

FEATURE

# How Does Climate Change Affect Emergent Properties of Aquatic Ecosystems?

**Michelle D. Staudinger**  | U.S. Geological Survey, U.S. Department of the Interior, Northeast Climate Adaptation Science Center, Amherst, MA 01003 | University of Massachusetts, Department of Environmental Conservation, Amherst, MA. E-mail: mstaudinger@usgs.gov

**Abigail J. Lynch**  | U.S. Geological Survey, National Climate Adaptation Science Center, Reston, VA

**Sarah K. Gaichas**  | NOAA NMFS Northeast Fisheries Science Center, Woods Hole, MA

**Michael G. Fox**  | Trent University, School of the Environment and Department of Biology, Peterborough, ON, Canada

**Daniel Gibson-Reinemer**  | Adams State University, Department of Biology, Alamosa, CO | Illinois Natural History Survey, Illinois River Biological Station, Havana, IL

**Joseph A. Langan**  | University of Rhode Island, Graduate School of Oceanography, Narragansett, RI

**Amy K. Teffer**  | University of British Columbia, Department of Forest and Conservation Sciences, Vancouver, BC | David H. Smith Conservation Research Fellowship, Society for Conservation Biology, Washington D.C

**Stephen J. Thackeray**  | UK Centre for Ecology & Hydrology, Lancaster Environment Centre, Lake Ecosystems Group, Bailrigg, Lancaster, UK

**Ian J. Winfield**  | UK Centre for Ecology & Hydrology, Lancaster Environment Centre, Lake Ecosystems Group, Bailrigg, Lancaster, UK

An adult Sockeye Salmon *Oncorhynchus nerka* at Adams River spawning grounds, British Columbia, Canada, showing skin *Saprolegnia* sp. infections. Adult Pacific salmon die naturally after spawning but carry multiple infections that can be accelerated by warming to affect longevity in freshwater and reproductive fitness. Photo credit: Amy Teffer.

Emergent properties of ecosystems are community attributes, such as structure and function, that arise from connections and interactions (e.g., predator-prey, competition) among populations, species, or assemblages that, when viewed together, provide a holistic representation that is more than the sum of its individual parts. Climate change is altering emergent properties of aquatic ecosystems through component responses, a combination of shifts in species range, phenology, distribution, and productivity, which lead to novel ecosystems that have no historical analog. The reshuffling, restructuring, and rewiring of aquatic ecosystems due to climate impacts are of high concern for natural resource management and conservation as these changes can lead to species extinctions and reductions in ecosystem services. Overall, we found that substantial progress has been made to advance our understanding of how climate change is affecting emergent properties of aquatic ecosystems. However, responses are incredibly complex, and high uncertainty remains for how systems will reorganize and function over the coming decades. This cross-system perspective summarizes the state of knowledge of climate-driven emergent properties in aquatic habitats with case studies that highlight mechanisms of change, observed or anticipated outcomes, as well as insights into confounding non-climate effects, research tools, and management approaches to advance the field.

## WHAT ARE EMERGENT PROPERTIES AND HOW CAN CLIMATE CHANGE MODIFY THEM?

Emergent properties of ecosystems refer to all ecological components of a community, including connections and interactions among species or assemblages, that when viewed together are more than the sum of their parts (Mayr 1982). Further, these holistic properties (e.g., community structure and interactions) are not generally predictable from individual attributes (e.g., individual species or population responses) when considered in isolation.

Climate change can modify emergent properties of freshwater and marine ecosystems as fishes and other aquatic species reshuffle across watersheds and seascapes through shifts in range, phenology, distribution, phenotype, and productivity (Carter et al. 2019; Weiskopf et al. 2020). These climate-induced responses alter the strength and intensity of established (i.e., historical) trophic interactions to restructure, rewire, and create novel combinations of community members or assemblages that have no historical analog (Hobbs et al. 2009; Pecl et al. 2017). As ecological interaction networks rewire and energy flows shift or are disrupted (Bartley et al. 2019) due to changes in habitat conditions, local extinctions, altered species dominance, and trophic mismatches, there is increasing concern about the future provisioning of ecosystem services that humans value and on which they depend (Carter et al. 2019; Weiskopf et al. 2020).

Our understanding of how climate change affects biodiversity, species interactions, community composition, and ecosystem function across ecological and spatiotemporal scales has advanced considerably through observational, experimental, and modeling approaches. The field is rapidly progressing from simple, negative predictions of the potential impacts and the ecological sensitivities of species, to more nuanced and balanced examinations of phenotypic and evolutionary mechanisms that allow for positive and neutral adaptive responses to changing environmental conditions (Dell et al. 2014; DeGregorio et al. 2015; Beever et al. 2016). The indirect effects of climate change resulting from altered trophic interactions have been predicted to be as, or more, influential on population dynamics as the direct impacts (Hunsicker et al. 2013; Gilbert et al. 2014; Howell and Filin 2014); yet until recently, we have had few examples of what these changes would actually look like.

In this article, we synthesize the current state of knowledge on observed and projected changes in emergent properties of aquatic systems due to climate change. Studies were synthesized using Web of Science and Google Scholar using the terms “climate change + trophic interactions,” “novel species interactions,” “novel ecosystems,” and “climate change + predator and prey.” Our findings primarily represent the

literature from 2009–2017, with additional recent studies added through expert elicitation. Based on recent national and global climate-impact assessments (Groffman et al. 2014; Pecl et al. 2017; Lipton et al. 2018; Carter et al. 2019), we expected to see mounting evidence in the literature for the reshuffling, restructuring, and rewiring of aquatic ecosystems through three broad, hypothesized mechanisms: (1) rearrangement and turnover of species, especially in temperate marine systems, with warm water species outcompeting and dominating cold water species, (2) novel assemblages resulting from component responses, especially from shifts in species range and phenology, and (3) declining biodiversity with increased dominance of generalists, and species with r-selected life history traits (e.g., early maturation, high fecundity), particularly in freshwater systems. We organize our findings to highlight patterns and exceptions in evidence around these three hypotheses (Figure 1).

Although many aquatic systems have already been altered in some way by anthropogenic stressors (e.g., pollution, habitat degradation, fishing pressure, stocking, dams), and the proliferation of non-native invasive species, which act as major agents of change, we focus specifically on climate-mediated shifts in ecosystems stemming from the redistribution of native species as they respond to climate impacts. This approach highlights how the reshuffling of biodiversity creates unique, and often poorly recognized management challenges for aquatic species of conservation concern. Our summary focuses on North America, but includes a long-term freshwater case study in the United Kingdom as an important comparison with insights into complex large-scale changes in fish communities and the consequences for fisheries management (Case Study 1). Results of this cross-system perspective are intended to inform future research efforts, fisheries management decisions, and conservation actions by highlighting potential mechanisms, consequences, vulnerabilities, and available adaptation options.

## WHAT IS THE CURRENT STATE OF KNOWLEDGE ON HOW CLIMATE CHANGE IS MODIFYING EMERGENT PROPERTIES OF AQUATIC ECOSYSTEMS?

We found varying support for all three hypotheses and aligned evidence in the following subsections each under a primary hypothesis. We also note where intersections occur with other hypotheses. In the first two subsections, we discuss and present examples of how aquatic species rearrangement and turnover is largely favoring warm water species and smaller body sizes. These changes, in concert with altered predatory demand and patterns in prey selection, have major implications for

