Climate Change Effects on North American Inland Fish Populations and Assemblages


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Climate Change Effects on North American Inland Fish Populations and Assemblages

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Climate is a critical driver of many fish populations, assemblages, and aquatic communities. However, direct observational studies of climate change impacts on North American inland fishes are rare. In this synthesis, we (1) summarize climate trends that may influence North American inland fish populations and assemblages, (2) compile 31 peer-reviewed studies of documented climate change effects on North American inland fish populations and assemblages, and (3) highlight four case studies representing a variety of observed responses ranging from warmwater systems in the southwestern and southeastern United States to coldwater systems along the Pacific Coast and Canadian Shield. We conclude by identifying key data gaps and research needs to inform adaptive, ecosystem-based approaches to managing North American inland fishes and fisheries in a changing climate.

**INTRODUCTION**

North American inland fishes, defined herein as fishes that reside in freshwaters above mean tide level and inclusive of diadromous fishes in their freshwater resident stages, include more than 1,200 freshwater and diadromous species (Burkhead 2012) that are ecologically, culturally, and economically important. These fishes contribute to biodiversity, ecosystem productivity, human well-being, livelihoods, and prosperity. As one example, inland recreational fisheries generate more than US$31 billion annually in Canada and the United States (DFO 2010; USFWS and USCB 2011).

Because inland fishes are so culturally and economically important, understanding how climate change will impact them is vital. Temperature and precipitation have direct effects on most of the physiological and biochemical processes that regulate fish performance and survival (see Whitney et al., this issue). Fishes are also uniquely vulnerable to climate-mediated changes in temperature and precipitation because they are confined to aquatic habitats, and movement to alternative habitats is often more restricted than in terrestrial systems (e.g., fragmented stream networks).

We conducted a literature review of the empirically documented effects of climate change on North American inland fish populations (e.g., changes to distribution, phenology, abundance, growth, recruitment, genetics) and assemblages structure (i.e., species richness, evenness, and composition). We limited our geographic scope to North America to provide a continental-scale synthesis on climate change impacts to inland
Fishes. We included only peer-reviewed studies conducted in North America and published between 1985 and 2015 (Bassar et al. 2016). We limited our search to studies of directional changes in climate (i.e., not climate variability) but did not require these studies to demonstrate a clear impact on the focal fish population or assemblage (i.e., negative results are as important as positive results). Through author expert knowledge, an online literature search (Google Scholar and Web of Science), and subsequent snowball sampling (i.e., using the references cited within confirmed studies of climate effects on inland fishes, as well as subsequent references to those studies; Goodman 1961), we identified 31 publications that directly characterized climate change effects on North American inland fishes.

The objectives of this synthesis are to (1) summarize climate trends that may influence inland fish populations and assemblages in North America, (2) compile and synthesize peer-reviewed studies of empirically documented (versus projected) climate change impacts on inland fishes within the region (i.e., distribution and phenology, demographic processes, evolutionary processes, and changes to assemblage structure), and (3) highlight case studies demonstrating the range of effects that climate change has had so far on North American inland fishes. Our synthesis was built upon a conceptual model that treated climate change effects and other anthropogenic stressors as principal interacting influences on fish populations and assemblages (Figure 1). By examining observed impacts of climate change on inland fishes, we sought to distinguish current knowledge from key data gaps that must be addressed. Our synthesis of North American fishes is constrained to Canada and the United States, due to the absence of peer-reviewed literature on climate change effects on inland fishes of Mexico (a clear data gap to be filled).

