warming is having wide-ranging effects on aquatic ecosystems. Fish are believed to adapt their feeding behavior as temperatures change, but empirical evidence of this behavior in nature and its impacts on individual fitness are lacking. We monitored the feeding behavior and growth of a temperature-sensitive fish population in a pristine lake for 11 y. Fish adjusted their feeding behavior annually in response to differences in temperature. In cooler years, fish ate more large prey from shallow nearshore regions, resulting in higher growth and condition than in warmer years, when fish ate more small prey from deep offshore regions. This suggests that the impacts of warming on aquatic ecosystems can scale from the individual to the food web level.

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See Commentary on page 9764.

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fish. In fact, multilake studies of temperate food webs have shown that cold-water predatory fish alter their littoral–pelagic coupling across gradients of abiotic factors that regulate the physiological costs of foraging in the littoral zone. For example, littoral energy use by lake trout (*Salvelinus namaycush*), a cold-water stenotherm, has been shown to increase with latitude, because lakes at higher latitudes have littoral zones that are either thermally favorable for longer periods or cooler in summer (3). Lake trout acquisition of littoral energy also has been shown to decrease with increasing littoral zone size due to the greater expanse of warm water to be traversed to access nearshore prey during summer (17). In both cases, the physiological constraint imposed by temperature was suggested as the key factor in controlling littoral energy use by lake trout, and together these studies suggest that the expected warmer conditions also could alter littoral–pelagic coupling by cold-water fish populations within single lakes.

Here, we sought to understand if and how annual variations in water temperatures altered littoral–pelagic coupling by a cold-water predatory fish population and what implications these dietary shifts had on individual fitness as inferred from growth and condition. Our study system was a small, oligotrophic north-temperate lake that did not contain pelagic prey fish. In such lakes, lake trout obtain the majority of their energy from prey fish and benthic invertebrates located in the littoral zone (18), presumably during the spring and fall, when water temperatures are cool. As the lake warms, water temperatures within the littoral zone exceed the thermal preference of lake trout ( $>15^{\circ}\text{C}$ ), and they move offshore to deeper water within the pelagic zone and begin to rely increasingly on smaller pelagic prey, including *Mysis diluviana* (i.e., freshwater shrimp) and zooplankton (Fig. 1) (13, 14, 18, 19). We hypothesized that because of the direct influence of temperature on fish physiology, annual changes in the phenology of littoral zone water temperatures, which are closely linked to air temperature variations (16), would influence littoral–pelagic coupling by lake trout (Fig. 1). We also expected that climate-driven year-to-year differences in access to prey-rich littoral regions would be manifested in the growth and condition of lake trout. To test these hypotheses, we used 11 consecutive years of acoustic telemetry and stable isotope data to quantify annual littoral habitat use and energy sources of our study population and related these findings to annual variations in water temperatures,

prey fish abundance, and the growth and condition of individual lake trout from annual mark–recapture sampling.

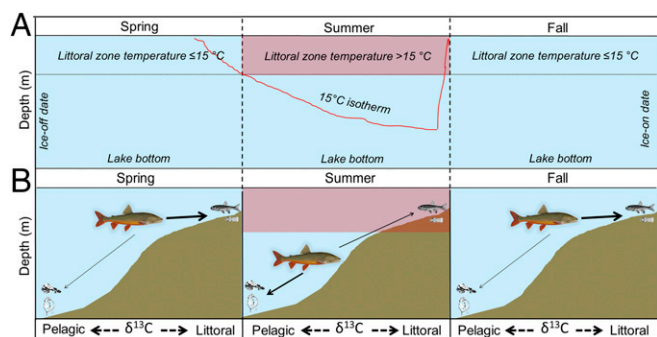
## Results

**Lake Temperatures.** The length of spring, when lake trout can access the littoral zone without thermal consequence ( $\leq 15^{\circ}\text{C}$ ), averaged 43 d and varied in duration by nearly a month (31–59 d) over the study. The summer period, when lake trout are putatively thermally restricted from accessing the littoral zone ( $>15^{\circ}\text{C}$ ), was on average 2.7 times longer than the spring and averaged 109 d with a difference of 1 mo (36 d) between the shortest (85 d) and longest (121 d) summers. Longer summers typically had warmer littoral zone temperatures (Pearson correlation:  $n = 11$ ,  $r = 0.79$ ,  $P < 0.01$ ). The length of the fall season, when lake trout spawn but can also use the littoral zone for feeding without thermal consequence, averaged 61 d (range: 51–72 d) and was on average 1.5 times longer than the spring and 1.8 times shorter than the summer. In a given year, the length of the spring and summer seasons showed a negative correlation ( $n = 11$ ,  $r = -0.59$ ,  $P = 0.06$ ), spring and fall lengths were not significantly correlated ( $n = 11$ ,  $r = 0.42$ ,  $P = 0.20$ ), and neither were fall and summer lengths ( $n = 11$ ,  $r = -0.32$ ,  $P = 0.34$ ).