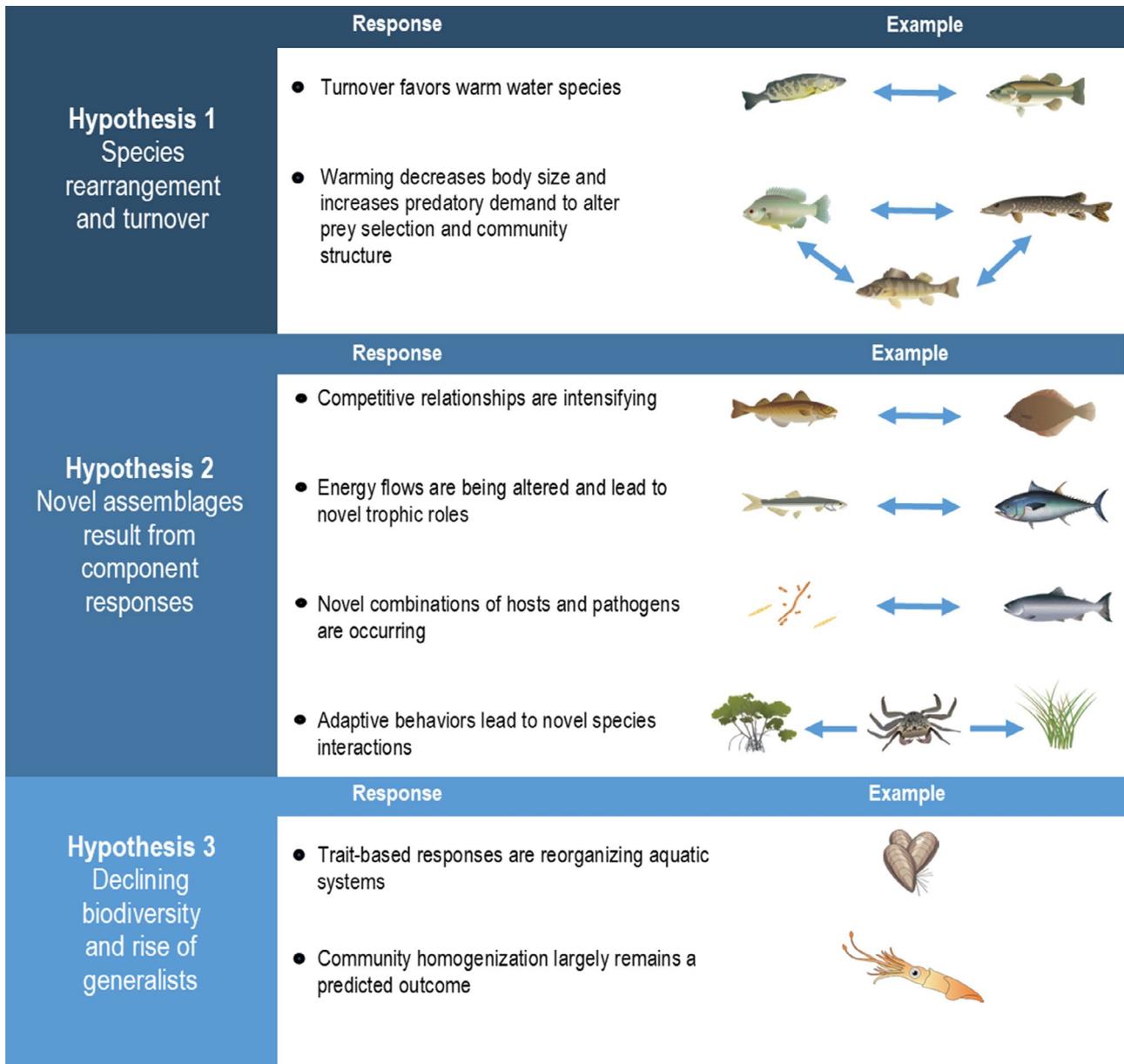


Figure 1. A conceptual model and road map for this synthesis that outlines the three hypothesized mechanisms for climate-induced changes in emergent properties in aquatic systems, various lines of evidence (bullets), and selected examples (icons) of observed and projected responses discussed in the main text. Symbols courtesy of the Integration and Application Network, University of Maryland Center for Environmental Science ([ian.umces.edu/symbols/](http://ian.umces.edu/symbols/)).

community structure and function (Hypothesis 1). In the next four subsections, we share the strongest and most complex evidence for novel assemblages arising from component responses that are leading to changes in competition, predator–prey interactions, host–parasite relationships, and affecting energy transfer through different communities and systems (Hypothesis 2). In the last subsection, we consider what is known about trait-based responses and how this can affect system reorganization and declines in biodiversity (Hypothesis 3).

**Biodiversity Rearrangement and Turnover Largely Favor Warm Water Species (Hypothesis 1)**

A key characteristic of climate-mediated emergent properties is that food webs may reorganize as novel species infiltrate and become established in new areas or become ecologically

dominant at new or expanded times of year. The resulting changes in biodiversity, for example through species turnover, can have ecological implications even if species richness remains relatively stable (Schindler et al. 2015; Gavioli et al. 2019). Species turnover is arguably a more sensitive indicator of climate change impacts than species loss, because species have to become less abundant before they go extinct, and because species richness may even rise temporarily with environmental change, before subsequently declining (Hillebrand et al. 2018). Functional approaches are also highly informative, as species traits mediate how they respond to climate change, and how they affect the wider ecosystem. New species that move into an ecosystem may not be functionally equivalent to the ones they out-compete and/or replace, and may therefore have different effects on emergent ecosystem behavior.

Changes in the distribution of species based on suitable thermal habitat have been observed (Nye et al. 2009; Henderson et al. 2017) and projected for a wide range of freshwater and marine fishes and invertebrates (Comte et al. 2013; Kleisner et al. 2017; Morley et al. 2018). There are fewer examples of altered migration phenology and seasonal residence times of warm water fishes, with implications for seasonal species diversity and dominance, but these patterns are increasing (Wood et al. 2009; Cohen et al. 2018; Staudinger et al. 2019). For example, a recent study analyzing a 60-year historical dataset of Narragansett Bay, Rhode Island, observed changes ranging from weeks to months in the migration phenology of 8 out of 12 fish and squid species, with summer species extending and winter species contracting residence times in the system (Langan et al. 2021). Friedland et al. (2020) used an ensemble of species distribution and habitat models to evaluate changes in hundreds of fishes and invertebrates across the Northeast continental shelf. Study findings showed major shifts in community structure through increases in diversity that were due to an influx of range shifting warm water species. The observed trends are consistent with the prior hypothesis that species will increasingly occupy higher latitudes as they follow thermal niches (Jones and Cheung 2015). Although similar patterns of increases in warm water species were observed in Long Island Sound, overall species diversity declined (Hypothesis 3), primarily due to losses of cold water species (Snyder et al. 2019). This contrasting trend to other coastal systems in the Northeast region is explained as this area represents the interface where range edges overlap (i.e., southern range boundary for cold water species, northern edge for warm water species).

In freshwater systems, warm water species such as Smallmouth *Micropterus dolomieu* and Largemouth Bass *M. salmoides* are also expanding their range in freshwater habitats with documented and projected impacts to cool and cold water communities including culturally and economically important species such as Walleye *Sander vitreus* (Sharma et al. 2009; Lawrence et al. 2012; Alofs et al. 2014; Case Study 2).

#### **Warming Decreases Body Size and Increases Predatory Demand to Alter Prey Selection Patterns and Community Structure (Hypothesis 1)**

There is strong evidence from global meta-analyses that warming temperatures result in smaller body size across aquatic taxa (Daufresne et al. 2009; Sheridan and Bickford 2011). Changes in body size affects predator–prey dynamics by directly influencing foraging success, prey vulnerability, and competitive exclusion (Peters 1986; Nilsson and Brönmark 2000; Claessen et al. 2002). Temperature also appears to have an interactive effect on prey size selection, resulting in relatively stronger interactions at the smallest and largest body sizes found across global marine systems (Gibert and DeLong 2014). The exact mechanisms underlying temperature-mediated predator–prey body size interactions are still uncertain, but are linked to activity levels, encounter rates, detectability, and energetic trade-offs associated with larger versus smaller body sizes (Ewald et al. 2013; Dell et al. 2014). Certainly, the selective nature of fishing pressure complicates emerging patterns *in situ*.

Predation rates generally increase with temperatures (Ewald et al. 2013) due to expanded growing seasons, metabolic rates, and energetic demands. This is especially true for

species and guilds that have broad habitat and foraging niches, or that can tolerate and rapidly adapt to warmer conditions; however, thermal response rates and performance (e.g., movement speed, growth) vary widely across species and systems (Dell et al. 2014; Luhring and DeLong 2016). Some species (e.g., cool or cold water) could also exhibit decreased consumption rates if temperatures surpass optimal thresholds. Trends toward decreasing body size, but increasing consumer demands have been shown to have cascading effects that can lead to greater biomass at lower and intermediate trophic levels (Jochum et al. 2012; West and Post 2016). Climate-induced shifts in the timing and location (e.g., range boundary or edge) of predator–prey relationships can also have multifaceted effects that lead to trophic mismatches when there is not enough biomass to support simultaneous increases in consumptive demands resulting from increased physiological rates. For example, simulations using bioenergetic models of warming in shallow midwestern freshwater lakes predict increased annual consumption rates by predatory Northern Pike *Esox lucius* and Largemouth Bass of Bluegill *Lepomis macrochirus* and Yellow Perch *Perca flavescens* over the next few decades (Breeggemann et al. 2016). In this system, predatory demand is predicted to increase to meet energetic needs and exhibit a seasonal shift, resulting in increased annual consumption with implications for assemblage structure (Hypothesis 2). Varying responses across consumers and habitats (e.g., warmer vs. cooler) are likely to lead to a range of outcomes that alter the biomass, abundance, structure, and function of aquatic ecosystems (Jochum et al. 2012; Gibert and DeLong 2014).

#### **Competitive Relationships Are Intensifying As A Consequence Of Component Responses (Hypothesis 2)**

Competitive relationships are intensifying due to increasing niche overlap in numerous systems as fishes either concentrate spatially in narrow thermal areas or undergo differential rates of distribution shifts (Hunsicker et al. 2013; Howell and Filin 2014; Fall et al. 2018; Rubenson and Olden 2019; Friedland et al. 2020). However, subsequent responses within multiple food webs show a range of trophic outcomes, depending on divergent thermal tolerances, species diversity, trophic redundancy, and the ability of existing communities to resist or accommodate influxes of new species (Harvey et al. 2004). For example, a modeling study found increased overlap resulted in generally higher productivity for Barents Sea Cod *Gadus morhua*, effectively increasing carrying capacity; however, when their Capelin *Mallotus villosus* prey declined due to predation pressure, cannibalism within the Cod population was predicted to increase (Howell and Filin 2014). Models using detailed spatial predator–prey information between Arrowtooth Flounder *Atheresthes stomias* and juvenile Alaskan Pollock *G. chalcogrammus* in the Bering Sea demonstrated trade-offs in mortality rates (Hunsicker et al. 2013). Warmer temperatures resulted in decreased juvenile pollock survival (Hypothesis 1), and greater (negative) impacts on pollock recruitment were predicted if flounder distributions maintain current temperature associations (Spencer et al. 2016).