**RECENT CLIMATE TRENDS FOR NORTH AMERICAN INLAND WATERS**

Earth’s climate system is changing with widespread impacts on inland aquatic systems. Climate change effects with the greatest significance for North American aquatic ecosystems include warming of the atmosphere and oceans, reduced snow and ice, and rising sea levels (IPCC 2014). Dramatic changes in precipitation patterns have already been observed, with wet regions becoming wetter and dry and arid regions becoming drier (Chou et al. 2013). For example, Arctic regions have experienced increased precipitation, whereas southern Canada has seen a significant decrease in spring snow extent (Dore 2005). Winter precipitation is predicted to increase at higher latitudes, and summer precipitation is expected to decrease in the southeastern United States (Dore 2005), with variability in precipitation increasing throughout the continent. Continental temperatures have progressively warmed, particularly at higher latitudes (IPCC 2014; Walsh et al. 2014). This warming has driven significant changes in spring snow accumulation and runoff timing in the western United States, causing significant hydrologic changes and, in the most extreme cases, hydrologic regime shifts (e.g., snowmelt driven to transient rain-on-snow; Mote et al. 2005; Stewart et al. 2005). Observed trends in snowmelt hydrology in the western United States are expected to continue into the future, particularly near the margins of heavy snowfall areas (Adam et al. 2009). Moreover, the frequency of extreme climatic events (e.g., <10th or >90th percentile daily means in temperature or precipitation within a season) is predicted to increase across North America (Saha et al. 2006).

Lentic habitats are directly impacted by climate-driven changes in precipitation and surface temperature. Consequently, lakes can serve as sentinels for climate change monitoring, providing early indications of effects on ecosystem structure, function, and services (Adrian et al. 2009; Williamson et al.
Over the last 30 years, many analyses of fish population demographics address the consequences of climate change, although response will also vary with local conditions (O’Reilly et al. 2015). On average, freeze and breakup dates of lake ice in the Northern Hemisphere have become later and earlier, respectively, and interannual variability in ice dynamics has increased over the past 150 years (Magnuson et al. 2000). Broadscale warming trends in lake epiplimnetic temperatures and water-level fluctuations have also been linked to climate variability (Coats et al. 2006; Williamson et al. 2009). In the future, changes in lake thermal structure (e.g., stratification) are expected to result in mixing regime shifts (e.g., polymictic to dimictic; Boehler and Schultze 2008) with concomitant impacts on lake ecosystem structure and function.

Lotic habitats are also responding to climate change. Alterations in the magnitude and timing of seasonal flow patterns have been observed in the western United States and are predicted to continue into the future (Mantua et al. 2010). Extreme flow events (i.e., flooding and drought) have also become more frequent in the past century, and this trend is projected to continue (Nijssen et al. 2001; Milly et al. 2002). Thermal regimes in rivers and streams are changing, with long-term increases in annual mean temperatures, particularly near urban areas (Kausahl et al. 2010; Rice and Jastram 2015). Though altered thermal regimes in lotic systems have been observed (Isaak et al. 2012), considerable variability is evident and observed patterns have been confounded by other anthropogenic factors, such as dams, diversions, and land use changes (Arismendi et al. 2012).

Wetland habitats are particularly sensitive to climate-induced hydrologic changes. They are directly impacted by reduced water levels in inland systems or inundation in coastal areas. In locations where a wetter, warmer climate and rising sea levels are predicted (Ingram et al. 2013), significant changes are expected for coastal wetlands that exist at the transition between aquatic and terrestrial systems (Burkett and Kusler 2000).

**CLIMATE IMPACTS ON NORTH AMERICAN INLAND FISHES**

Our literature review produced 31 studies documenting fish responses to climate change in Canada and the United States, published between 1985 and 2015 (Bassar et al. 2016). These responses were dominated by changes in demographic processes (e.g., abundance, growth, recruitment), distribution, and phenology (e.g., migration timing). The spatial distribution of the studies ranged primarily from 40°N to 50°N latitude and was somewhat concentrated along the east and west coasts and the Laurentian Great Lakes of Canada and the United States (Table 1, Figure 2). Within this latitudinal range, responses of salmonids to climate change were the most frequently documented, followed by percids, centrarchids, and other fish taxa (Table 1). Given the limited literature on climate-induced changes in species interactions and evolutionary shifts, we cannot report general trends for these phenomena. Below, we identify and discuss several key themes that emerged from our literature review. We also identify major knowledge gaps to be addressed in future research.

