Effects of differential habitat warming on complex communities

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Food webs unfold across a mosaic of micro and macro habitats, with each habitat coupled by mobile consumers that behave in response to local environmental conditions. Despite this fundamental characteristic of nature, research on how climate change will affect whole ecosystems has overlooked (*i*) that climate warming will generally affect habitats differently and (*ii*) that mobile consumers may respond to this differential change in a manner that may fundamentally alter the energy pathways that sustain ecosystems. This reasoning suggests a powerful, but largely unexplored, avenue for studying the impacts of climate change on ecosystem functioning. Here, we use lake ecosystems to show that predictable behavioral adjustments to local temperature differentials govern a fundamental structural shift across 54 food webs. Data show that the trophic pathways from basal resources to a cold-adapted predator shift toward greater reliance on a cold-water refuge habitat, and food chain length increases, as air temperatures rise. Notably, cold-adapted predator behavior may substantially drive this decoupling effect across the climatic range in our study independent of warmer-adapted species responses (for example, changes in nearshore species abundance and predator absence). Such modifications reflect a flexible food web architecture that requires more attention from climate change research. The trophic pathway restructuring documented here is expected to alter biomass accumulation, through the regulation of energy fluxes to predators, and thus potentially threatens ecosystem sustainability in times of rapid environmental change.

species interactions | thermoregulation | trophic structure | habitat coupling | heterogeneity

Natural systems are inherently complex entities, wherein organisms act as agents of material and biomass transport (1) weaving food webs through a mosaic thermal environment. Direct temperature effects on trophic interactions arise through thermal regulation of an organism's physiology and behavior (2–5). For ecotherms (that is, organisms whose body temperature is aligned with ambient temperature), several biological rates show unimodal responses to temperature (2, 3, 6), and correspondingly, studies have shown that consumption rates initially rise with warming to a peak rate and then fall rapidly approaching a critical temperature (6). Understanding the ways that these organism responses alter food webs, and how these food web responses affect ecosystem function, are key requirements to predicting climate change impacts on ecosystems (7–11).

A simple way to think about temperature's effects on any single trophic interaction is through the general linear consumption function:

$$\text{Consumption(per capita)} = a\, t_s\, R, \qquad [1]$$

where a is the attack rate, t_s is the time searching, and R is the resource biomass density. The direct effects of temperature on an organism's ability to encounter and capture resources in a given habitat may largely depend on a, and t_s (with potential indirect effects relative to the consumer through temperature influences on R). The argument for the temperature dependence

of attack rate (a) is relatively straightforward. Temperature mediates foraging velocity (3), and considering all else equal, velocity determines encounter rates and prey capture success. The influence of temperature on time searching is a little more complex, but the general expectation is that its influence will be shaped by the requirement that the organism allocate its feeding time in different patches or habitats to increase its fitness (5). Such thermal limitation of search time would lead to reductions of interaction strength in warming habitats—in effect, temperature would mediate prey availability (e.g., when temperature exceeds physiological limits). What remains to complete the consumption equation above is the effect of temperature on R, both the direct effects (for example, the impact of warming on R's productivity) and indirect effects (for example, impact of warming on the number and consumption capabilities of consumers competing for R) (12, 13). Note that the numerical response (i.e., biomass accumulation) of the consumer may depend on additional vital rates (e.g., conversion efficiency). The conversion of prey biomass to predator biomass (often denoted e) may not change with temperature (2, 3), although recent research suggests that e may be temperature dependent if consumers switch among resources with different elemental composition to balance changing metabolic and somatic demands (14). Nevertheless, we focus on consumption (a, t_s, R) as a means to build an argument for temperature's influence on trophic structure.

Here, we extend the logic that underlies this simple representation of temperature-dependent consumption to develop hypotheses that link temperature differentials, through direct

Significance

Organisms may adjust their behavior to stay cool as natural habitats differentially warm with rising air temperature. Undoubtedly, fundamental ecosystem properties will change in turn, but the impact of the dynamic thermal mosaic on food web interactions is not considered in traditional climate change research. To demonstrate differential warming effects on food webs, we use boreal lakes to show that the energy pathways leading to an apex predator shift, according to thermal preference, and the vertical pathway lengthened in warmer climate. Such a fundamental food web restructuring is expected to increase predator contaminant levels and alter community dynamics in ecosystems—a particular concern for conservation of boreal lakes, which house a significant portion of Earth's freshwater life.

and indirect means, to spatial food web structure. Spatially simple laboratory studies of food webs suggest that larger-bodied, higher trophic level organisms are likely to have high extinction risk with ambient warming (15). In natural systems, these higher-order predators provide a spatially unifying component to food webs: their high mobility enables them to forage among different habitats, coupling food chains with unique basal resource groups (16–18). This coupling structure can be an important part of sustaining higher-order consumers with consequences for food chain length, trophic control, and ecosystem stability (16, 19–21). For example, theory argues that reduced access to a novel resource compartment may decrease a consumer's biomass (19, 20), thereby increasing the chance of local extinction from a random event. When accessibility is limited, reduced coupling may alter food chain length if habitats contain prey that differ in trophic position (22) or if higher level prey increase, with reduced trophic control, and consequently predators become less omnivorous (19, 21). Given that temperature change can drive asymmetric responses in species that differ in thermal tolerance, the influence of spatially structuring elements on the response of a food web to warming will depend not only on the direct responses of consumers to temperature (2, 3, 5) but also those responses of other interacting community members (i.e., resources and competing predators) (12, 13, 23). We test notions of the structuring effects of differential temperature on spatially coupled food webs (thermal-accessibility hypothesis), using boreal lakes as a natural study system (Fig. 1). To make this test, we assembled one of the largest comparative food web datasets on record: 54 ecosystems, characterized using >3,000 isotope (N and C) samples.