Novel competitive interactions have also been examined in freshwater lakes throughout Ontario, Canada (Van Zuiden et al. 2016), where observed and projected changes lead to major shifts in species abundance and community structure (Hypothesis 1). Mid- to end-of-century (2050–2070) warming scenarios predict warm water fishes such as Smallmouth Bass will out compete cool and cold water fishes such as Walleye and Lake Trout

*Salvelinus namaycush* (Van Zuiden et al. 2016). However, the presence of a key prey, Cisco *Coregonus artedii*, was hypothesized to buffer Walleye declines in lakes where Walleye and Smallmouth Bass co-occur. In addition, a retrospective analysis of empirical data found that Walleye populations were negatively affected by increased primary productivity and decreased water clarity resulting from warming (Robillard and Fox 2006). In contrast, bottom-up forcing benefitted *Micropterus* spp. due to their ability to detect and hunt for prey in turbid and more complex environments (i.e., high abundance of macrophytes). The compounding effects of climate and non-climate stressors on this complex of competing freshwater piscivores is discussed in more detail in Case Study 2.

### **Energy Flows Are Being Altered Through Component Responses, Leading to Novel Trophic Roles and Changes in Prey Quality (Hypothesis 2)**

Temperature-driven changes in community structure and abundance create novel ecological conditions through the rewiring of species interactions and energy flows, which can affect ecosystem stability (Bartley et al. 2019). For example, laboratory and empirical modeling studies of freshwater pond and lake systems have shown that species that advance their phenology due to earlier seasonal warming gain predatory advantages (Rasmussen et al. 2014; Nosaka et al. 2015). When phenology shifts were strong and resulted in pronounced size differences between competitors, trophic relationships switched from competitive to predator-prey interactions (Borcherding et al. 2010). In Alaska, changes in phenological overlap during years with warm springs resulted in Kodiak brown bear *Ursus arctos middendorffi* becoming more aligned with red elderberry *Sambucus racemosa* and less aligned with Sockeye Salmon *Oncorhynchus nerka*. This shifted bear foraging patterns to decouple this well-established historical relationship, which resulted in reduced mortality rates on Sockeye Salmon and decreased dispersion of marine-derived nutrients across surrounding terrestrial habitats (Deacy et al. 2017).

Climate-induced changes in prey quality also disrupt energy flows through negative impacts on predator growth, reproduction, and condition. Declines in the size structure of the Atlantic Herring *Clupea harengus* population in the Gulf of Maine is believed to have reduced the condition of Bluefin Tuna *Thunnus thynnus*, even as this key prey became more abundant (Golet et al. 2015). In the northwestern Atlantic, changes in production at the base of the food chain decreased trophic transfer of lipid reserves to Capelin, whose mean energy content decreased in recent decades, thus reducing the foraging efficiency of Atlantic Salmon *Salmo salar* (Renkawitz et al. 2015). In addition, marine heat waves in the Pacific Northwest were implicated in nutritional declines of Pacific Sand Lance *Ammodytes personatus* through reductions in body size and energy density that resulted in population declines and breeding failures of several predator guilds (von Biela et al. 2019).

### **Novel Combinations of Hosts and Pathogens Are Consequences of Component Responses (Hypothesis 2)**

The reshuffling of ecosystem composition, size structure, and species dominance can also redistribute and unbalance pathogen-host relationships, with unprecedented and unpredictable consequences on individual fitness and survival (Pecl et al. 2017; Bartley et al. 2019). Further, as fishes and other aquatic biota adapt to new environments, they will likely

encounter novel pathogens for which they have not developed immune resistance, and can affect establishment success rate (e.g., Stricker et al. 2016). Climate change impacts how infectious agents (e.g., viruses, bacteria, protozoan microparasites) interact with each other and their hosts, which may have disease outcomes, even for historically non-pathogenic agents (Altizer et al. 2013; Selakovic et al. 2014; Buck and Ripple 2017). For example, in British Columbia, Canada, adult Pacific salmon *Oncorhynchus* spp. exposed to chronic thermal stress during their spawning migration showed accelerated infection development for some bacteria and microparasites, altered physiological indices, and decreased longevity relative to fish in cool water (Teffer et al. 2017, 2018, 2019; cover image).

Infectious agents may therefore reduce host resilience to changes in environmental conditions associated with climate change for which there may not be plasticity in host phenology or behavior to mitigate fitness consequences (i.e., alterations in migration timing to avoid high temperatures). Further, little is known regarding pathogen dynamics at the leading edge of species range shifts given several factors: minimal long-term data on how infectious agents range geographically across marine and freshwater systems and hosts, differences in pathogen transmission dynamics in aqueous environments, and the complexity of food webs and (or) species interactions (Harvell et al. 2002; Lafferty 2017).

### **Adaptive Behaviors Can Lead to Novel Species Interactions (Hypothesis 2)**

Adaptive behaviors can alter biotic interactions that allow species to “persist in place” as temperature and food resource conditions change, such as by altering the diel or seasonal timing of activity levels to avoid heat stress or track prey (Beever et al. 2016; Monaco et al. 2016). Adaptive behaviors can also help species test novel foraging conditions, allowing them to alternate between historical and new prey options as they become available. For example, *in situ* observations of mangrove tree crabs *Aratus pisonii* showed they exhibited strong site fidelity in their native mangrove tree habitats, but this behavior was not observed as they colonized novel salt marsh habitats in Florida (Cannizzo and Griffen 2016). In a Canadian lake, Lake Trout, a cold water piscivore, exhibited distinct changes in foraging locations and prey size consumed during warmer years, which led to changes in individual growth rates and food web structure (Guzzo et al. 2017).

Changes in established behaviors are likely to be important in determining a species vulnerability to predation risk, starvation, or sub-lethal effects (e.g., predator avoidance or trade-offs in growth rates), especially if prey are naive or locally adapted to specific predators or conditions (Herstoff and Urban 2014; Miller et al. 2014; Luhning and DeLong 2016). However, a study of a suite of freshwater amphibians by Herstoff and Urban (2014) found that in common garden experiments, when prey were exposed to a novel range-shifting predator, survival was not compromised if they were familiar with a similar native predator. These results suggest that species are able to recognize analogues from other systems as threats, and that evolutionary and ecological histories are important to understanding future species responses.

### **Trait-Based Responses Are Reorganizing Aquatic Systems (Hypothesis 3)**

Species responses to climate change are heterogeneous across spatial and temporal scales, and their ecological traits

and trophic niches (generalist vs. specialists) largely dictate how adaptive they will be to changing and novel conditions. The more specialized a fish species is to a particular prey or habitat, the more vulnerable it typically is to changes in the availability of those resources (Chin et al. 2010; Hare et al. 2016). These trait-based responses directly contribute to how species redistribute, dominate, and colonize aquatic habitats in a changing climate (Dell et al. 2014). However, it is important to note that landscape factors often play a more substantial role than climate change in freshwater ecosystems as distribution shifts are blocked by natural and anthropogenic barriers (LeMoine et al. 2020). The consequences of which are most severe for sessile invertebrates. For example, freshwater mussels (Unionida) that are host generalists and long-term brooders are more able to disperse than host specialists and short-term brooders (Archambault et al. 2018).

Biodiversity loss from climate change is projected at provincial (e.g., Jackson and Mandrak 2002), continental (e.g., Markovic et al. 2014), and global scales (e.g., Xenopoulos et al. 2005). Additionally, losses or decreases of fish species occupying particular niches within communities are hypothesized to lead to abrupt community shifts (e.g., regime shifts; Beaugrand 2014). The paleo record provides historical evidence for nonlinear changes across geological time, where climate-driven mass extinctions of specialists were preceded by the rise and dominance of generalists (Blois et al. 2013). Another major shift observed over historical periods is the reduction in body sizes (Sheridan and Bickford 2011). Such changes are closely related to trends in smaller size-at-age and maturity relationships and are increasingly being documented as a result of modern climate change (Daufresne et al. 2009).

### **Community Homogenization Largely Remains A Predicted Outcome, Unless Non-Native Invasives Are Considered (Hypothesis 3)**

There are relatively few modern day examples of aquatic homogenization, unless non-native invasive species are considered (Scott and Helfman 2001; Villéger et al. 2011, 2015; Magurran et al. 2015). One exception is the rapid range and phenology expansions of squid populations in coastal areas, including the Humboldt squid *Dosidicus gigas* in the California Current (Stewart et al. 2014), and longfin inshore squid *Doryteuthis pealeii* in the Gulf of Maine (Mills et al. 2013) and Narragansett Bay systems (Langan et al. 2021). These short-lived (i.e., life spans of 1–2 years), and highly opportunistic predators, have taken advantage of warming waters and changes in oxygen minimum zones to expand into habitats and exert biological control on prey in novel habitats (Pershing et al. 2019). Further, homogenization of habitats and life history traits in historical and novel ecosystems also contribute to enhanced competition among species (Lancaster et al. 2017). However, extreme events and increased environmental and seasonal variability could also have the opposite effect through competitive exclusion after major disturbances (Sheil 2016).