**Population Structure**
**Distribution and Phenology**

Some of the most dramatic fish population responses documented with climate change are shifts in species’ spatial distributions and the timing of key behaviors (e.g., migrations, spawning). Over the last 30 years, many analyses have projected fish distributional shifts in response to climate change, but comparatively few studies have documented observed changes (reviewed in Heino et al. 2009; Comte et al. 2013). Most reports of observed distributional changes come from Europe (Comte and Grenouillet 2013; Pletterbauer et al. 2014), and we are aware of only four studies from North America (Table 1). At mid-latitudes (40°N to 50°N), warm- and coolwater species have exhibited increased presence, abundance, and distribution (Johnson and Evans 1990; Allof et al. 2014), and a coldwater species (Bull Trout Salvelinus confluentus) has experienced range contraction (Eby et al. 2014). At higher latitudes (>50°N), Sockeye Salmon Oncorhynchus nerka and Pink Salmon O. gorbuscha have expanded northward in the Northwest Territories, Canada (Babaluk et al. 2000).

Phenological shifts in the timing of seasonal migrations or spawning are better documented than distributional shifts (Parmesan and Yohe 2003; Crozier and Hutchings 2014); our literature review produced 15 examples from North America (Table 1). In general, milder winters, earlier spring warming, and warmer summers have led to earlier spring phenological events (e.g., migration, spawning), although responses have been mixed. At lower latitudes, for example, Striped Bass Morone saxatilis exhibited earlier spawning migrations with earlier spring warming (Peer and Miller 2014). At mid-latitudes, Alewife Alosa pseudoharengus (Ellis and Vokoun 2009), Atlantic Salmon Salmo salar (Juanes et al. 2004; Russell et al. 2012; Otero et al. 2014), American Shad A. sapidissima (Quinn and Adams 1996), and Sockeye Salmon (Quinn and Adams 1996; Cooke et al. 2004; Crozier et al. 2011) have begun spring migration events earlier in response to accelerated warming in the spring and to overall warmer spring and summer temperatures. In Lake Erie, Yellow Perch Perca flavescens did not spawn earlier in the spring following shorter, warmer winters (Farmer et al. 2015), but in Lake Michigan, Yellow Perch did (Lyons et al. 2015), as did Walleye Sander vitreus in some Minnesota lakes (Schneider et al. 2010). At higher latitudes, several juvenile Pacific salmon Oncorhynchus spp. populations have been observed migrating to the ocean earlier, in concert with warmer winter temperatures (Taylor 2008; Kovach et al. 2013). However, many fall-spawning Pacific salmon populations in southeast Alaska are also beginning their freshwater migrations earlier than in the past (Kovach et al. 2015). This consistent trend across species and populations strongly suggests that a shared environmental driver (i.e., climate change) is responsible (see Pacific salmon case study). Unfortunately, these altered behaviors can be maladaptive (e.g., Cooke et al. 2004); therefore, we suggest that additional research is needed to better understand the mechanisms and consequences of these changes.