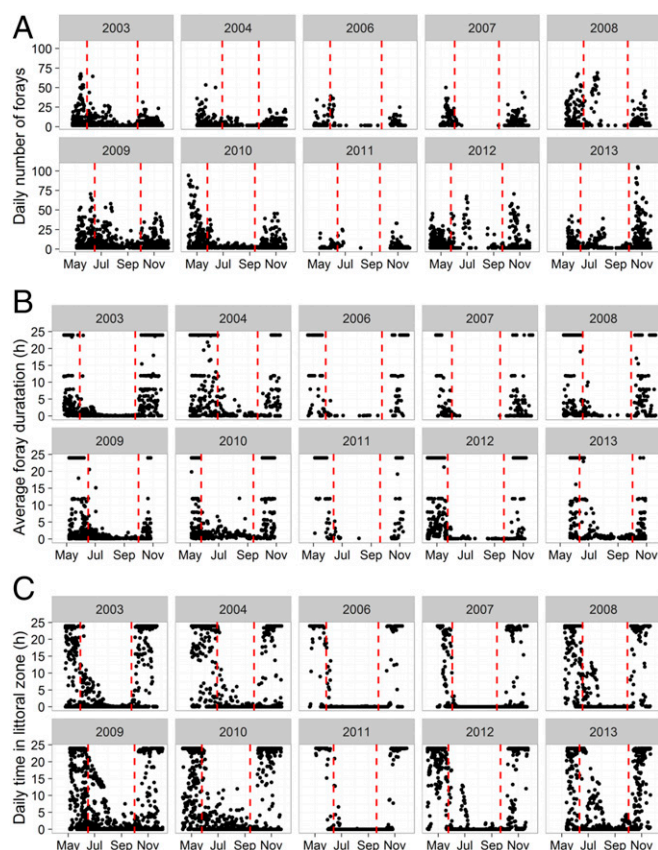
**Habitat Use.** Lake trout displayed clear seasonal shifts in habitat use and behavior that followed changes in mean littoral zone temperatures (Fig. 2). Immediately following ice-out, lake trout often spent several hours or entire days within the littoral zone (Fig. 2). As mean littoral zone water temperatures exceeded  $15^{\circ}\text{C}$  (summer), lake trout greatly reduced their forays into the littoral zone until water temperatures cooled to  $15^{\circ}\text{C}$  in the fall, when lake trout quickly reoccupied the littoral zone (Fig. 2). The total time spent by lake trout in the littoral zone during the spring of each year averaged 550 h and increased with spring length ( $\log_{10}$ ;  $F_{1,8} = 6.75$ ,  $P = 0.03$ ,  $r^2 = 0.46$ ) (Fig. 3A). In contrast, the number ( $F_{1,8} = 0.28$ ,  $P = 0.61$ ) or average duration ( $F_{1,8} = 1.13$ ,  $P = 0.32$ ) of littoral forays made in the spring was not predicted by spring length. Rather, lake trout made a greater number ( $F_{1,8} = 12.22$ ,  $P < 0.01$ ,  $r^2 = 0.60$ ) of shorter ( $F_{1,8} = 5.24$ ,  $P = 0.05$ ,  $r^2 = 0.40$ ) forays in springs with higher prey fish densities (Fig. S1 A and B). The contrasting effect of number and duration of forays meant that prey fish abundance (measured as catch per unit effort, CPUE) did not alter the total time lake trout spent in the littoral zone during the spring but only how they used that time ( $F_{1,8} = 0.00$ ,  $P = 0.98$ ) (Fig. S1C).