### **HOW ARE NON-CLIMATIC EFFECTS CONFOUNDING EMERGENT PROPERTIES OF AQUATIC SYSTEMS?**

There are a range of factors that can affect emergent properties of ecosystems to create counter intuitive or unanticipated changes, including the interactive effects of climate with non-climate stressors (Lynch et al. 2016), lag effects (Phillips et al. 2010; Henderson et al. 2017), and portfolio

effects (Schindler et al. 2015). First and foremost, freshwater and marine ecosystems have a long history of disruption and stress from non-climate threats such as nutrient loading, pollution, fishing pressure, stocking or introduction of non-native or invasive species, and land use change (Lynch et al. 2016). Consequently, the degree of alteration (or management) must be considered when evaluating any of these hypotheses regarding emergent properties. As climate change impacts continue to increase, and fewer and fewer unaltered systems remain, these legacy stressors will continue to intensify or exacerbate ecological relationships and processes, potentially pushing them over critical tipping points that cause population declines (Powell et al. 2017). For example, higher temperatures often lead to increased primary production, which can result in bottom-up or even trophic-cascade effects on aquatic ecosystems (Case Study 2).

These impacts are not novel, seasonal algal blooms and eutrophication have long affected aquatic habitats, but the rate and locations where they occur as a result of climate change may differ from historical areas to cause novel effects (USGCRP 2019). Relationships are also becoming increasingly complex for management and conservation efforts to navigate. For example, regulated rivers like the Columbia, Colorado, and Mississippi are highly altered and restoring connectivity may (in some situations) reduce climate refugia for existing fish populations dependent on hypolimnetic releases.

Emergent ecosystem responses may be lagged with respect to changes in individual or combined climate and non-climate stressors, making it difficult to attribute changes to their source drivers (Robillard and Fox 2006; Graham et al. 2007; Case study 2). Lag effects are likely to cause complex and surprising outcomes that confound fisheries management, due to high variation in species responses stemming from differences in life histories and other factors including historical alterations (e.g., fishing, habitat loss) that influence event timing and manifestation (Bell et al. 2015; Langan et al. 2019). For example, lag effects were found for numerous marine species when the effects of climate change were greater on juvenile recruitment than adult survival because of the time necessary to propagate the effect throughout populations (Henderson et al. 2017). In addition, pathogens may lag behind their hosts as species shift their ranges (Crowl et al. 2008; Burge et al. 2014), especially if density dependent processes are in play (Phillips et al. 2010). Monitoring across ecological scales, consideration of system histories, and explicitly planning for uncertain futures (e.g., using approaches such as scenario planning [Borggaard et al. 2019]) are steps management could take to avoid surprising outcomes resulting from lagged ecosystem behaviors.

Trait-based approaches can help increase understanding of whether aquatic systems can function similarly at broad scales, even after species have reshuffled, food webs have restructured, and energetic pathways have been rewired (Schindler et al. 2015). This could occur through compensatory effects that average out across all responses (i.e., positive, negative, or neutral) within the study system (Olsen et al. 2018). For example, regional-scale range shifts driven by climate and species introductions could bring about community turnover in specific local ecosystems. In these communities, among-species synchrony in responses to temporal environmental variation could maintain temporal stability of aggregate ecosystem properties (e.g., total biomass and yield, the strength

of top-down control). If climate-driven range shifts result in the local colonization of novel species with different environmental responses to historically dominant species, and thus asynchronous population dynamics occur, this could also increase the temporal stability of emergent ecosystem properties. Conversely, colonization of new combinations of species (native and/or non-native invasives) with similar and synchronous population responses and dynamics, could dampen stability at the aggregate level. Compensatory effects can also scale up to aggregated effects across species guilds that are smaller overall than those on individual species (Olsen et al. 2018).

#### **WHAT TOOLS ARE ADVANCING THE UNDERSTANDING OF EMERGENT PROPERTIES OF AQUATIC SYSTEMS?**

Currently, modeling studies and sensitivity analyses of results represent the best available tools for understanding and anticipating potential changes in emergent properties. This is because, for most aquatic habitats, we lack data and holistic observational networks to sufficiently track complex responses at an ecosystem level. However, there are exceptions (Box 1) that can provide insights to direct future research priorities (Masi et al. 2017; Sturludottir et al. 2018; Hansen et al. 2019) and estimate the effects of measurement error (Masi et al. 2017). Furthermore, we must ask how diverse data sources representing component responses can combine effectively to generate new and holistic understanding of ecosystem function, and emergent behavior (Thackeray and Hampton 2020). For example, when ecological surveys and models are paired together, such efforts offer opportunities to simultaneously track and evaluate individual and multiple systems across landscapes or seascapes for novel conditions (Letcher et al. 2016; Read et al. 2016; Hansen et al. 2017). In this context, we must recognize that the full range of species and ecosystem state responses to climate change, including null (no-change) results obtained for a single species or species assemblage, will be equally informative for model parameterization, capturing population stability (e.g., adaptation in place), and the quantification and reduction of uncertainty in ecosystem characteristics and vital rates. Consequently, models and experimental and observational research can form an iterative process to fill areas of data scarcity and improve our understanding of abrupt ecosystem changes (Kirby and Beaugrand 2009; Beaugrand 2014; Lynam et al. 2017).

Novel system properties and configurations, with no historical analog, will be difficult to predict with confidence (Lynch et al. 2021). Abrupt changes in ecosystem structure and function have been observed around the globe (Möllmann et al. 2015) and attributed to complex, indirect, and (or) nonlinear relationships between climate processes, harvest, and trophic structure (Lynam et al. 2017; Olsen et al. 2018; Hansen et al. 2019). Improvements in the process–representation and bio-complexity of modeling platforms, and learning based upon regular model testing using current data are therefore key to testing novel hypotheses about system responses and thresholds at different scales under future scenarios of change.

To meet these needs, recent investigations have constructed ecosystem-level models for evaluating freshwater and marine communities around the globe (Nyamweya et al. 2017; Sturludottir et al. 2018; Fay et al. 2019). For example, food web models leveraging the results of observational or experimental studies have often been used to enhance understanding of the structure of an ecosystem and identify leading indicators or nodes most sensitive to perturbation spanning multiple levels

of biodiversity (e.g., genes, species, guild; Masi et al. 2017; Sturludottir et al. 2018; Fu et al. 2019; Hansen et al. 2019). As models continue to advance, they can be augmented to allow for more nuanced and complicated dynamics, like nonlinear and multispecies interactions (Chevalier et al. 2018), disease, or evolutionary processes. Efforts that synthesize data across ecosystems or areas with insufficient data (e.g., small lakes or ponds, deep ocean basins) to build broad scale predictive models are important exercises to evaluate where to focus new data collections or execute experiments to fill gaps in understanding.

There are not only ecological consequences to climate-induced changes in emergent properties, but also socioeconomic and cultural considerations for communities that rely upon these resources for their income, nutrition, cultural heritage, and wellbeing, including Indigenous peoples and local fishing communities with historical ties to resource availability (Daigle et al. 2019). End-to-end ecosystem modeling approaches, which seek to represent all components of socio-ecological systems, have enabled comparisons of system-level outcomes from different scenarios and cost–benefit analyses of management actions (Beaugrand 2014; Möllmann et al. 2015). Such models have served as tools to explore the socioeconomic implications of changing ecosystem structure (Fay et al. 2019), evaluate resource management strategies (Nyamweya et al. 2017), and project the impacts of future climatic and harvest scenarios (Olsen et al. 2018). For example, Fay et al. (2019) modeled the northeastern United States and found that changes in fishing effort led to strong responses, with clear tradeoffs among species and fishery sectors, but that regional market sales scaled nonlinearly with total landings, and regional income was relatively similar across scenarios. In addition, Olsen et al. (2018) found across many ecosystems that cumulative negative and positive impacts of ocean acidification and marine protected areas, respectively, were generally greater than effects from altering fishing mortality. Ultimately, the reshuffling of and novel combinations of commercially, recreationally, and subsistence species are expected to benefit some communities (e.g., as species shift north and become viable new fisheries), while others suffer due to decreased access and economic value, as well as loss of cultural identity and practices.

#### **WHAT POLICY AND MANAGEMENT ACTIONS SUPPORT EMERGENT PROPERTIES?**

Advancements in our understanding of climate-induced changes in emergent properties and related topics can be tracked over time by their explicit consideration in national and global assessments, such as the U.S. National Climate Assessment, the Intergovernmental Panel on Climate Change, the Intergovernmental Science–Policy Platform on Biodiversity and Ecosystem Services, and the Convention on Biological Diversity. These synthesis efforts are conducted over broad taxonomic, geographic, and temporal scales, and provide a barometer of the state of the science and the pace at which knowledge is advancing. Indeed, the treatment of emergent properties increased considerably between the third and fourth U.S. National Climate Assessments (Groffman et al. 2014; Lipton et al. 2018). Such a shift in focus provides an important indicator to guide policymakers on where to direct resources to reduce information gaps and risk to critical natural resources (MA 2005; Jones et al. 2015; Carter et al. 2019; Ruckelshaus et al. 2020). However, effective communication of complex results and high uncertainty to managers and policymakers

Box 1. Climate change and emergent properties for policymakers and managers.



**Climate change is altering emergent properties of aquatic ecosystems.**

Emergent properties make aquatic communities more than the sum of individual parts. Communities are networks of biological connections and interactions. If climate change disrupts one component (a species, a habitat, an interactive relationship) it can reshape the dynamics of the entire community.



**Ecosystems are reshuffling, restructuring, and rewiring due to climate change impacts.**

North American ecosystems are reorganizing in favor of warm-water species, smaller body sizes, and changes in foraging patterns. Novel species interactions and assemblages are forming due to species and population responses to climate change. Biodiversity loss and more generalist organisms (e.g., non-native invasives) are expected as a result.