**Demographic Processes**

Climate change is altering North American fish population dynamics through changes to abundance, growth, and recruitment. Fish population demographics describe the dynamics of population structure with respect to multiple life history forms and vital rates (i.e., survival, growth, and recruitment). Populations are balanced by recruitment, mortality, and migration; climate factors can influence these dynamics additively or interactively (Walther et al. 2002; Letcher et al. 2015). Though numerous examples of correlations between climatic variation and fish population dynamics exist, relatively few studies have directly identified climate change as the proximate driver (i.e., a directional climate shift has influenced population demography over time).
<table>
<thead>
<tr>
<th>Map Data Point</th>
<th>Response</th>
<th>Driver (climate/habitat)</th>
<th>Geographic area and habitat</th>
<th>Response (species or biological variable)</th>
<th>Response (type, direction)</th>
<th>Response level</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Assemblage composition change</td>
<td>Warmer temperatures</td>
<td>Ontario watersheds (n = 137)</td>
<td>Species richness</td>
<td>Increase in species richness</td>
<td>Assemblage level</td>
<td>Minns and Moore (1995)</td>
</tr>
<tr>
<td>2</td>
<td>Demographic change (growth/biomass)</td>
<td>Warmer water temperatures</td>
<td>Auke Lake, Alaska</td>
<td>Sockeye Salmon, Coho Salmon</td>
<td>Greater size and biomass of Sockeye Salmon smolts</td>
<td>Species level</td>
<td>Kovach et al. (2014)</td>
</tr>
<tr>
<td>3</td>
<td>Demographic change (recruitment)</td>
<td>Greater flow variability</td>
<td>Washington rivers (n = 21)</td>
<td>Chinook Salmon</td>
<td>Declines in recruitment</td>
<td>Species level</td>
<td>Ward et al. (2015)</td>
</tr>
<tr>
<td>4</td>
<td>Demographic change (abundance)</td>
<td>Warmer air temperatures</td>
<td>Kwasartha Lake, Ontario</td>
<td>Walleye, black basses</td>
<td>Walleye abundance declined, black basses increased</td>
<td>Species level</td>
<td>Robillard and Fox (2006)</td>
</tr>
<tr>
<td>5</td>
<td>Demographic change (abundance)</td>
<td>Warmer summers, longer growing season</td>
<td>Minnesota lakes (n = 634)</td>
<td>Cisco</td>
<td>Declines in abundance</td>
<td>Species level</td>
<td>Jacobson et al. (2012)</td>
</tr>
<tr>
<td>6</td>
<td>Demographic change (growth)</td>
<td>Warmer water temperatures, earlier spring</td>
<td>Wood River, Alaska</td>
<td>Sockeye Salmon</td>
<td>Increased zooplankton densities, increased growth of juveniles</td>
<td>Species level</td>
<td>Schindler et al. (2005)</td>
</tr>
<tr>
<td>7</td>
<td>Demographic change (growth)</td>
<td>Warmer summer temperatures</td>
<td>Nephijee River, Lake Gatun, Matias, and Lake Tasiapik, Québec</td>
<td>Arctic Charr</td>
<td>Growth decreased in one lake</td>
<td>Species level</td>
<td>Murdock and Power (2013)</td>
</tr>
<tr>
<td>8</td>
<td>Demographic change (population size/survival)</td>
<td>Warmer stream temperatures, lower flows</td>
<td>Massachusetts streams (n = 4)</td>
<td>Brook Trout</td>
<td>Reduced recruitment and population sizes</td>
<td>Species level</td>
<td>Bassar et al. (2016)</td>
</tr>
<tr>
<td>9</td>
<td>Distributional shift</td>
<td>Warmer air temperatures, less ice cover</td>
<td>Ontario lakes (n = 1,527)</td>
<td>13 game and non-game species</td>
<td>6 gamefishes expanded their range northward, 5 of 7 non-gamefishes had range contractions</td>
<td>Assemblage level</td>
<td>Alofs et al. (2014)</td>
</tr>
<tr>
<td>10</td>
<td>Distributional shift</td>
<td>Warmer ocean and river conditions in summer</td>
<td>Northwest Territories</td>
<td>Sockeye Salmon, Pink Salmon, Coho Salmon, Chum Salmon</td>
<td>Range expanded northward</td>
<td>Species level</td>
<td>Babaluk et al. (2000)</td>
</tr>
<tr>
<td>11</td>
<td>Distributional shift</td>
<td>Warmer air and water temperatures</td>
<td>Great Lakes</td>
<td>White Perch</td>
<td>Range expanded in Great Lakes</td>
<td>Species level</td>
<td>Johnson and Evans (1990)</td>
</tr>
<tr>
<td>12</td>
<td>Distributional shift</td>
<td>Warmer water temperatures</td>
<td>East Fork Bitterroot River, Montana</td>
<td>Bull Trout</td>
<td>Greater site abandonment and shifts in local distributions</td>
<td>Species level</td>
<td>Eby et al. (2014)</td>
</tr>
<tr>
<td>13</td>
<td>Evolutionary changes (migration timing)</td>
<td>Earlier/warmer spring/summer</td>
<td>Auke Creek, Alaska</td>
<td>Pink Salmon</td>
<td>Natural selection for earlier adult migration</td>
<td>Species level</td>
<td>Kovach et al. (2012)</td>
</tr>
<tr>
<td>14</td>
<td>Evolutionary changes (migration timing)</td>
<td>Earlier/warmer spring/summer</td>
<td>Columbia River and Snake River, Washington/Oregon</td>
<td>Sockeye Salmon</td>
<td>Natural selection for earlier adult migration</td>
<td>Species level</td>
<td>Crozier et al. (2011)</td>
</tr>
<tr>
<td>15</td>
<td>Hybridization and Distributional shift</td>
<td>Warmer spring/summer temperatures</td>
<td>Flathead River drainage, Montana</td>
<td>Rainbow Trout, Westslope Cutthroat Trout</td>
<td>Rainbow Trout expanded upstream; greater hybridization</td>
<td>Species level</td>
<td>Muhfeld et al. (2014)</td>
</tr>
<tr>
<td>17</td>
<td>Phenological shift</td>
<td>Earlier/warmer spring/summer</td>
<td>Southeastern Alaska streams (n = 21)</td>
<td>Pacific salmon</td>
<td>Sockeye Salmon generally migrated later, Coho, Pink, and Chum salmon migrated earlier</td>
<td>Species level</td>
<td>Kovach et al. (2015)</td>
</tr>
<tr>
<td>18</td>
<td>Phenological shift</td>
<td>Earlier/warmer spring/summer</td>
<td>Auke Creek, Alaska</td>
<td>Salmonoid species; 14 life histories</td>
<td>Generally earlier fry/ juvenile and adult migrations</td>
<td>Species level</td>
<td>Kovach et al. (2013)</td>
</tr>
<tr>
<td>19</td>
<td>Phenological mismatch</td>
<td>Earlier spring, less snow, lower summer flows</td>
<td>Rio Grande River; New Mexico</td>
<td>8 cyprinid, catosomid, and poeciliid species</td>
<td>Earlier spawning and egg hatching; lentic species increased</td>
<td>Assemblage level</td>
<td>Krabbenhoft et al. (2014)</td>
</tr>
<tr>
<td>20</td>
<td>Phenological shift</td>
<td>Earlier/warmer spring/summer</td>
<td>Southern New England streams (n = 6)</td>
<td>Alewife</td>
<td>Earlier spawning migrations</td>
<td>Species level</td>
<td>Ellis and Vokoun (2009)</td>
</tr>
<tr>
<td>21</td>
<td>Phenological shift</td>
<td>Earlier/warmer spring/summer</td>
<td>Columbia River, Washington/Oregon</td>
<td>American Shad</td>
<td>Earlier spawning migrations</td>
<td>Species level</td>
<td>Quinn and Adams (1996)</td>
</tr>
</tbody>
</table>
### Table 1. (Continued) Documented climate change effects on North American inland fish populations and assemblages.