Freshwater lakes are particularly sensitive to climate change as lake habitats are structured by climate-driven water temperature and many biota are vulnerable to ambient temperature change (24). A key habitat feature of boreal lakes is thermal stratification, an effect of antagonistic physical forces of mixing by wind energy and resistance to mixing by solar heating that separates cold, more dense water (hypolimnion) from warmer, less dense surface water (epilimnion) (25). The stratification process creates a potential for temperature differentials between deeper offshore and shallower near-shore subhabitats within a lake, as temperatures remain relatively constant in deep habitats, whereas shallower near-shore temperatures are strongly influenced by air temperatures (26). Monitoring in the boreal region (27, 28) has shown that rising air temperature warms surface waters, accelerates the stratification process, and extends the duration of stratification; thus, air temperature is a primary determinant of lake thermal heterogeneity.

Most aquatic organisms (e.g., invertebrates, amphibians, fish) are ectotherms; therefore, the demands of the thermal environment arguably form the most influential set of abiotic factors aquatic organisms must satisfy (29, 30) (including increased oxygen requirements in warmer water). Thermal differentiation in lakes typically corresponds with the species differences that characterize offshore and near-shore habitats. Conveniently, biomass flow from these habitats through a food web can be traced using stable carbon and nitrogen isotope ratios due to isotope differences at the base of the food web between phytoplankton (offshore) and benthic algae (near-shore) (18, 22, 31, 32).

We focus our study on the trophic pathways that flow from basal resources to lake trout (*Salvelinus namaycush*), a vulnerable, cold-adapted (10–12 °C preference) apex predator (33) estimated to reside in 66,500 Canadian lakes (34) (Fig. 1). Previous studies show that lake trout play a keystone structural role in integrating resource pools in offshore and near-shore habitats (18, 21, 22, 31). In what follows, we test the direct and indirect effects of differential warming on this natural system (lake trout food web) across a summer mean temperature gradient ranging 15–20 °C. At the warmer end of this range, surface water temperatures will often exceed the physiological tolerance of lake

Fig. 1. Simple schematic showing expected effects of differential warming on habitat coupling (horizontal axis) and habitat use (vertical axis) by lake trout in cold (*Upper*) and warm (*Lower*) lakes. A thermal accessibility argument predicts that lake trout couple into the thermally exposed near-shore resource channel less and should use (proportionally) that habitat less under warmer conditions (indicated by lake trout position). The arrow direction and thickness indicate coupling direction and strength. The letters in the upper diagram identify trophic groups used in both cold (*Upper*) and warm (*Lower*) lake depictions: lake trout (a), pelagic forage fish (b), pelagic invertebrates (c), pelagic phytoplankton (d), littoral fish (e), littoral invertebrates (f), and benthic algae (g). To the right in the diagram, we show thermal profile data contrasting temperature at depth from Victoria Lake [cold; summer air temperature, 15.5 °C; latitude (lat), 49.62306; longitude (long), –91.54889] and Charleston Lake (warm; summer air temperature, 19.7 °C; lat, 44.53611; long, –76.01194) taken at the time of sampling. Temperature is visually highlighted with darker blue (cold) and darker red (warm) hues. These lakes experience temperatures near the cold and warm endpoints for our dataset and are of the same order of magnitude in size, and both had thermal profiles recorded to 30 m.

trout and should restrict accessibility into the near-shore habitat (Fig. 1, *Lower*). Given this thermal mechanism, we predict that lake trout in warmer climates may change their habitat use to deeper waters and this spatial behavior may shift the degree that near-shore resource pools are coupled by this predator relative to cooler climates (Fig. 1). We further consider whether spatial responses are associated with a shift in the length of the apex predator's food chain. This thermal-accessibility–mediated restructuring of fundamental food web structure is considered along with complementary notions of warm-tolerant competitor effects and relative prey abundance changes with climate.

Results and Discussion

Food Web Structure Shifts in Response to Climate. Resource contributions from near-shore exposed habitats to lake trout were clearly reduced relative to open coldwater habitats in warmer temperatures (Fig. 2 *A* and *B*). Under these warmer conditions, lake trout carbon signatures shifted toward cold-water baseline

sources (Fig. 2*A*), indicating a proportionally stronger dependence on offshore phytoplankton production. In addition, this shift toward offshore carbon sources was accompanied by a parallel diet shift toward more coldwater prey fish (Fig. 2*B*). Concurrently, the trophic position of lake trout increased with warmer temperatures (Fig. 2*C*). Hence, a shift in consumption to deepwater resources seems to correspond with a lengthening of the trophic pathways to lake trout (Pearson's $r = -0.28$, df = 53, $P = 0.032$). Lake trout typically hold the highest trophic position in temperate lakes (32), and so for many lakes this increased trophic position likely amounts to an increase in overall food chain length. Furthermore, this food web response is theoretically predicted by a previous study that argues that decreasing accessibility in these lakes may result in a habitat coupling contraction of the food web (21). Our previously unidentified findings suggest that temperature may be an important mediator of this accessibility effect.