The amount of time that lake trout spent in the littoral zone each summer averaged 43 h and was not predicted by summer length ( $F_{1,8} = 0.09$ ,  $P = 0.77$ ) (Fig. 3B) or prey fish CPUE ( $F_{1,8} = 0.01$ ,  $P = 0.93$ ). The number or average duration of littoral forays made by lake trout in the summer also was not predicted by summer length ( $\log_{10}$ ; number of forays:  $F_{1,8} = 0.55$ ,  $P = 0.48$ ; average foray duration:  $F_{1,8} = 2.31$ ,  $P = 0.17$ ) or prey fish CPUE ( $\log_{10}$ ; number of forays:  $F_{1,8} = 0.69$ ,  $P = 0.43$ ; average foray duration:  $F_{1,8} = 0.09$ ,  $P = 0.78$ ). The mean summer water temperature in the littoral zone also did not predict the time spent by lake trout within the littoral zone during the summer ( $F_{1,8} = 0.01$ ,  $P = 0.92$ ) Fig. S1D or the number of littoral forays ( $\log_{10}$ ;  $F_{1,8} = 1.76$ ,  $P = 0.22$ ). However, lake trout made shorter forays as mean summer littoral zone water temperatures increased ( $F_{1,8} = 3.79$ ,  $P = 0.08$ ,  $r^2 = 0.32$ ) (Fig. S1 E and F). The time spent within the littoral zone the during summer was not related to the length of the preceding spring ( $F_{1,8} = 0.01$ ,  $P = 0.92$ ).

The amount of time that lake trout spent in the littoral zone each fall averaged 301 h but, unlike spring, was not predicted by fall length (square-root;  $F_{1,8} = 1.13$ ,  $P = 0.32$ ) (Fig. 3C) or prey fish CPUE (square-root;  $F_{1,8} = 0.04$ ,  $P = 0.85$ ). The number or average duration of littoral forays made by lake trout in fall also was not predicted by fall length (number of forays:  $F_{1,8} = 3.14$ ,  $P = 0.12$ ; average foray duration:  $F_{1,8} = 0.02$ ,  $P = 0.90$ ) or prey



**Fig. 1.** Theoretical illustration of how seasonality in water temperatures during the open-water season impacts foraging behavior of lake trout in small Boreal Shield lakes. (A and B) Cold water temperatures immediately after ice-out in the spring and before ice-on in the fall allow lake trout to access the littoral zone ( $<6$  m depth) without thermal consequence. However, during summer warm littoral temperatures impose an energetic cost to lake trout accessing the littoral zone. Therefore, (B) lake trout should exhibit greater use of littoral habitat and prey (prey fish and benthic invertebrates/aquatic insects) when springs and falls are longer, and conversely, should use more pelagic habitat and prey (*Mysis* and zooplankton) when summers are longer. In B, increasing arrow thickness denotes expected increased use of energy pathways based on littoral water temperatures.



**Fig. 2.** Daily estimates of littoral zone use by individual lake trout implanted with acoustic transmitters during each annual open-water period ( $n = 420\text{--}1,906$  per year), including (A) the number of littoral forays, (B) the average foray duration in hours, and (C) the total time in hours. Red vertical dashed lines indicated the start and end dates of the summer period (i.e., when the mean littoral zone temperature exceeds  $15\text{ }^{\circ}\text{C}$ ) each year. Each data point is a daily estimate for an individual fish. Note there were no telemetry data for 2005 (see *Materials and Methods*).

fish CPUE (number of forays:  $F_{1,8} = 0.58$ ,  $P = 0.47$ ; average foray duration:  $F_{1,8} = 0.24$ ,  $P = 0.64$ ). The time spent within the littoral zone during the fall also was not related to the length of the preceding spring (square-root;  $F_{1,8} = 0.20$ ,  $P = 0.67$ ) or summer (square-root;  $F_{1,8} = 0.14$ ,  $P = 0.72$ ).

**Energy Sources.** The proportion of littoral energy assimilated by lake trout, estimated using  $\delta^{13}\text{C}$  values (logit-transformed for analyses), averaged 0.66 (range 0.40–0.95) over the study and was positively related to spring length ( $F_{1,9} = 12.66$ ,  $P < 0.01$ ,  $r^2 = 0.59$ ) (Fig. 4A) and negatively related to summer length ( $F_{1,9} = 12.58$ ,

$P < 0.01$ ,  $r^2 = 0.58$ ) (Fig. 4B). The proportion of littoral energy assimilated by lake trout was not predicted by prey fish CPUE ( $F_{1,9} = 1.53$ ,  $P = 0.25$ ) but was negatively related to mean summer littoral zone temperature ( $F_{1,9} = 7.49$ ,  $P = 0.02$ ,  $r^2 = 0.45$ ).