<table>
<thead>
<tr>
<th>Map Data Point</th>
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<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>22</td>
<td>Phenological shift</td>
<td>Earlier/warmer spring/summer</td>
<td>Connecticut, Maine, New Brunswick, Newfoundland rivers (n = 4)</td>
<td>Atlantic Salmon</td>
<td>Earlier spawning migrations</td>
<td>Species</td>
<td>Juanes et al. (2004)</td>
</tr>
<tr>
<td>23</td>
<td>Phenological shift</td>
<td>Earlier/warmer spring/summer</td>
<td>European and North American rivers (n = 67 and 16, respectively)</td>
<td>Atlantic Salmon</td>
<td>Earlier smolt outmigration</td>
<td>Species</td>
<td>Otero et al. (2014)</td>
</tr>
<tr>
<td>24</td>
<td>Phenological shift</td>
<td>Earlier/warmer spring/summer</td>
<td>European and North American rivers (n = 31)</td>
<td>Atlantic Salmon</td>
<td>Earlier smolt outmigration, reduced marine survival</td>
<td>Species</td>
<td>Russell et al. (2012)</td>
</tr>
<tr>
<td>25</td>
<td>Phenological shift</td>
<td>Earlier/warmer spring/summer</td>
<td>Auke Creek, Alaska</td>
<td>Pink Salmon</td>
<td>Earlier fry and adult migrations</td>
<td>Species</td>
<td>Taylor (2008); Kovach et al. (2015)</td>
</tr>
<tr>
<td>27</td>
<td>Phenological shift</td>
<td>Earlier/warmer spring/summer</td>
<td>Fraser River, British Columbia</td>
<td>Sockeye Salmon</td>
<td>Earlier spawning migrations</td>
<td>Species</td>
<td>Cooke et al. (2004)</td>
</tr>
<tr>
<td>28</td>
<td>Phenological shift</td>
<td>Earlier/warmer spring/summer</td>
<td>Potomac River and upper Chesapeake Bay, Maryland/Virginia</td>
<td>Striped Bass</td>
<td>Earlier spawning migrations</td>
<td>Species</td>
<td>Peer and Miller (2014)</td>
</tr>
<tr>
<td>29</td>
<td>Phenological shift</td>
<td>Earlier/warmer spring/summer</td>
<td>Minnesota lakes (n = 12)</td>
<td>Walleye</td>
<td>Earlier spawning in one-third of lakes</td>
<td>Species</td>
<td>Schneider et al. (2010)</td>
</tr>
<tr>
<td>30</td>
<td>Phenological shift</td>
<td>Earlier spring</td>
<td>Lakes Michigan and Superior</td>
<td>Yellow Perch, Lake Trout</td>
<td>Yellow Perch spawned earlier, no change for Lake Trout</td>
<td>Species</td>
<td>Lyons et al. (2015)</td>
</tr>
<tr>
<td>31</td>
<td>Demographic change</td>
<td>Shorter, warmer winters</td>
<td>Lake Erie</td>
<td>Yellow Perch</td>
<td>No shift in spawning time, reduced recruitment</td>
<td>Species</td>
<td>Farmer et al. (2015)</td>
</tr>
</tbody>
</table>