Our results extend predictions from consumption and spatial theory to include climate. In cross-system comparative studies, other factors may influence ecological processes, and thus these factors may influence the relationship between climatic conditions and food web structure. For this reason, we provide supplementary analysis that explores additional physical lake characteristics and nutrient status as determinants of food web structure (*SI Results and Discussion*). Despite evidence that lake morphometry and nutrient status may be important in some cases, our supplemental analysis further supports a strong climatic influence on all food web response variables presented above. Such consideration of thermal/productive space may provide some interesting future extensions of our findings.

Focal Predator Alters Habitat Use in Response to Climate. The general food web structure shift we document corresponds with data on lake trout habitat use. Abundance data from a subset of lakes used in the trophic analysis show that the relative proportion of lake trout caught in near-shore habitat decreased as temperatures increased (Fig. 2*D*). Detailed field studies have previously found that lake trout behaviorally thermoregulate seeking cold-water refuges in the summer months (33, 35, 36). Despite a preference for cold water, summer tracking data have shown that lake trout occasionally take short forays into the littoral zone, in the summer, which is expected to be driven by the search for prey (35). Interestingly, a classic account of lake trout natural history anecdotally notes that fishermen claim to catch lake trout from shore all year long in northern areas, whereas at the southern end of the species' range this is not the case (37). Our systematic study shows that these notions of temperature-mediated habitat use occur across a climate gradient in many lakes, and these findings link this climate-mediated spatial behavior to a shift in lake trout reliance on different trophic pathways that structure the food web. Considering our findings with previous observations, we argue that consumer habitat use may be an important component of the food web response (Fig. 2 *A–C*) across the climatic gradient.

Nonfocal Predators and the Food Web Shift. Smallmouth bass (*Microterus dolomieu*) and walleye (*Sanders vitreus*) are apex predators that inhabit the near-shore zone in several lake trout lakes in our study area. Because these species are expected to benefit from warmer summer temperatures over the climate range of our study (26), they may be an indirect cause of the overall decoupling effect observed across the climate gradient. In contrast to the prediction that warm-water predators are the primary driver of decoupling across a warming climatic gradient, our analysis of lakes without bass and walleye shows a similar if not stronger relationship between warming and the decoupling of lake habitats (Fig. 3*A*). Furthermore, bass abundance estimates in lakes where these species are present are independent of the temperature gradient measured in our study, and walleye abundance is somewhat higher but not significantly so in the colder lakes (Fig. 3*B*). Note that our findings do not discount the previous findings that competitors may act to decouple lake trout from near-shore fish production (22), nor that the distribution of bass is restricted by climate (26). In fact, bass are more likely to be present on average in our warmer study lakes ($F = 4.393$, $n = 54$, $P = 0.041$). Our findings instead suggest that the existence of these predators is not the force driving the relationship between air temperature and trophic structure across the climatic gradient. Said differently, temperature may alter the accessibility of resources to predators in a similar way but independently of its effects on other components of the food web.

Near-Shore Prey Abundance in Relation to the Climate Gradient. Examination of prey abundance in the exposed littoral habitat further contradicts the idea that indirect effects account for the observed food web restructuring. Prey abundance estimates did not vary predictably with warmer temperature conditions (Fig. 3*C*). This result suggests that abiotic limiting factors like temperature may explain exceptions to the general prediction that habitat coupling may depend on relative prey abundance in an alternate habitat (17).
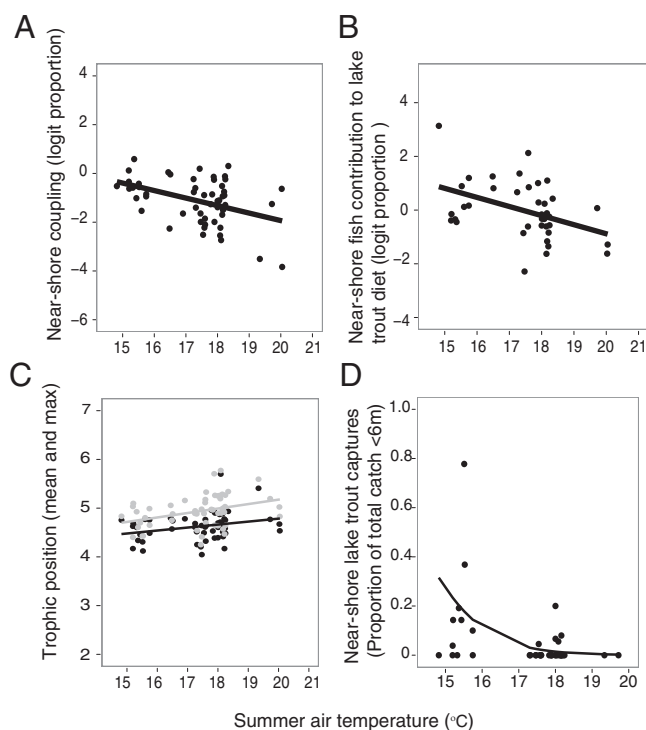