**Confounding effects make links to climate difficult in some cases.**

Non-climate stressors also impact emergent properties. As climate change impacts continue to increase, they will intensify or exacerbate other stressors to disrupt ecological relationships, processes, and emergent properties.



**Scientific tools are improving our understanding of climate-induced changes in emergent properties.**

Scientific models and decision frameworks are improving our ability to anticipate novel ecosystem-level changes and evaluate trade-offs of different ecological outcomes and management actions. Data gaps remain that require additional monitoring and research to reduce uncertainty and avoid surprises.



**Emergent properties are important to acknowledge for climate policy and management.**

Explicit consideration of emergent properties in climate action recognizes the importance of aquatic community interactions and the importance of ecosystem-based management approaches. Such broader interpretations of stewardship will be essential for restoration, conservation, and sustainable management as novel communities are on the rise.

will continue to be challenging and require additional effort and engagement by researchers to ensure their findings are used appropriately.

At regional and local scales, more nuanced understanding of component and emergent responses of aquatic systems provide opportunities for fisheries and other natural resource managers to identify (e.g., through climate vulnerability and cumulative risk assessment frameworks) and prioritize species and ecological processes for targeted conservation actions (Colburn et al. 2016; Hare et al. 2016; Gaichas et al. 2018). In many cases, familiar conservation tools can be modified to meet the challenges of managing aquatic systems in a changing climate. However, managing for change and desired system properties is becoming increasingly necessary as historical restoration targets may no longer be attainable (Stein et al. 2013; Lynch et al. 2021; Thompson et al. 2021). Local depletion or species-level extinction is of utmost importance to natural resource managers with responsibilities for species of

conservation concern and for commercial harvest, due to the ecosystem services biodiversity provides to socio-ecological communities (Seddon et al. 2016). Maximizing biodiversity remains a fundamental conservation and management goal, as well as in an emergent properties context, as it supports trophic generalism and redundancy (Stein et al. 2013).

Reducing non-climate stressors can increase the resilience not just of individual species, but also entire ecosystems through improvements in fitness, survival, and the competitive abilities of sensitive species (Floury et al. 2013; Staudt et al. 2013; Lynch et al. 2016). Familiar actions such as increasing habitat connectivity enhance species (e.g., diadromous fishes) ability to recover from long-term depletion and expand ecological roles within food-webs and socio-economic systems (Dias et al. 2019). Increasing connectivity also allows species to adapt to climate impacts and colonize new areas by providing corridors to follow thermal optima (Krosby et al. 2010). In addition, identifying and protecting areas containing

climate refugia will facilitate such movements (Morelli et al. 2016), particularly in freshwater systems where distribution and colonization is more limited than in marine systems. All of these actions, however, are context dependent and should be assessed relative to local conditions and threats. For example, although increasing connectivity has clear benefits in (re)gaining access to critical habitat, such actions can also act to increase novel interactions and communities or the spread of disease and non-native invasive species (Havel et al. 2015; Lafferty 2017). Cost–benefit analyses can help weigh the consequences of different actions prior to their implementation and develop a monitoring plan with decision thresholds to prompt additional actions (e.g., to limit spread and establishment of non-native invasive) as needed post action.

Emergent properties of marine and freshwater systems are especially challenging to observe and track as well as the events that precede their manifestation due to the difficulties of making observations underwater and determining the appropriate scale to detect such changes. Therefore, maintaining, expanding, and coordinating monitoring networks across spatial and temporal scales, as well as at the multispecies and system levels is critical to understand the causes, frequency, and impacts of climate-induced changes in emergent properties and identify system tipping points (Möllmann et al. 2015; Powell et al. 2017; Proença et al. 2017; Langan et al. 2021). Tracking and characterizing how novel species occupy or create new or redundant ecological roles can inform actions with respect to maintaining desired key ecosystem processes and ecosystem services. Such information will be key to helping fishing communities identify and transition to new species, in some cases moving away from historically and culturally important stocks (Pershing et al. 2019).

A key step by the natural resource management community is to simultaneously monitor climate variables and multispecies trophic interactions. New technologies, such as satellite imagery of primary production over ecoregional scales to genomic tools, such as eDNA metabarcoding, can help track the reshuffling of species, especially changes in cryptic species and difficult-to-sample habitats (Ruppert et al. 2019). Coordinated monitoring across programs and networks of networks allows for improved assessment of change while making efficient use of scarce resources. The Great Lakes Fishery Commission Sea Lamprey *Petromyzon marinus* control program is an excellent example of such coordination—it is a partnership among multiple Tribal, state, provincial, and federal research and management programs, across the United States and Canada—to work together to address ecosystem-scale impacts of the invasive parasite (Siefkes et al. 2013). Such collaborations also create opportunities for researchers and managers to share information and increase the overall effectiveness of their combined programs (Staudinger et al. 2013; Ruckelshaus et al. 2020).

There are a variety of management approaches and tools that can be used in combination to evaluate competing strategies in the face of climate-driven changes in emergent properties in aquatic systems. Ecosystem-based management approaches are well suited to observing and responding to changes in emergent properties due to the holistic consideration of environmental changes, changes in species interactions across multiple trophic levels, and the direct and indirect effects of human activities (e.g., fisheries) on socio-ecological systems (Link 2010; Beard et al. 2011). Integrated ecosystem assessment is an analytical framework to implement

ecosystem-based management approaches (Levin et al. 2009, 2014), which employs scoping and objective setting, indicator analysis, risk assessment, and management strategy evaluation (Holland 2010).

Integrative ecosystem analyses and models have proven capable of supporting management decisions, in both research and applied management contexts (Townsend et al. 2019) by simulating alternative management strategies in complex systems and under high uncertainty (Punt and Donovan 2007; Punt et al. 2014; Dawson et al. 2016; Kaplan et al. 2020). For example, uncertainty in Atlantic Herring growth and productivity was addressed by implementing a range of models representing both historical and current states to ensure ecosystem and prey conditions were evaluated for impacts on predators as a new harvest control rule for Atlantic Herring was tested (Deroba et al. 2018).

Within such frameworks, multi-model inference approaches can address complex dynamics by combining results from climate-driven single species population models and multi-species models with or without climate drivers (Trifonova et al. 2015; Koenigstein et al. 2016). In addition, suites of models can also be used to inform adjustments of management reference points for climate and ecosystem interactions (Hare 2014; Holsman et al. 2016; Ianelli et al. 2016). Ecosystem-based approaches that include species interactions and cumulative system risk are already being implemented in the United States, making management systems more prepared to address climate-driven changes in emergent properties. For example, in August 2020, the Atlantic States Marine Fisheries Commission approved the use of Ecological Reference Points to manage Atlantic Menhaden, *Brevoortia tyrannus* (Available: <https://bit.ly/2OkKYIk>), a prey species subject to a high volume fishery. Under this system, maximum and target fishing rates for Atlantic Menhaden were established to sustain Striped Bass *Morone saxatilis*, a key predator and target of important recreational and commercial fisheries. The resulting linked management system can more readily adapt to climate-driven changes in predator–prey dynamics that arise in the future, whereas this was not possible previously when the two fisheries were managed separately. The Mid-Atlantic Fishery Management Council’s ecosystem risk assessment supports another operational ecosystem approach, where environmental, habitat, fishery, economic, and management indicators are evaluated annually (Gaichas et al. 2018). Changes in risk levels highlight areas where further integrative analysis is warranted (Gaichas et al. 2016), and scoping is proceeding for a management strategy evaluation that potentially links changing thermal habitat, distribution shifts, fishery shifts, and management measures (Muffley et al. 2021).

## CONCLUSIONS

Over the past decade, the field of emergent properties has made substantial progress to advance our understanding of how aquatic ecosystems are reshuffling, restructuring, and rewiring through observed and projected climate impacts. We found substantial evidence in support of predictions from previous assessments (Carter et al. 2019), however, the number of published examples varied by hypothesis and habitat type (i.e., freshwater vs. marine). We often found it difficult to align specific emergent responses with a single hypothesis, as outcomes of rearrangement and turnover (Hypothesis 1), novel assemblages (Hypothesis 2), declining biodiversity and the rise of generalists (Hypothesis 3) were either documented simultaneously or as a progression within and across studies under each

topic. In addition, we found that the range of results reported in the literature transcended our initial framework as the three hypotheses did not well capture interim responses and all potential outcomes exhibited by aquatic communities as they transition from historical to novel states of organization.

Our findings found strong support for species rearrangement and turnover to favor warm water species (Hypothesis 1), which are infiltrating new areas and seasonal periods in both marine and freshwater habitats. In addition, complex and sometimes counterintuitive changes in foraging patterns due to declining body size and faster bioenergetics lead to altered community structure. There was also considerable support for Hypothesis 2, with novel trophic interactions (e.g., intensification of competition, host–pathogen relationships) and species assemblages forming primarily as a result of shifts in range and phenology, but also through adaptive behavioral and metabolic responses that disrupted or shifted energy flows and resource use. Numerous examples from multiple systems show component responses are scaling up to affect ecological networks through both top-down (changes in biological control) and bottom-up (changes in productivity and prey quality) mechanisms. There was mixed evidence for declines in species diversity and proliferation of generalists in North American aquatic systems (Hypothesis 3). In transitional habitats, places where warm water species were moving in from lower latitudes and cold water species are still persistent, biodiversity was found to increase; exceptions were found at the interface of range edge boundaries and some freshwater systems. These are likely interim ecosystem states, and as warming continues, losses of cold water species are expected (Jackson and Mandrak 2002; Xenopoulos et al. 2005; Markovic et al. 2014).