### Figure 2. Documented impacts of climate change on inland fishes of Canada (green background) and the United States (tan background) based on a 2015 literature review of 772 peer-reviewed publications (1985–2015). Each circle represents an individual fish species or assemblage response type (i.e., demographic changes, distributional or phenological shifts, changes in assemblage structure, changes in community processes, or a combination of responses) to changing climatic factors. In some instances, point locations were slightly offset to enhance clarity. Points correspond to Table 1 and are ordered numerically by response type. Inset panel shows the annual number of publications reporting documented climate change effects (31 total studies).
Seven studies in our review documented climate-induced demographic changes in North American inland fishes (Table 1). These included changes in abundance, growth, and recruitment, with the majority focused on temperature-related effects on coldwater fishes. Decreased growth and abundance of some coldwater species has been linked to increased temperature (e.g., Arctic Char *S. alpinus*, Murdoch and Power 2013; Cisco *Coregonus artedi*, Jacobson et al. 2012) or to increased hydrologic variability (e.g., Chinook Salmon *O. tshawytscha*, Ward et al. 2015). Conversely, increased temperatures and altered aquatic conditions have facilitated increased recruitment and abundance for coldwater species (e.g., Sockeye Salmon, Schindler et al. 2005; Kovach et al. 2014) as well as for warmwater species (e.g., black basses *Micropterus* spp., Robillard and Fox 2006). Although compensatory dynamics can buffer some populations from climatic change, research on Brook Trout *S. fontinalis* suggests that rapid climatic shifts may exceed compensatory processes and ultimately cause population declines (Bassar et al. 2016). Demographic impacts of climate change are widely predicted, but the paucity of documented examples where climate change influences population demography underscores the need for continued monitoring efforts and a critical examination of our ability to accurately predict climate change impacts on inland fishes.