Fig. 2. Relationship between temperature, trophic structure, and predator habitat use across individual lake ecosystems. (*A*) As temperature increases, the contribution of material derived from basal resources in near-shore habitat to lake trout diet (near-shore coupling) is reduced (linear regression, $R^2 = 0.18$, df = 53, $P = 0.001$). (*B*) Similarly higher temperatures are related to a reduced contribution of carbon from near-shore fish relative to offshore fish, indicating the decreased reliance on prey fish from near-shore habitat under warmer temperatures (linear regression, $R^2 = 0.18$, df = 36, $P = 0.008$). (*C*) Trophic position of lake trout estimated as the population mean (black, linear regression, $R^2 = 0.07$, df = 53, $P = 0.045$) and the highest individual value recorded for each lake (gray, linear regression, $R^2 = 0.13$, df = 53, $P = 0.007$). (*D*) The proportion of the lake trout population captured near-shore (<6 m) in each lake decreased with summer air temperature indicating a shift to offshore habitat use [logistic regression (binomial), D explained = 0.45, df = 39, $P < 2.0 \times 10^{-16}$]. Summer air temperature is the mean monthly temperature averaged for June, July, and August for the year each lake was sampled. Near-shore coupling is the proportional contribution of $\delta^{13}C$ from near-shore resources relative to offshore resources ultimately assimilated in lake trout tissue (*Materials and Methods*).

Taken together with the predator effects mentioned above (Fig. 3 *A* and *B*), we argue that temperature differentials can decouple food web interactions across habitats independent of the complex indirect interactions between cold-water predators and warm-water fish species.

Conclusions

Historically, climate change research on communities has largely focused on the magnitude of regional temperature change and focal species thermal sensitivity (10). Increasingly researchers recognize that predicting organism responses to climate change is more ecologically complex than simple thermal limitations of species (7). Some recent research suggests that inconsistencies in mapping climate change to organism responses may be reduced by considering biotic interactions (10, 13). Until recently, however, few studies considered the impacts of any directional environmental change on the fundamental consumptive pathways that structure food webs (but see refs. 32 and 38–40), and thus climate change impacts on food web structure remain elusive. Our finding, that air temperature mediates a predictable shift in food web structure as a predator integrates different habitats, contributes to an emerging research area that considers biotic interactions in climate change effects. Moreover, these findings support the general idea that consumptive effects and spatial conditions in food webs cannot be overlooked if we aim to understand climate impacts on communities (12, 13, 23).

With ongoing climate change, ecotherms in aquatic and terrestrial systems may increasingly face the challenge of staying cool. By shifting from warm habitats (for example, aquatic = near-shore, terrestrial = direct sun) to cold refuge habitats (for example, aquatic = offshore, terrestrial = shade), organisms avoid detrimental and potentially lethal thermal exposure in their environment. Indeed, we found that the apex predator in these boreal lakes did, in fact, alter its habitat use in a manner expected by thermal tolerance (33, 36), as we detected a decreased proportion of lake trout in near-shore habitat with relatively warmer air temperatures (Fig. 2*D*). Such behavioral thermal buffering by organisms is well known for individual species (6), but the implications of this climate-mediated behavior on the integration of food web pathways has not been studied.

Data show that over a climatic gradient the trophic pathway that couples two lake habitats contracts, and the height of the food chain pathway linking basal resources to the focal predator lengthens, as warming air temperature drives a thermal differential within lakes. This decoupling of resource pathways and increased predator trophic position occurs independently of the abundance of near-shore prey species and the presence of two warm-tolerant predators that can be found in some of the systems we studied. We recognize that this may not always be the case and expect that warm-water predators and negative temperature effects on prey species along with indirect behavioral effects (12) can magnify the consumptive shift we identify. We do argue that our study provides evidence that thermal accessibility can be an important mediator of the biomass uptake by predators from different habitats and thus can influence the structure of food webs across climatic conditions. This result aligns with previous food chain research that has argued that behavioral responses and altered habitat use in response to climatic conditions can mediate prey encounter and biomass structure at different trophic levels (12). Our findings extend previous knowledge by showing that thermal effects act to shift consumptive pathways according to spatial temperature features across systems. In a general sense, this result supports recent research that argues for spatial conditions as an important regulator of the fundamental pathways of energy flow from basal resources to predators in food webs (19, 21, 32, 40).