Although we found a range of studies (e.g., multispecies and meta-analyses) demonstrating changes in biodiversity of aquatic systems, a rigorous trait-based analysis that goes beyond the scope of this study is needed to determine if the newly prevalent species represent more generalist lifestyles. One ecosystem response that we had anticipated examples of in the literature that did not manifest was direct evidence for trophic cascades. Although there are mounting case studies documenting changes in species relationships, most involve pairs of species or linkages between one or two trophic levels. Trophic cascades involving multiple trophic levels (>2) are notoriously difficult to document (Pershing et al. 2015), and it seems this phenomena has yet to be fully realized in North American aquatic systems and remains a predicted consequence of climate impacts.

Overall, emergent responses were complex and high uncertainty remains for how many systems will reorganize and function over the coming decades. Because the field is quite nuanced and studies are not necessarily categorized as “emergent,” our search criteria undoubtedly missed relevant studies that would provide additional examples and evidence in support and in contrast to prior predictions and hypotheses as well as more explicit and holistic examples of compensatory or spiraling system responses to climate. Analytical tools that track and evaluate changes in emergent properties of aquatic systems are becoming more sophisticated (e.g., multispecies models and multi-model techniques), but are often limited, or even biased by data availability, gaps in information on species-specific traits, and the scale at which studies are conducted (Kirby and Beaugrand 2009; Beaugrand 2014; Schindler et al. 2015). Basic

research and expanded monitoring can improve understanding of evolutionary, behavioral, and ecological responses, and is still needed in many systems to quantify the occurrence and strength of trophic interactions and underlying mechanisms that regulate complex community responses. Finally, holistic management and conservation strategies (e.g., ecosystem-based management, integrative ecosystem analyses, adaptive management) that are robust to uncertainty and can be implemented, given a range of potential outcomes are crucial to tracking and evaluating emergent properties in a warming world.

#### CASE STUDY 1

##### When the Heat Came Down: Long-Term Lake Observations from a Warming Lake Windermere, UK

Although most evidence presented in this review is from North America, long-term ecological changes have occurred globally. The freshwater ecosystem of Windermere, the largest natural lake in England (Figure A), provides an example of a sentinel large temperate lake that has undergone considerable changes in emergent properties over recent decades; this includes changing phenologies, resulting mismatches, altered trophic interactions, and community turnover. Long-term lake observations at Windermere spans over 75 years of continuous study, ranging from physics to fish (Maberly and Elliott 2012). Detailed records have documented a long history of cultural eutrophication and recent warming, involving a step-change in lake water temperatures at the end of the 1980s. These changes have contrasting implications for the aquatic biota of the lake, including its diverse native and introduced cold water (e.g., Arctic Char *Salvelinus alpinus*), cool water (e.g., Eurasian Perch *Perca fluviatilis*), and warm water (e.g., Roach *Rutilus rutilus*) fish populations.

The biological manifestations of such long-term environmental changes start at the base of the lake’s food web, in the plankton. The seasonality of the lake ecosystem changed (Hypothesis 1), with spring blooms of the dominant diatom *Asterionella formosa* shifting earlier at a rate of approximately 4 days per decade (Thackeray et al. 2008) and similar phenological advance in the lake’s zooplankton, specifically *Daphnia* spp. (Thackeray et al. 2012). Peak spawning in Eurasian Perch, the lake’s most abundant fish species, also advanced to align with rising temperatures to represent a regime shift in the late-1980s (Winfield et al. 2004). Differential phenological shifts within the fish community at Windermere led to climate-induced predator–prey asynchrony in the form of Eurasian Perch–*Daphnia* sp. mismatches, which can increase variability in predator abundance (Thackeray et al. 2013; Ohlberger et al. 2014). Marked changes in trophic interactions and food web structure have also been observed at higher levels in the food web of Windermere (Hypothesis 1). The lake’s top predator, Northern Pike *Esox lucius*, and its diet composition, has been studied continuously with a standardized methodology since 1976 (Winfield et al. 2012). Over the 34-year period, the dietary importance of the native cold water salmonids, Arctic Char and Brown Trout *Salmo trutta*, decreased while the introduced warm water cyprinid Roach increased. Over approximately the same period, the individual condition of Northern Pike decreased (Winfield et al. 2008b), likely due to a marked population decline in Arctic Char (Winfield et al. 2008a, 2019). Local decline of this high-profile salmonid is also related to

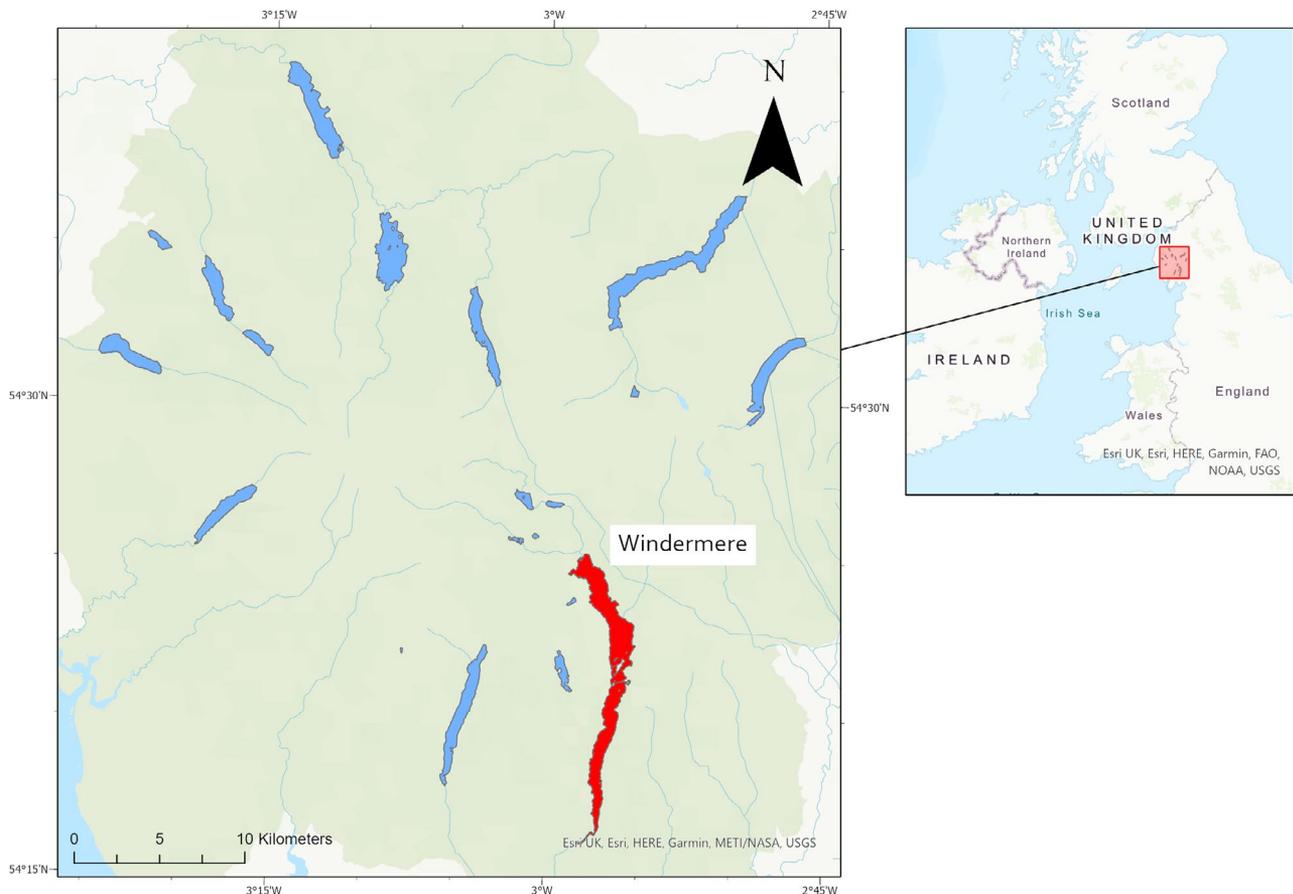


Figure A. a map of Windermere (red) in the context of the major water bodies (blue) of the English Lake District (left), within the United Kingdom (right).

reduced oxygen availability at greater depths (Jones et al. 2008) and increased sedimentation on its spawning grounds (Winfield et al. 2015), both of which are driven in large part by eutrophication and climate change. These contrasting population dynamics are just two components of the changing nature of the Windermere fish community (Figure B), but also includes a dramatic increase in the warm water and non-native cyprinids Roach and Common Bream *Abramis brama* (Winfield and Thackeray, unpublished data; Hypothesis 2). The abilities



Figure B. Arctic Char anglers on Windermere. Photo credit Ian J. Winfield.

of these two non-native cyprinids to alter zooplankton communities and nutrient dynamics are well known from other European locations (e.g., Volta et al. 2013); consequently, there is a significant risk that increases of these non-native species in Windermere will result in further changes to the lake's emergent properties in the future (Figure C).

