Warmer climate squeezes aquatic predators out of their preferred habitat

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Ecosystems are mosaics of different habitats, each of which provides its own opportunities and risks to the organisms that inhabit it. The profitability of any habitat depends on a variety of biotic and abiotic variables including the abundance of prey, vulnerability to predators, and physical features such as temperature that modify physiology and behavior. Because biological and physical conditions are continuously varying, and it is rare that any single habitat satisfies all requirements for successfully completing life cycles, organisms must navigate across habitat landscapes to fulfill their resource needs. Human modifications to habitats are presenting new challenges to many organisms. One underappreciated effect humans are having on the profitability of landscapes is via climate warming, where we are changing the rules of the game controlling how consumers can move among habitats. In PNAS, Guzzo et al. (1) show that warmer water temperatures in lakes restrict the daily movements of a top predator between habitats that are profitable for feeding and those that provide cold water for maintaining physiological functions. Intensified thermal barriers to movement under warmer climate conditions reduce feeding rates in productive habitats, thereby slowing growth of the predator. Surprising stories such as this continue to emerge from field ecology and serve as a sharp reminder that human perturbations to the Earth's climate system have many untold consequences for the biosphere.

Navigating Thermal Landscapes

Water temperature varies considerably within aquatic ecosystems, generating both opportunities and constraints for their inhabitants. In some habitats water is sufficiently cold that it depresses metabolic rates and therefore growth rates of predators. Other habitats provide metabolic opportunity because temperatures are warm enough to increase the potential for growth in organisms whose body temperatures track the water temperatures they are exposed to (2). Water temperatures can also exceed physiological limits of cold-adapted species, forcing them to seek refuge in pockets of cold habitat (3, 4), but often at the cost of reduced foraging opportunity. Climate change is altering the thermal characteristics of the landscapes that aquatic organisms occupy; however, the ecological consequences remain only superficially understood.

The boreal biome contains most of the world's lakes and nearly all of these are ice-covered during winter months. In spring, the absorption of solar radiation melts ice and heats surface waters, eventually leading to stable vertical stratification in thermal conditions of the water column. Temperature differences between warm, surface and deep, cold waters can exceed 15 °C over a few meters of depth, a gradient which typically persists for several months. This stratification can produce a physiological barrier to predators such as the widely distributed lake trout (*Salvelinus namaycush*), whose physiology is adapted to cold temperatures, forcing them to spend most of their time in deep, cold water and avoid warm surface habitats during summer. Under these conditions lake trout are spatially segregated from their preferred prey, which live in near-shore (littoral) habitats bathed in warm water. To access these prey, lake trout must make directed movements to the littoral zone to feed but run the risk of experiencing thermally stressful conditions in doing so.

Working in small, undeveloped lakes at the IISD-Experimental Lakes Area in northwestern Ontario, Canada, Guzzo et al. (1) studied the foraging behavior of lake trout by implanting them with telemetry tags to track the habitats used during the ice-free season. Daily movements by lake trout between deep, cold-water habitats and the warm littoral habitat were quantified over an 11-y period during which there was substantial variation in the seasonal timing and duration of thermal stratification. Contrasts in climate conditions among years enabled Guzzo et al. (1) to assess whether lake trout behavior responded to changes in the time it took lakes to form strong thermal stratification during the spring. Most littoral habitat feeding occurred during the spring season as surface habitats were in the process of warming, but before they exceeded the upper thermal tolerance of lake trout. Feeding forays into warm littoral habitats were rare during summer when surface waters exceeded 15 °C. Warmer summers were associated with more abrupt vernal warming that reduced the time during which lake

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trout could access the littoral zone without experiencing excessively warm water. Thus, warmer climate conditions reduced the opportunities for lake trout to access the productive littoral habitat where their preferred prey live.

Guzzo et al. (1) also used carbon stable isotope ratios to determine whether thermally induced changes in lake trout behavior affected their capacity to acquire energy from productive littoral habitats. Prey from alternative habitats in lakes typically have distinct carbon stable isotope ratios due to the differences in physical conditions that affect the kinetics governing how algae fix carbon dissolved in the surrounding water (5). Algae form the trophic foundation of lake food webs, and this isotope signature is passed reliably into consumers of the algae and eventually to top predators such as lake trout. Thus, the carbon stable isotope signatures of fish reflect their reliance on the dominant energy pathways originating from different habitats. Guzzo et al. (1) report that during years when spring warming was abrupt and lake trout were constrained to cold, deep-water habitat longer, fewer littoral resources were assimilated by lake trout by the end of the growing season. The decreased reliance on littoral food resources led to reduced body condition such that lake trout were distinctly leaner during warm summers compared with years when spring warming was more protracted. Thus, changes in the timing and pace of spring warming fundamentally changed how organic matter flowed from algae to top predators.

Lake trout have been remarkably adaptable to the variation in climate conditions they experience across their geographic range. In North America, their native distribution spans the northern United States through much of the Canadian arctic. Thus, it is not too surprising that this species can alter its behavior to cope with the local climate conditions. However, Guzzo et al. (1) show that that this species is capable of adapting its behavior over the short time frames associated with interannual variation in lake thermal conditions. This adaptability should offer some optimism about the potential for lake trout to persist with ongoing climate warming. However, their ability to cope with new climate conditions will depend on the maintenance of habitat options to which they can adapt their behavior. Increasing human development of lakeshores often leads to increased algal growth, which hastens the depletion of oxygen in deep waters, potentially eliminating that habitat as a cold-water refugium (6). Development of lakeshores also runs the risk of degrading littoral habitats (7) such that they may be less profitable to lake trout during the spring when they rely on them heavily. Invasions by species tolerant of warmer conditions, such as smallmouth bass, will also compete with lake trout in littoral habitats (8), thereby reducing their ability to capitalize on near-shore resources.

Predators in a Warmer Future

Guzzo et al. (1) also show that rapidly warming springs produced physiological costs to lake trout, associated with reduced opportunity to feed in the most profitable habitats during this season. Thus, even if viable habitat options are maintained that enable lake trout to adapt their foraging behavior to warming climate, we should expect that the productivity of lake trout populations will also respond. Fisheries managers who regulate harvest on this culturally important species must be cognizant that exploitation rates that were sustainable in the past might not be in the future (9), particularly in more southerly ecosystems where warming climate may intensify thermal constraints on lake-trout foraging. Alternatively, lake-trout populations in arctic ecosystems might actually become more productive, thereby being able to support higher exploitation rates under warmer conditions.

Climate change has left a distinct footprint on the thermal conditions of temperate lakes globally. Most lakes with long-term observational records have shown distinct warming trends (10) and much of this warming is occurring during the late winter and spring. Temperate lakes are experiencing earlier dates of spring ice breakup (11) and timing of thermal stratification (12), conditions that place thermal constraints on the abilities of lake trout to forage in profitable habitats. Further climate change will intensify these changes, although the consequences for lake trout and for other aquatic species remain only vaguely understood.

This case study serves as a convincing example of the complexities involved in how ecological systems respond to warming climate. A priority for management and conservation should be to maintain functioning habitat options for organisms so that they can respond to new constraints and opportunities as warming climate alters the attributes of ecosystems. Without such options in a warmer future, organisms such as lake trout will not likely persist throughout their range. Accurate predictions of how specific ecosystems will respond in a warmer world will remain elusive, and management regimes need to remain vigilant to change through active monitoring and assessment and flexible for adapting policies to accommodate new conditions and ecological dynamics as they reveal themselves (13).

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