The habitat avoidance and the shift in trophic interactions we document may have important implications for the sustainability
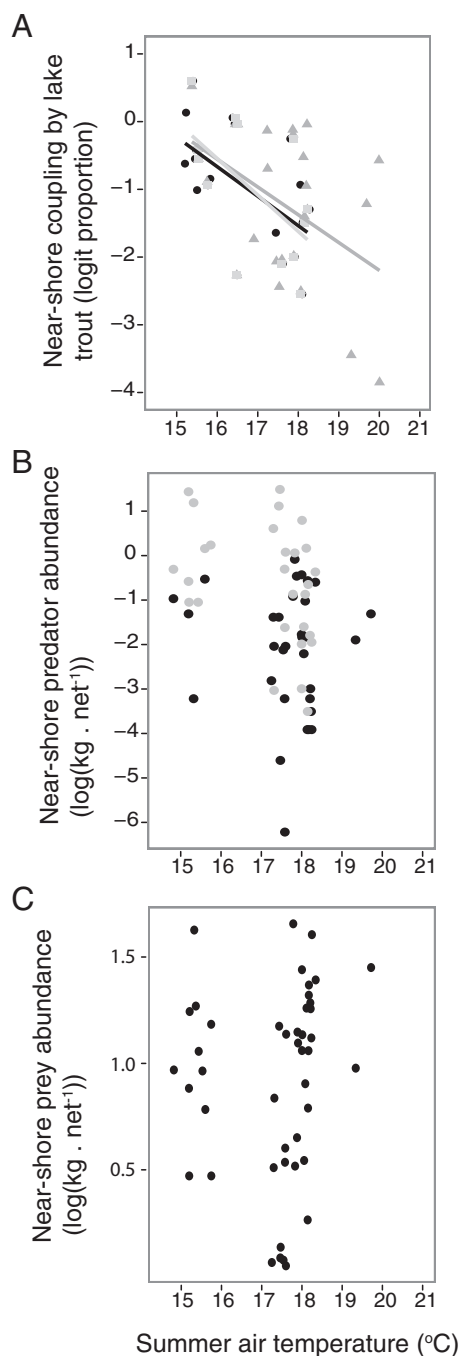

Fig. 3. Relationship between temperature and near-shore coupling is independent of measured indicators of indirect effects in study lakes. (*A*) The negative relationship between temperature and near-shore coupling [logit($\delta^{13}C_{lake\ trout} - \delta^{13}C_{mussel}$)/($\delta^{13}C_{snail} - \delta^{13}C_{mussel}$)] occurs with smallmouth bass absent [black line (black circle); $R^2 = 0.33$, df = 17, $P = 0.009$], walleye absent [dark gray line (gray triangle); $R^2 = 0.22$, df = 24, $P = 0.01$], and both near-shore predators absent [light gray line (gray square); $R^2 = 0.35$, df = 11, $P = 0.03$]. (*B*) Smallmouth bass (black circle; $R^2 = 0.007$, df = 30, $P = 0.65$) and walleye (gray circle; $R^2 = 0.12$, df = 26, $P = 0.07$) biomass per net are not significantly related to the temperature gradient in lakes where these predators are present. (*C*) Near-shore prey biomass per net is independent of the climatic gradient ($R^2 = 0.0064$, df = 43, $P = 0.599$). Summer air temperature is the mean monthly temperature averaged for June, July, and August for the year each lake was sampled. Near-shore coupling is the proportional contribution of $\delta^{13}C$ from near-shore basal resources relative to offshore basal resources ultimately assimilated in lake trout tissue. For display in *A*, circles have been jittered 0.1 on *x*-axis and triangles 0.1 on *y*-axis to reduce overlap.

of these freshwater food webs and for complex food webs in general. A reduced energy flux to predators can lower predator population size (19, 20) and leave predators more susceptible to extinction by other stressors in their environment (for example, harvest). In addition to the potential for predator extinction from lowered access to production, intolerable conditions also limit a predator's ability to switch habitats in response to prey variability. Such behavior can reduce the potential for "adaptive" stabilization of the food web. For example, if prey species have the potential to oscillate, predators may suppress this potential by switching from prey at low abundance to feed on abundant prey. In the absence of this flexibility, predators may continue to reduce prey in disturbed habitats, or food chains without weak predator coupling may be more prone to rapid dynamic fluctuations with improved conditions (16, 19, 20). These kinds of responses are recognized as potential implications of this food web structural shift on community dynamics, and sustainability. Understanding the nature of the relationships between food web structure and dynamics remains a challenge for climate research, and clarifying the relationship between structure and function of food webs is a central problem in ecology.

Our study uses a food web approach to relate climate to the biodiversity inherent in the world's ecosystems. In particular, we expect our findings to have major implications for climate impacts on an integral part of global freshwater biodiversity on which mankind relies. Boreal lakes in particular house a large part of Canada's 37% share of global freshwater (34). Furthermore, freshwater communities in these lakes support recreational and subsistence fisheries of substantial social and economic value (e.g., Canadian recreational fishery value of >4.9 billion dollars annually) (41). Aside from the dynamic implications of food web shifts, increased trophic positions of the predators in these systems have been linked to greater accumulation contaminants (42), adding to potential considerations when assessing the influence of climate on the services that humans rely on in these ecosystems. More generally, given the widespread recognition of consumer thermoregulation, such a fundamental shift in dominant trophic pathways may extend to a number of aquatic and terrestrial ecosystems. Finally, we suggest that flexible food web structure may serve as an important diagnostic tool for the detection of climate change effects, and so we argue for more research on the implications of food web restructuring for use in conservation efforts.