## CASE STUDY 2

### As Temperatures Rise: Long-Term Changes in the Freshwater Fish Communities in the Kawartha Lakes (Ontario, Canada) and the Upper Mississippi River (USA)

Changes in temperature can influence the relative abundance of fishes because effects on year-class strength, recruitment, growth, and survival depends on individual species thermal requirements (Shuter and Post 1990; Tonn 1990; Casselman 2002). Determining the effects of climate change on fish communities is often complicated by other environmental (e.g., pollution) and/or ecological changes (e.g., fish community homogenization; Cazelles et al. 2019) that are either associated with warming, or which have occurred concurrently at local or regional scales. Elevated temperatures often result in increased primary production, leading to bottom-up trophic-cascades (Carpenter et al. 1985) that would ultimately affect resource availability to fishes at higher trophic levels. Greater primary production may also increase turbidity (Oviatt et al. 2017), which confers a feeding advantage to some fishes but not others (Lester et al. 2004; Huenemann et al. 2012). However, in some

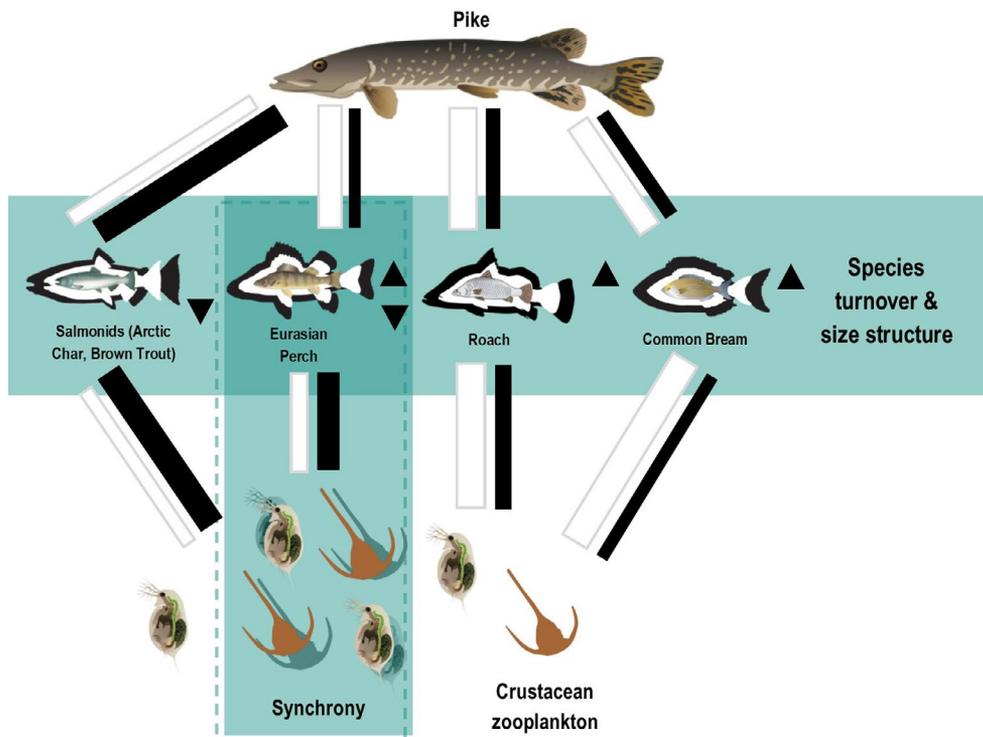


Figure C. Conceptual model showing climate change complexity and emergent effects through the Windermere food web. Since the mid-1940s, along with warming of the lake, there has been turnover in the prey community available to Northern Pike *Esox lucius*. Arctic Char *Salvelinus alpinus* have become less abundant (downward arrow), while the reverse is true of Roach *Rutilus rutilus* and Common Bream *Abramis brama* (upward arrow). Eurasian Perch *Perca fluviatilis* populations have fluctuated among years (double-headed arrow). At the same time, salmonids have become less prevalent in Pike diets than Roach, Perch, and Bream (changes in linkage width between recent decades and previous decades [white and black bars, respectively] indicate qualitative change in interaction strength). Size structure (shown for prey fish), may also decline due to warming, parasitism, trophic interactions, and fishing pressure. Seasonal events have shifted earlier; perch spawning has shifted more slowly than seasonal peaks in zooplankton abundance (especially *Daphnia* spp. in spring). How will community composition, size structure, and seasonality continue to change in the future to alter emergent properties of this system?

systems, such as the Great Lakes catchment, turbidity has shown historical declines in the face of rising temperatures as a result of phosphorus removal from detergents (Robillard and Fox 2006).

In two freshwater fish communities of the Midwestern United States and Ontario, Canada, changes in the piscivore community due to warming and other non-climate factors were evaluated over multi-decadal periods. In the Kawartha Lakes region, Ontario, Canada (Figure D), observations were made across a 26–35 year period in four lakes (Robillard and Fox 2006), and updated to cover an additional 5–10 years. In the upper Mississippi River, patterns in the fish community were evaluated over a 25-year period and across several navigational pools (Figure E). Both systems have been the subject of repeated fish community surveys using standardized sampling at various intervals, and both systems have experienced increased air or water temperatures by at least 0.5°C per decade.

Walleye, Largemouth Bass, and Smallmouth Bass, are important piscivores in the Kawartha Lakes and the Upper Mississippi River. Changes in the abundance of these three species were consistent across the two study areas and match expectations of species turnover due to climate change (Hypothesis 1). Walleye, a cool water species, decreased in abundance while one or both warm water Bass species increased over time (Figure F). In the upper Mississippi River,

the warm water Largemouth Bass displayed larger body sizes as they became more abundant, in concert with rising water temperatures (Figure G). This was a counter-intuitive result, as it is in contrast to expected trends in body size predicted on a global scale due to warming (Daufresne et al. 2009; Sheridan and Bickford 2011). In the Kawartha Lakes, the proportion of Walleye to total piscivores as well as their relative abundance in catches declined over the study period in all four lakes, and was negatively related to mean air temperature. Concurrently, Largemouth Bass and Smallmouth Bass increased over time (Figure F), mirroring trends in the upper Mississippi River.

Similar trends across regions that vary in other environmental factors, and across lentic and lotic systems, suggest warming temperatures affect the piscivore guild at the regional level by favoring warm water species over cool water species. However, the effects may also be exacerbated by declines in turbidity precipitated by decreases in primary production. There are cases, however, where turbidity can decline even as temperature increases as a result of human activities, such as the removal of phosphorus from detergents as was true in the Great Lakes region (Robillard and Fox 2006). Increased water clarity and increased turbidity benefit Bass over Walleye due to differences in their ability to feed in turbid waters (Lester et al. 2004; Huenemann et al. 2012; Oviatt et al. 2017). Therefore,

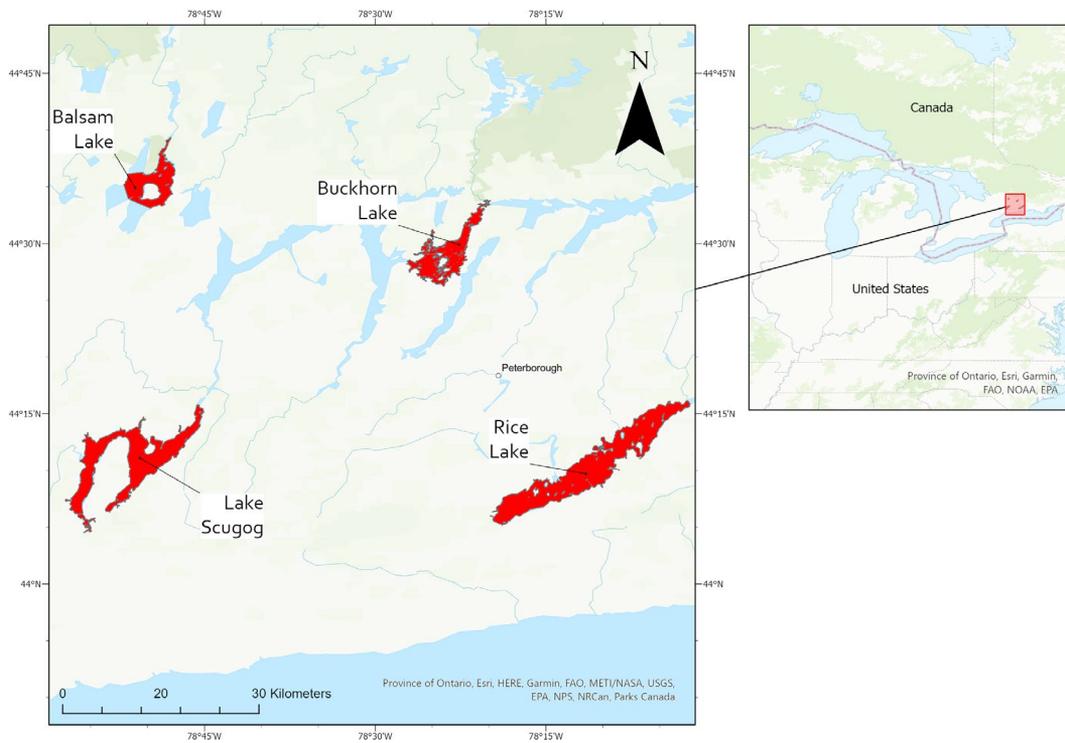


Figure D. Location of the four Kawartha lakes: Balsam, Buckhorn, Rice, and Scugog (red) in Ontario, Canada, used in a long-term study of changes in the piscivore community.