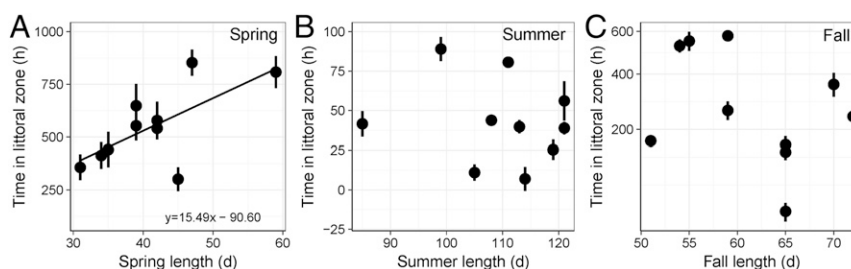
Lake trout stomachs contained more prey in spring ( $6.33 \pm 6.15$  g, mean  $\pm$  SD) than in summer ( $1.73 \pm 1.45$  g) and fall ( $3.45 \pm 2.75$  g), and the composition of these prey items varied seasonally. Stomach contents collected in spring contained 60% benthic invertebrates and insects, 37% littoral prey fish, 3% *Mysis*, and no zooplankton. Stomachs collected in summer contained 45% littoral prey fish, 2% benthic invertebrates and insects, 27% *Mysis*, and 26% zooplankton. Fall stomach contents contained 22% littoral prey fish, no benthic invertebrates or insects, 72% *Mysis*, and 6% zooplankton.

**Growth and Condition.** The growth (i.e., change in weight) and condition of individual lake trout were positively related to the time spent within the littoral zone during the spring (weight:  $F_{[1,127]} = 8.69$ ,  $P < 0.01$ ,  $r^2 = 0.07$ ; condition:  $F_{[1,127]} = 5.82$ ,  $P = 0.02$ ,  $r^2 = 0.04$ ) (Fig. 5 A and B) and summer (weight:  $F_{[1,126]} = 30.39$ ,  $P < 0.01$ ,  $r^2 = 0.19$ ; condition:  $F_{[1,126]} = 11.95$ ,  $P < 0.01$ ,  $r^2 = 0.09$ ) (Fig. 5 C and D). Growth and condition were also positively related to the proportion of littoral energy assimilated (weight:  $F_{[1,139]} = 13.96$ ,  $P < 0.01$ ,  $r^2 = 0.09$ ; condition:  $F_{[1,138]} = 5.44$ ,  $P < 0.01$ ,  $r^2 = 0.04$ ) (Fig. 5 E and F). Consistent with behavioral data, growth and condition of individual lake trout were also positively correlated to spring length (weight:  $F_{[1,139]} = 8.56$ ,  $P < 0.01$ ,  $r^2 = 0.06$ ; condition:  $F_{[1,138]} = 6.74$ ,  $P = 0.01$ ,  $r^2 = 0.05$ ); however, neither was related to summer length (weight:  $F_{[1,139]} = 0.17$ ,  $P = 0.68$ ; condition:  $F_{[1,138]} = 0.56$ ,  $P = 0.46$ ).

## Discussion

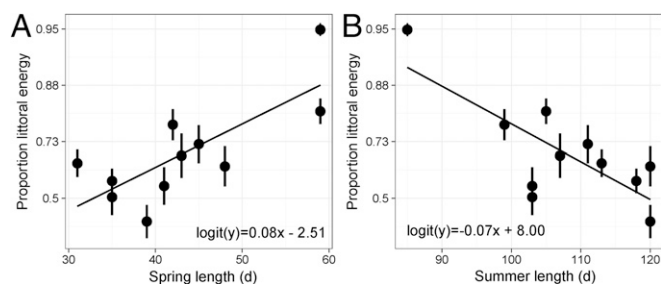
We found that lake trout, a mobile cold-water predator, made consistent and predictable seasonal shifts in habitat use that were triggered by changes in lake-water temperatures. As the phenology of littoral zone temperatures shifted from year to year, so did lake trout use of nearshore habitat and acquisition of energy from this prey-rich habitat. In warmer years, when littoral energy acquisition was lower, individual lake trout had reduced growth and condition. This ability of a single population of aquatic top predators to adjust its foraging behavior rapidly to interannual changes in climatic conditions and the corresponding impacts on measures of fitness highlight the adaptability of this glacial relict species to persist under adverse conditions. Indeed, recent evidence that many fish species from various thermal guilds and trophic levels may be capable of flexible foraging behavior (20) suggest that our results may be broadly applicable for understanding the impact of climate change on aquatic ecosystems.