Materials and Methods

General Lake Sampling. In 2009, we began collecting data to estimate food web relationships using stable isotope techniques from lakes across the Canadian province of Ontario in conjunction with ongoing Ontario Ministry of Natural Resources (OMNR) lake biodiversity surveys. Full details for the fish community netting protocol and isotope collection can be found elsewhere (43). Our general methodology for isotope processing and analysis follows previously published studies (18, 22, 32). In an attempt to extend our sampling range, we supplemented the whole-lake sampling with isotope data collected from a few lakes using a less intensive sampling effort. In what follows, we provide details necessary to understand our general methodology and data analysis.

Summer air temperature data were obtained for each lake for the year the lake was sampled from a climate database (historical climate analysis tool) maintained by the OMNR (44). Five additional temperature measures along with some general study lake characteristics were used in analyses appearing in SI Results and Discussion [OMNR database and Environment Canada database (44, 45)]. Lake characteristic measurements were obtained from historical government (OMNR) databases or were measured during the biological survey.

Stable Isotope Data Collection. Food web structure was procured from tissue-based stable isotope analysis of a representative set of organisms in the lake trout food web of boreal lakes (Fig. 1). We used carbon as a tracer of spatial structure as isotope ratios (δ^{13}C) exhibit little to no (<1‰) ^{13}C enrichment with transfer among trophic levels but differ between primary producers in offshore and near-shore habitats (21, 30, 31). Nitrogen (δ^{15}N) is used to estimate the number of trophic transfers in the pathway from basal resource

to an apex predator. This is possible as nitrogen isotope ratios exhibit a 3–4‰ fractionation between predators and prey, and have been shown to correspond with diet data in freshwater lakes (31, 38, 46). Using this approach, we are positioned to obtain estimates of the reliance of lake trout on near-shore and offshore resources (habitat coupling) and the food chain length of the sink food web that leads to lake trout.

For most lakes, lake trout and forage fish tissue samples were collected according to a standard gill netting methodology where nets were assigned to random locations based on a depth-stratified design (43). Mussels [Unionidae, zebra mussels (Dreissena sp.) (two lakes)] were collected by snorkeling or dip nets and were used as an integrated indicator of pelagic isotope baselines. Gastropods were used as indicators of the near-shore resource baseline and were collected by the same methods as mussels. Near-shore benthic insects were also obtained for the near-shore zone using a kick net and by hand picking individuals from the rocks and woody debris. Mesh nets, 150–200 μm, were retrieved five times from below 20 m of the water's surface from the deepest part of the lake to collect zooplankton.

From larger fish, a muscle sample (~2 g) was removed in the field from behind the dorsal fin and above the lateral line to keep the tissue sample consistent (43). Smaller fish were frozen whole and dorsal muscle tissue was removed in the laboratory (target 500 μg dried sample). Mussels and snails were removed from their shell so that only soft tissue was used. Zooplankton and near-shore invertebrates were kept whole. Samples were dried at 65–70 °C for 48–72 h. Dried samples were ground into powder and were sent to the University of New Hampshire stable isotope laboratory for analysis.

Stable Isotopes-Based Food Web Measures. We used established methodology and two source mixing models to determine the contribution of near-shore carbon in lake trout diets and their trophic position. The number of lake trout isotope samples obtained ranged from 2 to 24, with an average of 13 individual trout sampled per lake. Lake trout, 250 mm in fork length (snout tip to fork of tail) and larger, were used, as fish of this size were expected to be capable of predating on small forage fish as well as invertebrates. We only used lakes where both littoral and pelagic forage fish were present in an attempt to preserve the general trophic structure across lakes.

If one of the key baseline organisms (that is, mussels or snails) was not collected, which occurred in a few lakes, we used linear regression models to estimate missing baseline values from other organisms from the same lake. Carbon isotope ratios were estimated with the following equations: $\delta^{13}C_{mussel} = 0.7071(\delta^{13}C_{pelagic\ forage\ fish}) - 7.9513(R^2 = 0.35)$ and $\delta^{13}C_{snail} = 1.0377(\delta^{13}C_{mussel}) + 9.5952(R^2 = 0.17)$. Nitrogen baseline values were estimated in the same way, e.g., $\delta^{15}N_{snail} = 0.895(\delta^{15}N_{mussel}) - 0.3275(R^2 = 0.71)$.

Estimates of near-shore carbon contribution are based on the mean δ^{13}C for lake trout, mussel, and snails in each lake using the following equation (22): proportion near-shore carbon in lake trout diet = $(\delta^{13}C_{lake\ trout} - \delta^{13}C_{mussel})/(\delta^{13}C_{snail} - \delta^{13}C_{mussel})$. The same equation was used for the forage fish based calculation with $\delta^{13}C_{pelagic\ forage\ fish}$ and $\delta^{13}C_{littoral\ forage\ fish}$ replacing $\delta^{13}C_{mussel}$ and $\delta^{13}C_{snail}$, respectively: Proportion near-shore fish carbon in lake trout diet = $(\delta^{13}C_{lake\ trout} - \delta^{13}C_{pelagic\ forage\ fish})/(\delta^{13}C_{littoral\ forage\ fish} - \delta^{13}C_{pelagic\ forage\ fish})$. Trophic position of lake trout was calculated using the following equation (32): trophic position = $2 + (\delta^{15}N_{lake\ trout} - (\delta^{15}N_{mussel} \times (1 - \alpha) + \delta^{15}N_{snail} \times \alpha))/3.4$, where 3.4 is the assumed per-trophic level increase due to fractionation in ^{15}N, 2 is the trophic position of the organism used to estimate baseline values, α is the proportion of littoral carbon and weighs the trophic position estimate according to baseline contributions.