**Evolutionary Processes**

Evolutionary responses to climate change in freshwater ecosystems are poorly documented, but a small number of studies indicate that North American inland fishes are already exhibiting genetic change. Climate-driven changes in freshwater habitats have, and likely will, strongly influence evolutionary processes (i.e., heritable dynamics) in fishes and other organisms (Pauls et al. 2013). Although empirical evidence for adaptive microevolution in response to climate change is rare (Crozier and Hutchings 2014), with time, changes to this and other evolutionary processes, such as genetic drift and gene flow (e.g., range contractions, decreases in the effective population size) are likely to be more frequent (Pauls et al. 2013).

Our review identified three studies that report climate-induced evolutionary changes in North American inland fish populations (Table 1), including adaptive changes due to natural selection and neutral or potentially maladaptive changes associated with increased interspecific introgression. Crozier et al. (2011) demonstrated that a shift toward earlier adult migration in a Sockeye Salmon population may be an evolutionary response, where natural selection is now acting against the latest-migrating individuals; these late migrants will tend to experience relatively harsh climatic conditions and, consequently, have decreased survival during migration. Similarly, Kovach et al. (2012) used long-term genetic data to reveal an evolutionary basis for a strong temporal trend toward earlier migration in an adult Pink Salmon population, likely in response to increasing stream temperatures and shifting oceanic conditions. Increasing stream temperature and shifts in spring precipitation in the Flathead River, Montana, have promoted rapid upstream expansion of nonnative Rainbow Trout *O. mykiss* into habitats occupied by native Westslope Cutthroat Trout *O. clarkii lewisi*, with spatial overlap between the two species’ ranges now leading to introgression and declines in genetically pure Westslope Cutthroat Trout (Mullhfeld et al. 2014). Genetic diversity in inland fish populations has also been linked to climatic variables (e.g., drought) that have changed in recent decades (Turner et al. 2014), suggesting that changes in genetic diversity may prove to be a common but currently understudied effect of climate change (Pauls et al. 2013).

**Assemblage Structure**

Species interactions are often the proximate driver of climate-induced changes in fish population dynamics and extirpation. Species interactions, including trophic linkages (e.g., predation, parasitism, and herbivory), as well as competition, influence species distributions and assemblage structure (i.e., species richness, evenness, and composition; Wisz et al. 2013). Changes in assemblage structure can alter ecosystem functioning (e.g., production, trophic dynamics) and consequently energy flow through food webs (Carey and Wahl 2011).

Mechanisms by which climatic drivers may influence species interactions are diverse. To date, four studies document climate change–induced changes in North American inland fish assemblages through expansion of species’ ranges and novel interactions as well as phenological shifts to increase spatial and temporal overlap of species and competitive interactions (Table 1). In Ontario lakes, species richness has increased over time as a warmer, wetter climate has facilitated natural range expansions and novel species interactions (see Smallmouth Bass *M. dolomieu* case study, Minns and Moore 1995; Mandrak 1995). Similarly, Alofs et al. (2014) have observed northward expansions of gamefishes in Ontario lakes, even as the ranges of their prey have contracted. Krabbenhoft et al. (2014) documented a phenological shift in hatching times in an assemblage of eight fishes in the Rio Grande, New Mexico, associated with changes in flow regimes due to increased overlap and larval competition for food, particularly in dry years (see Rio Grande case study, Turner et al. 2010). Alternatively, some interspecific relationships may be unaffected by climate change. For instance, migrations of piscivorous Dolly Varden *S. malma* have tracked the changes in the timing of Pacific salmon migrations because Dolly Varden appear to use salmon migration as a cue (Sergeant et al. 2015). With increasing changes in species distributions, altered species interactions are often the proximate causes of species declines (Cahiil et al. 2013; Ockendon et al. 2014). These changes highlight the need for future research focused on the potential ecological and social consequences of novel species interactions including the concepts of ecological replacement and surrogate species (i.e., species used in conservation planning as a proxy for other species or a particular environment).