Our results suggest that water temperature phenology (i.e., seasonality) supersedes prey density as the main controller of littoral–pelagic coupling by lake trout. Although prey fish abundance and summer littoral zone temperature influenced foraging strategy (i.e., the balance of the number and duration of littoral



**Fig. 3.** Relationships between the length of (A) spring, (B) summer, and (C) fall and time spent in the littoral zone by acoustically tagged lake trout. Note differences in y-axis scales. Least squares mean ( $\pm$ SD) estimates of time in the littoral zone are shown. Spring data were  $\log_{10}$  transformed for analysis.





**Fig. 4.** Relationships of mean estimates ( $\pm$ SD) of littoral energy use (logit-transformed;  $n = 11$ ) to the number of (A) spring and (B) summer days.

forays), these factors did not affect the overall time spent within the littoral zone. Rather, longer springs resulted in greater occupation of littoral habitat and acquisition of littoral energy. Conversely, littoral energy use declined with increasing summer length, which was negatively correlated to spring length in a given year. These results suggest that changes in temperature can fundamentally rewire energy pathways, a result that has the potential to impact food web stability (7–9, 21), but of course the direction and magnitude of these impacts would vary depending on the how future warming alters the phenology of water temperatures.

Reductions in the growth and condition of individual lake trout observed in years with reduced littoral habitat use and littoral energy use could result from a combination of factors. First, increased reliance on *Mysis* and zooplankton would be less energetically efficient than foraging on larger prey fish or benthic invertebrates because predatory fish are more active when forced to feed on numerous, smaller prey (22). This increased energetic cost of feeding on small prey has been illustrated by studies that found predatory fish in lakes without pelagic prey fish had increased muscle activity and greater activity rates than those same species in lakes containing pelagic prey fish (23–25) and by studies showing that more active fish generally grow more slowly (26). Additionally, in oligotrophic lakes, the littoral zone is often more productive and smaller in volume than the pelagic zone (6, 17), and therefore the probability of a lake trout's encountering prey would be higher in the littoral zone than in the pelagic zone, increasing foraging success but also reducing the time required to find prey.

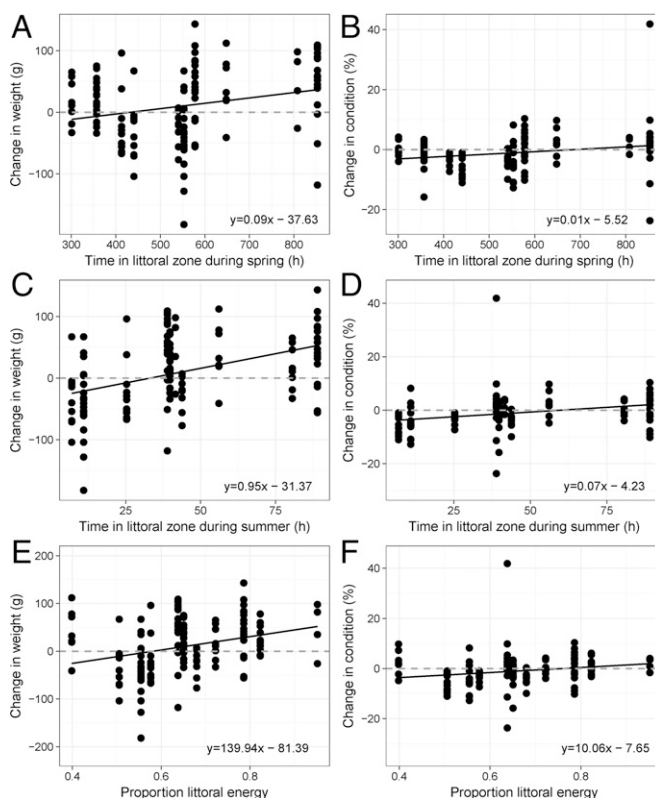
Despite thermally suboptimal temperatures in littoral regions during summer, lake trout used this habitat to access preferred prey in all years. Regular, although limited, foraging into waters with temperatures above their thermal preference indicates the energetic importance of acquiring large, energy-dense prey (27). This suggests that capturing prey fish in warm water could be a more efficient strategy than foraging on small prey within the pelagic zone—at least for some parts of summer. These rapid forays into warm, shallow water have been documented previously for lake trout (28, 29). However, during the peak of summer, when littoral temperatures were highest, lake trout seemed to reduce greatly and even stop use of the littoral zone. This behavior also has been exhibited by other temperature-sensitive fish, including brook trout (*Salvelinus fontinalis*) and rainbow trout (*Oncorhynchus mykiss*), which have been documented to stop foraging and seek cool-water refuge when temperatures exceed their thermal preferences (30, 31). Therefore, continued warming of surface-water temperatures during the summer (15, 16) could extend periods of limited littoral access in salmonids, increasing their reliance on pelagic-derived energy.