Catch Data Analysis. Catch estimates were obtained from lakes used in the isotope analysis that were sampled using whole-lake standardized netting protocols (43). Near-shore habitat use by lake trout was determined as the number of lake trout caught from nets in less than 6 m of water relative to the total catch for the whole lake. Presence and absence of smallmouth bass and walleye were determined by biodiversity surveys and historical records for each lake. Catch per unit effort estimates for smallmouth bass, walleye, and littoral species were estimated for the whole lake and predator catch estimates were area weighted by depth stratum using lake bathymetry. The basic unit of the catch estimate used in our analysis of predator catch is kilograms of fish per gang, where a gang is the equivalent to 25 m of net. The number of individuals per gang is used for the forage species according to their presence in each lake (34 sp.).

Statistical Approach. We used linear, logistic (binomial), and multivariate regression models in our analyses. We transformed data according to statistical requirements (47). Logit transforms were used for isotope proportion data (48). Catch per unit effort estimates used as fish abundance measures were log transformed. To avoid extreme zero inflated catch distributions,

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we analyzed smallmouth bass and walleye biomass per net for lakes where the species are present and where we had catch data. We felt this was an appropriate way to meet statistical assumptions and considering we examined the effects of the absence of these predator species in another analysis. We excluded an outlier from the analysis for Fig. 2B and in the near-shore fish coupling summary in *SI Results and Discussion*. This single measure had a large effect on the linear regression model as identified by Cook's distance (48) and was the highest value in the dataset. All analyses were performed using the R language statistical environment.