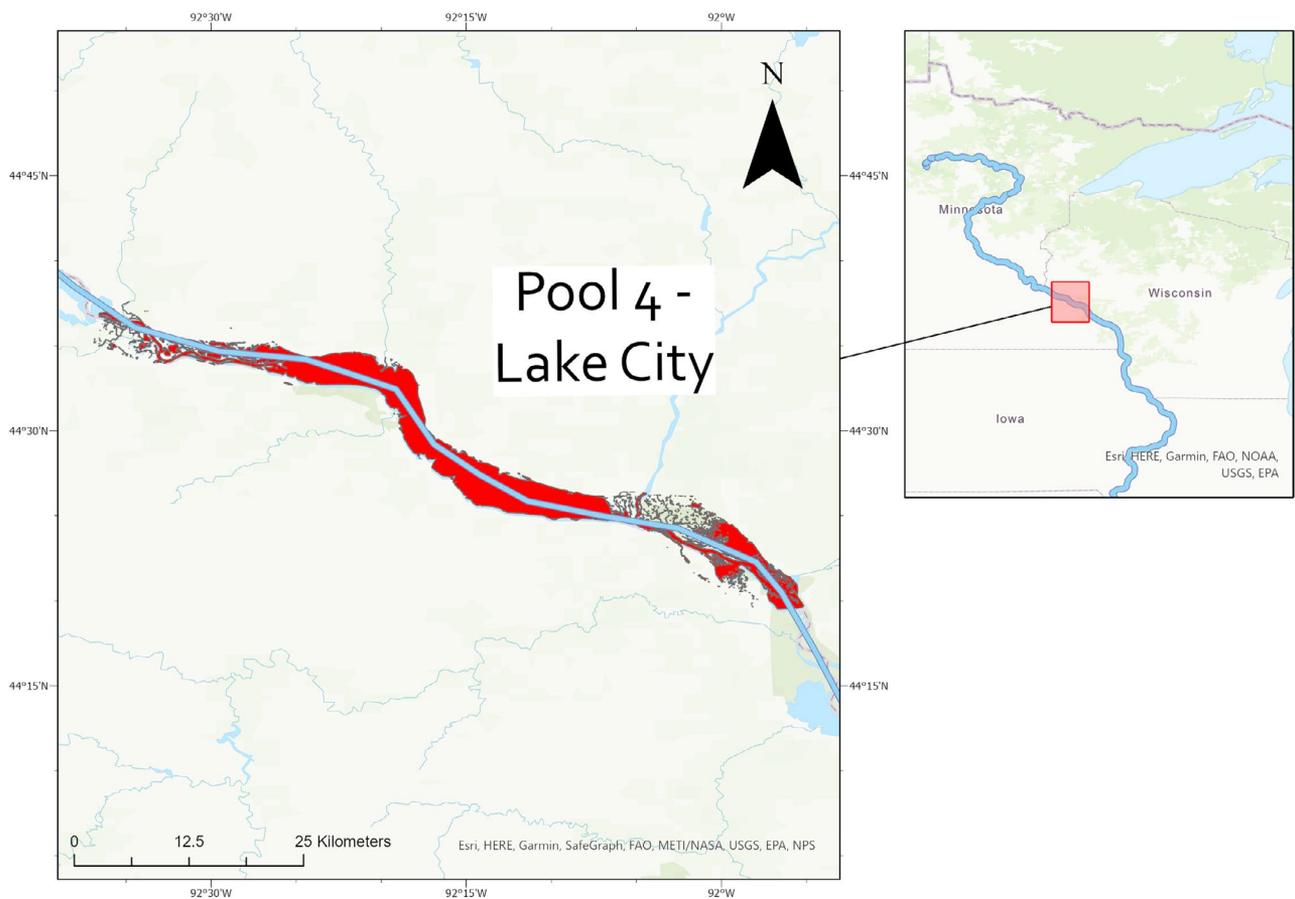


Figure E. Map of the upper Mississippi River and locations of Pool 4, Lake City (red) where long-term monitoring was conducted.

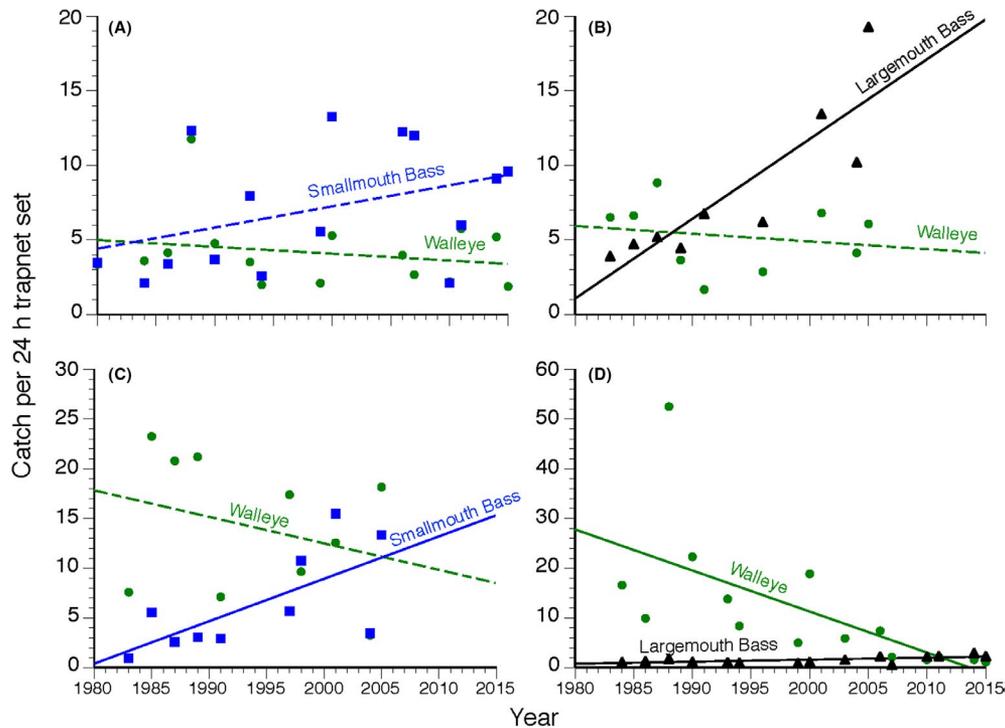


Figure F. Historical trends in Largemouth Bass *Micropterus salmoides* (black triangles) and Smallmouth Bass *M. dolomieu* (blue squares) and Walleye *Sander vitreus* (green circles) abundance in four Kawartha lakes (A) Balsam Lake, (B) Buckhorn Lake, (C) Rice Lake, and (D) Scugog Lake in central Ontario, Canada, based on standardized trap netting. Lines are best-fit regressions; solid lines are statistically significant ( $p < 0.05$ ). Data courtesy of Michael Fox.

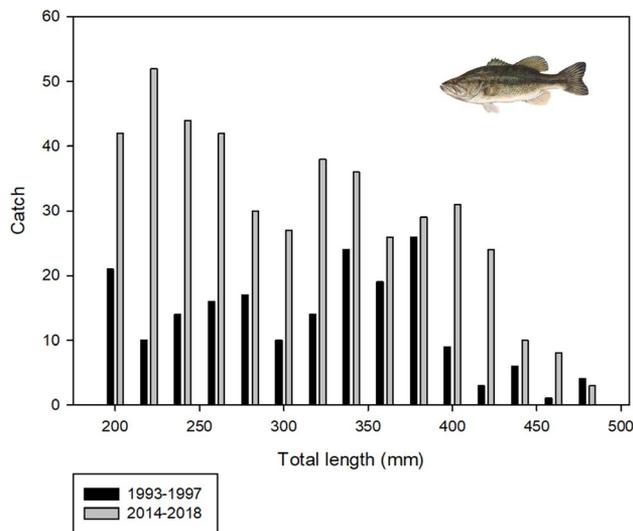


Figure G. Length-frequency histogram comparing the size distribution of stock-size Largemouth Bass *Micropterus salmoides* in Pool 4 of the Mississippi River from 1993–1997 (black bars) and 2014–2018 (grey bars) captured with daytime electrofishing. A two-tailed Kolmogorov-Smirnov test found significant differences ( $p = 0.002$ ) between size frequencies captured in the two time periods with higher abundance and larger-sized individuals. Sampling effort is standardized but differed slightly between the two time periods with 80.6 samples/year (403 samples total) in 1993–1997 and 81.8 samples/year (409 samples total) in 2014–2018 from electrofishing. Data are from the long-term resources monitoring element of the U.S. Army Corps of Engineers Upper Mississippi River Restoration Program (available: <https://bit.ly/2PFf89P>). Data courtesy of Daniel Gibson-Reinemer.

the reduction of non-climate stressors can have important consequences on the fitness, survival, and competitive interactions of sensitive species influenced by the separate or interactive effects of water quality (or other stressors) and climate change (Floury et al. 2013).

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#### ORCID

Michelle D. Staudinger <https://orcid.org/0000-0002-4535-2005>

Abigail J. Lynch <https://orcid.org/0000-0001-8449-8392>

Sarah K. Gaichas <https://orcid.org/0000-0002-5788-3073>

Michael G. Fox <https://orcid.org/0000-0001-9941-9677>

Daniel Gibson-Reinemer  <https://orcid.org/0000-0002-8992-014X>

Joseph A. Langan  <https://orcid.org/0000-0002-6438-6390>

Amy K. Teffer  <https://orcid.org/0000-0001-5322-2617>

Stephen J. Thackeray  <https://orcid.org/0000-0003-3274-2706>

Ian J. Winfield  <https://orcid.org/0000-0001-9296-5114>

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