The fall period also provides thermal conditions in which lake trout could exploit littoral prey without consequence and presumably could offset the constraints imposed by the stressful conditions during the preceding seasons. Although the fall periods generally were longer than the spring periods, lake trout on average spent less time in the littoral zone during the fall than in

the spring, even though the littoral zone is also the region where spawning occurs. Moreover, lake trout did not increase their use of this habitat in fall periods that were preceded by stressful conditions (i.e., shorter spring and/or longer summers), and their fall diet reflected a reliance on pelagic prey, mainly *Mysis*, as earlier studies have noted (13, 14). At least in our study system, the fall does not seem to be a period when lake trout make extensive use of littoral resources. Based on the apparent limited acquisition of littoral energy in summer and fall periods, it appears that the spring period, which is strongly influenced by climate (16), is critical for the annual growth and condition of lake trout.

Observed reductions in individual growth and condition associated with reduced access to littoral energy also have important implications for population persistence through impacts on reproduction and recruitment. Further reductions in access to littoral regions with future warming could prevent lake trout from accumulating sufficient energy to spawn in the fall (27), potentially increasing the frequency of skip-spawning (32, 33). The prospective smaller postadult body size with warming could also lead to reductions in fecundity, which is positively correlated with body size (34). Furthermore, increased reliance on pelagic energy by adult lake trout during longer and/or warmer summers would increase competition with juvenile lake trout that rely almost exclusively on *Mysis* and zooplankton (35, 36). Together, the potential for less frequent spawning, production of fewer eggs, and lower recruitment to adulthood posed by warming could have severe implications for the ability of lake trout populations within small lakes to persist through future climate change.

It is worth noting that our study lake did not contain pelagic prey fish (e.g., cisco, *Coregonus artedii*), and this type of food web represents only a subset of lake trout lakes (18). In lakes with



**Fig. 5.** Annual changes in the weight and condition of individual lake trout captured in consecutive years as a function of spring littoral habitat use (A and B) ( $n = 129$ ), summer littoral habitat (C and D) ( $n = 129$ ), and littoral energy use (E and F) ( $n = 141$ ). The gray dashed lines indicate zero.

cisco, lake trout would be able to access prey fish throughout periods of thermal limitation (13), and so the impacts of seasonal phenology on foraging behavior and fitness in cisco-containing lakes may differ from our findings. However, a study by King, et al. (37) found that lake trout inhabiting a cisco-containing lake had reduced growth in years with earlier onset of thermal stratification, likely because of reduced access to littoral prey in the spring. This suggests that the impacts of seasonal phenology on the foraging behavior and fitness of lake trout may be similar across lake types; however, the magnitude of these changes may vary. Finally, the adaptive behavior of lake trout illustrated here also has implications for predicting how future warming may alter the geographic distribution of cold-water fish species, particularly around southern range borders, where surface temperatures may exceed thermal limits. At these southern edges, adaptive foraging behavior and use of refuge may allow cold-water populations to persist for extended periods when simple surface models would predict range contractions (2).

## Materials and Methods

**Study Site.** The study occurred over 11 y (2003–2013) within the International Institute for Sustainable Development (IISD)-Experimental Lakes Area, Canada (49°40'N, 93°44'W) (38). Lake 373 (L373) is an unmanipulated long-term reference lake used to monitor natural variation. It is a small (surface area 27.3 ha, maximum depth 20.5 m), single-basin lake that thermally stratifies during summer, when mean littoral zone temperatures typically range from 17–21 °C. The lake supports a native, naturally reproducing lake trout population that consisted of ≈285 adults during our study. The lake does not contain pelagic prey fish, and the main prey items for adult lake trout are littoral prey fish (*Phoxinus eos*, *Phoxinus neogaeus*, *Margariscus margarita*, and *Cottus cognatus*), benthic invertebrates, insects, *Mysis*, and zooplankton. The lake also contains white sucker (*Catostomus commersonii*). We considered the littoral zone to be water depths <6 m (39). Because L373 is bowl-shaped, with no islands or shoals, littoral regions were located only along the perimeter of the lake.