1. Levin S (1998) Ecosystems and the biosphere as complex adaptive systems. *Ecosystems* 1(5):431–436.
2. Huey RB, Stevenson RD (1979) Integrating thermal physiology and ecology of ectotherms: A discussion of approaches. *Am Zool* 19(1):357–366.
3. Dell AI, Pawar S, Savage VM (2011) Systematic variation in the temperature dependence of physiological and ecological traits. *Proc Natl Acad Sci USA* 108(26): 10591–10596.
4. Dell AI, Pawar S, Savage VM (2014) Temperature dependence of trophic interactions are driven by asymmetry of species responses and foraging strategy. *J Anim Ecol* 83(1):70–84.
5. Kearney M, Shine R, Porter WP (2009) The potential for behavioral thermoregulation to buffer "cold-blooded" animals against climate warming. *Proc Natl Acad Sci USA* 106(10):3835–3840.
6. Brett JR (1971) Energetic responses of salmon to temperature. A study of some thermal relations in the physiology and freshwater ecology of sockeye salmon (*Oncorhynchus nerkd*). *Am Zool* 11(1):99–113.
7. Walther GR, et al. (2002) Ecological responses to recent climate change. *Nature* 416(6879):389–395.
8. Schmitz OJ, Post E, Burns CE, Johnston KM (2003) Ecosystem responses to global climate change: Moving beyond color mapping. *Bioscience* 53:1199–1205.
9. Suttle KB, Thomsen MA, Power ME (2007) Species interactions reverse grassland responses to changing climate. *Science* 315(5812):640–642.
10. Post E (2013) *Ecology of Climate Change: The Importance of Biotic Interactions* (Princeton Univ Press, Princeton).
11. Post E, Pedersen C (2008) Opposing plant community responses to warming with and without herbivores. *Proc Natl Acad Sci USA* 105(34):12353–12358.
12. Barton BT, Schmitz OJ (2009) Experimental warming transforms multiple predator effects in a grassland food web. *Ecol Lett* 12(12):1317–1325.
13. Gilman SE, Urban MC, Tewksbury J, Gilchrist GW, Holt RD (2010) A framework for community interactions under climate change. *Trends Ecol Evol* 25(6):325–331.
14. Schmitz OJ (2013) Global climate change and the evolutionary ecology of ecosystem functioning. *Ann N Y Acad Sci* 1297:61–72.
15. Petchey OL, McPhearson PT, Casey TM, Morin PJ (1999) Environmental warming alters food-web structure and ecosystem function. *Nature* 402:69–72.
16. Rooney N, McCann K, Gellner G, Moore JC (2006) Structural asymmetry and the stability of diverse food webs. *Nature* 442(7100):265–269.
17. Schindler DE, Scheuerell MD (2002) Habitat coupling in lake ecosystems. *Oikos* 98: 177–189.
18. Dolson R, McCann K, Rooney N, Ridgway M (2009) Lake morphometry predicts the degree of habitat coupling by a mobile predator. *Oikos* 118:1230–1238.
19. McCann KS, Rasmussen JB, Umbanhowar J (2005) The dynamics of spatially coupled food webs. *Ecol Lett* 8(5):513–523.
20. Post DM, Conners ME, Goldberg DS (2000) Prey preference by a top predator and the stability of linked food chains. *Ecology* 81:8–14.
21. Tunney TD, McCann KS, Lester NP, Shuter BJ (2012) Food web expansion and contraction in response to changing environmental conditions. *Nat Commun* 3:1105.
22. Vander Zanden MJ, Casselman J, Rasmussen J (1999) Stable isotope evidence for the food web consequences of species invasions in lakes. *Nature* 401:464–467.
23. Post E, Peterson RO, Stenseth NC, McLaren BE (1999) Ecosystem consequences of wolf behavioural response to climate. *Nature* 401:905–907.
24. Woodward G, Perkins DM, Brown LE (2010) Climate change and freshwater ecosystems: Impacts across multiple levels of organization. *Philos Trans R Soc Lond B Biol Sci* 365(1549):2093–2106.
25. Kalff J (2002) *Limnology: Inland Water Ecosystems* (Prentice Hall, Upper Saddle River, NJ).
26. Sharma S, Jackson DA, Minns CK, Shuter BJ (2007) Will northern fish populations be in hot water because of climate change? *Glob Change Biol* 13(10):2052–2064.
27. Keller W (2007) Implications of climate warming for Boreal Shield lakes: A review and synthesis. *Environ Rev* 15:99–112.
28. Schindler DW, et al. (1990) Effects of climatic warming on lakes of the central boreal forest. *Science* 250(4983):967–970.
29. Magnuson JJ, Crowder LB, Medvick PA (1979) Temperature as an ecological resource. *Am Zool* 19(1):331–343.
30. Beitinger TL, Fitzpatrick LC (1979) Physiological and ecological correlates of preferred temperature in fish. *Am Zool* 19(1):319–329.
31. France RL (1995) Differentiation between littoral and pelagic food webs in lakes using stable carbon isotopes. *Limnol Oceanogr* 40(7):1310–1313.
32. Post DM, Pace ML, Hairston NG, Jr. (2000) Ecosystem size determines food-chain length in lakes. *Nature* 405(6790):1047–1049.
33. Plumb JM, Blanchfield PJ (2009) Performance of temperature and dissolved oxygen criteria to predict habitat use by lake trout (*Salvelinus namaycush*). *Can J Fish Aquat Sci* 66(11):2011–2023.
34. Minns CK, Moore JE, Shuter BJ, Mandrak NE (2008) A preliminary national analysis of some key characteristics of Canadian lakes. *Can J Fish Aquat Sci* 65(8):1763–1778.
35. Morbey Y, Addison P, Shuter BJ, Vascotto K (2006) Within-population heterogeneity of habitat use by lake trout Salvelinus namaycush. *J Fish Biol* 69(6):1675–1696.
36. Snucins E, Gunn J (1995) Coping with a warm environment—behavioral thermoregulation by lake trout. *Trans Am Fish Soc* 124(1):118–123.
37. Scott WB, Crossman EJ (1985) *Freshwater Fishes of Canada* (Gordon Soules Book Publishers, Vancouver).
38. Tylianakis JM, Tscharntke T, Lewis OT (2007) Habitat modification alters the structure of tropical host-parasitoid food webs. *Nature* 445(7124):202–205.
39. Schoener T (1989) Food webs from the small to the large. *Ecology* 70(6):1559–1589.
40. Vander Zanden MJ, Shuter BJ, Lester N, Rasmussen JB (1999) Patterns of food chain length in lakes: A stable isotope study. *Am Nat* 154(4):406–416.
41. Shuter BJ, Minns CK, Regier HA, Reist JD (1998) Canada country study: Climate impacts and adaptation: Fishery sector. *Canada Country Study: Climate Impacts and Adaptation: National Sectoral Volume*, eds Koshida G, Avis W (Environment Canada, Toronto), pp 257–318.
42. Cabana G, Rasmussen JB (1994) Modelling food chain structure and contaminant bioaccumulation using stable nitrogen isotopes. *Nature* 372(6503):255–257.
43. Sandstrom S, Rawson M, Lester N (2013) *Manual of Instructions for Broad-Scale Fish Community Monitoring; Using North American (NA1) and Ontario Small Mesh (ON2) Gillnets* (Queen's Printer for Ontario, Peterborough, ON, Canada).
44. Cross J, et al. (2012) *Historic Climate Analysis Tool*, ed Ontario Ministry of Natural Resources (Ontario Ministry of Natural Resources, Thunder Bay, ON, Canada).
45. Government of Canada (2013) National Resources Canada Canadian Forest Service climate estimates. Available at http://gmaps.nrcan.gc.ca/cl_p/climatepoints.php. Accessed July 20, 2013.
46. Vander Zanden MJ, Cabana G, Rasmussen JB (1997) Comparing trophic position of freshwater fish calculated using stable nitrogen isotope ratios (δ15N) and literature dietary data. *Can J Fish Aquat Sci* 54(4):1142–1158.
47. Sokal RR, Rolf FJ (1969) *Biometry : The Principles and Practice of Statistics in Biological Research* (Freeman, San Francisco).
48. Crawley MJ (2013) *The R Book* (Wiley, Chichester, UK), 2nd Ed.