**Lake Temperatures.** Annual ice-on and ice-off dates were monitored at nearby (≈12 km) Rawson Lake (54.3 ha) and were assumed to be the same for L373 because the lakes are similar in size and depth. Water temperatures in L373 were measured every 30 min using a string of data loggers (HOBO Temp Pro H20-001; Onset) deployed over the deepest point of the lake (19). Logger data from 29 April to 20 June 2003 were not available, and biweekly temperature profile data were supplemented.

We estimated the mean daily temperature of the littoral zone during each open-water season using data from temperature loggers at 1–6 m. The period between ice-off and the date that the mean littoral zone temperature exceeded 15 °C was denoted “spring.” The period when the mean littoral zone temperature exceeded 15 °C was denoted “summer.” “Fall” was the period between the date that the lake cooled to ≤15 °C and ice-on. “Winter” was considered the ice-covered period. Because lake trout spawn inshore in the fall (40), we were unable to distinguish between foraging and spawning behavior. By using the date when littoral water temperatures exceeded 15 °C, we provide a measure of how access to littoral energy is controlled by temperature (19, 41). We did not use the existence of a planar thermocline to define summer, because this can occur when littoral temperatures are ≤15 °C and would not represent a physiological barrier for lake trout (41).

**Habitat Use.** We monitored the depths of lake trout using acoustic telemetry. Telemetry data were collected from 41 individual fish (fork length 380–501 mm) implanted with depth-sensing transmitters (V16P-4L or V13P-1L; VEMCO Ltd.) that randomly transmitted a coded signal every 16–64 s (V16) or every 120–300 s (V13) (see [Tables S1](#) and [S2](#) for transmitter and biological details). The depths of transmitter-implanted fish were monitored year-round using four or five omnidirectional hydrophone receivers (VR2; VEMCO Ltd.) with overlapping detection ranges distributed throughout the lake (19, 42).

Raw telemetry data were filtered before analyses (details are given in [Supporting Information](#) and [Figs. S2](#) and [S3](#)). The final telemetry dataset for estimation of spring, summer, and fall habitat use consisted of 1,979,775 detections (range 63,016–368,755 per year) from 29 individual fish (range two to nine fish per year). No telemetry data from 2005 were available, because all new transmitters were implanted that spring, and we did not use data from the year in which transmitters were implanted to avoid potential effects of tagging on behavior. Using data for each fish, we calculated daily estimates of (i) the number of forays into the littoral zone; (ii) the average duration of each

littoral foray; and (iii) the total time spent in the littoral zone during the spring, summer, and fall of each open-water season. A littoral foray was denoted by a fish's depth changing from ≥6 m to <6 m between consecutive detections. The total number of forays performed by an individual fish on a given day was then summed. Daily estimates of the total time spent in the littoral zone by each fish were calculated as the ratio of littoral zone detections to total detections scaled to a 24-h period. Daily estimates of average foray duration for each fish were then calculated as the total time spent in the littoral zone divided by the number of littoral forays on that day. We note that our method would categorize a lake trout moving into depths <6 m in offshore regions as a littoral foray, but we assumed all forays occurred in the nearshore region.

**Energy Sources.** We used stable carbon ( $\delta^{13}\text{C}$ ) isotopes to estimate use of littoral- vs. pelagic-derived energy by lake trout (35). Pectoral fin-ray tips (lake trout) and dorsal muscle (littoral prey fish) were collected each fall. *Mysis* and bulk zooplankton were collected monthly during each open-water season. Samples were dried, ground, loaded into tin capsules, and analyzed using standard methods at the University New Brunswick or the University of Waterloo. Stable isotope values were conveyed in  $\delta$  notation (‰):  $\delta^{13}\text{C} = [(^{13}\text{C}/^{12}\text{C}_{\text{sample}} / ^{13}\text{C}/^{12}\text{C}_{\text{standard}}) - 1] \times 1,000$ .

The  $\delta^{13}\text{C}$  values of lake trout fins were first corrected to equivalent muscle values using the equation  $\delta^{13}\text{C}_{\text{muscle}} = 0.73 \times \delta^{13}\text{C}_{\text{fin}} - 8.11$  (43). We mathematically lipid-corrected the  $\delta^{13}\text{C}$  values of prey fish and *Mysis* using  $\delta^{13}\text{C}_{\text{muscle}} (\text{normalized}) = \delta^{13}\text{C}_{\text{muscle}} + [-3.32 + (0.99 \times \text{C:N})]$  (44). The correction was not applied to lake trout because lipids should not be an issue for fin tissue. From 2003–2005, stable isotope data for prey fish were not available; in these years we estimated the  $\delta^{13}\text{C}$  values of prey fish by adding the mean difference in  $\delta^{13}\text{C}$  values of prey fish and littoral mayflies during years when both these items were analyzed to the mean values of littoral mayflies. We note that lake trout fin-ray tips have been found to turn over at similar rates to white muscle (43). We determined the proportion of littoral energy assimilated by each lake trout using a two-source mixing model that treated *Mysis* and littoral prey fish as the pelagic and littoral end members, respectively (45): proportion littoral energy =  $(\delta^{13}\text{C}_{\text{lake trout}} - \delta^{13}\text{C}_{\text{Mysis}}) / (\delta^{13}\text{C}_{\text{prey fish}} - \delta^{13}\text{C}_{\text{Mysis}})$ . The lake trout  $\delta^{13}\text{C}$  dataset contained 194 samples ( $n = 15$ –20 per year) with fork lengths ranging from 199–502 mm.

A small number of lake trout stomach contents obtained from nonlethal gastric lavages were collected in the spring (23 and 28 May,  $n = 14$ ) and summer (12 August,  $n = 4$ ) of 2014 and from fall mark-recapture sampling mortalities (various dates between 1–21 October 1986–2012,  $n = 24$ ) to support stable isotopes. Prey items from each stomach were identified and grouped into the following groups: benthic invertebrates and insects, prey fish, *Mysis*, and zooplankton. We then calculated the proportion of the total stomach content weight for each diet item.

**Growth and Condition.** Lake trout growth was examined using data from annual mark-recapture sampling. Fish were captured each fall using trap nets and short (<30 min) evening gill net sets on spawning shoals (46, 47). Following capture, the weights, fork lengths (in millimeters), and tag numbers from previously captured fish were recorded. Newly captured fish received a tag for future identification. Condition was estimated as a percentage of standard weight specific for lake trout (48). We identified 141 instances in which an individual fish was captured in consecutive years during the study period.

**Prey Fish Abundance.** The relative abundance of littoral prey fish were calculated as CPUE based on annual collections (46, 49). Each spring, two or three small-diameter mesh trap nets were set for 27–39 consecutive days to target the nearshore-littoral zone. Annual CPUE estimates were calculated by dividing the total number of prey fish by the number of net days (i.e., number of trap nets  $\times$  number of fishing days). We included all cyprinid species and slimy sculpin in putative littoral prey fish CPUE values.

**Statistical Analysis.** Analyses were carried out in R, v. 3.3.2 (50). Assumptions of linear mixed effect models (LMMs) and linear regression were evaluated (51, 52). Where necessary, data were transformed to meet assumptions as reported in *Results*. LMMs were fit using the *nlme* package (53), and fits were evaluated (51, 52). We calculated least squares means for each factor level in LMMs using the *lsmeans* package (54). Because of the small sample size (11 y), we considered  $P < 0.1$  as statistically significant.

We analyzed habitat use data from spring, summer, and fall seasons separately. LMMs were applied to each habitat measure (number of littoral forays, average foray duration, and total time in littoral zone) over all years for each season, for a total of nine LMMs, which treated year as a fixed factor and individual fish as random intercepts. Mean estimates ( $\pm$ SD) of habitat use for each year/season were obtained using the least squares means from each LMM and were subsequently used as response variables in linear regression

to test if each seasonal habitat use measure was predicted by the corresponding season length, prey fish CPUE, length of the preceding season (summer and fall only), and mean summer littoral zone temperatures (summer only).

Mean estimates of the proportion of littoral energy assimilated for each study year were obtained by calculating means ( $\pm$ SD) over all individual lake trout analyzed for  $\delta^{13}\text{C}$  within each year. The linear regression procedure described above for habitat use then was used to test if the mean proportion of littoral energy was predicted by season length (spring or summer), prey fish CPUE, and summer littoral zone water temperatures. Isotope data were not related to fall length, because samples were collected near the start of the fall in each year.

We determine how variations in littoral energy and habitat use translated to growth by treating annual changes in individual lake trout weight and condition as response variables in separate linear regressions with spring–

summer littoral energy use, spring and summer littoral habitat use, and the length of the spring, summer, and winter periods used as predictor variables. Fall habitat use or fall length was not used as a predictor for annual growth because fish collections occurred throughout this period.

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