**Links with Other Stressors**

Complex interactions between climate change and other anthropogenic stressors make it difficult to partition and understand their relative effects. Climate change acts on aquatic ecosystems in concert with other anthropogenic stressors, and together these stressors may have complex, compounded effects on inland fishes (see Southeast case study). Some important stressors that are known to interact with climate change are altered land use, water pollution, stream and river impoundments and flow alterations, invasive species, disease and parasites, and fishing exploitation (Kwak and Freeman 2010; Staudt et al. 2013). Water impoundment and withdrawal can alter flow patterns and modify geomorphic features, and dams can alter flow regimes, water availability, water quality, thermal environments, stream connectivity, and aquatic habitats (Collier et al. 1996; Pringle et al. 2000). Beyond habitat changes, invasive species, diseases, parasites,
and fishing pressure influence fish populations and assemblages (Cooke and Cowx 2004; Marcos-López et al. 2010). Introduced species, in particular, are frequently cited as the greatest threat to native aquatic biodiversity in North America along with habitat degradation and loss (Crossman 1984; Fuller et al. 1999; Jelks et al. 2008).

These stressors interact with each other and climate change at multiple scales to transform the physical and biotic environment of aquatic systems. Changes in land and water use that occur concurrently with climate change compound climate impacts to aquatic habitats through increased sedimentation and contaminant input, nutrient enrichment, hydrologic alteration, exotic aquatic vegetation, riparian clearing and canopy destruction, and loss of woody debris (Allan 2004). Rising temperature and drought may compel accelerated water extraction and consumption for human uses, thereby exacerbating the direct climate effect. These feedbacks between climate and other anthropogenic stressors, which may be nonlinear, make separating their individual effects on inland fishes challenging. However, the occurrence of compounded effects suggests that actions to lessen other anthropogenic stressors can mitigate climate change impacts (Parmesan et al. 2013).

**CASE STUDIES**

**Diverse Responses to Climate Change in Pacific Salmon**

Freshwater conditions are changing rapidly throughout northern latitudes, often at rates that exceed those observed in more southern latitudes (IPCC 2014). These environmental changes will impact Pacific salmon through numerous processes, with many potential consequences for ecological and social systems (e.g., Schindler et al. 2008). Growing evidence already suggests that recent climatic change has influenced spatial and temporal shifts in salmon growth, phenology, population dynamics, and natural selection (Table 1).

Pacific salmon responses to climate change vary across biological scales ranging from individuals to populations and species (Figures 3 and 4). Increasing temperatures have influenced growth in multiple salmon populations across Alaska, but observed relationships vary among locations, among co-occurring species at the same location, and among differing smolt life histories within species (Griffiths et al. 2014; Kovach et al. 2014). Climate-induced changes in juvenile (Kovach et al. 2013) and adult (Quinn and Adams 1996; Crozier et al. 2011; Kovach et al. 2015) migration timing have occurred throughout the Pacific range. These responses are variable across species and locations and in some instances may reflect natural selection (Crozier et al. 2011; Kovach et al. 2012). In general, salmon populations in Alaska demonstrate surprisingly diverse demographic responses to climate change (e.g., Rogers et al. 2013), and this diversity will ultimately contribute to long-term population stability, a phenomenon that has major implications for human harvest and ecosystem dynamics (Hilborn et al. 2003; Schindler et al. 2010). For example, salmon consumers, such as bears and gulls, actively exploit and benefit from spatial heterogeneity in salmon phenology and population dynamics (Schindler et al. 2013).

Salmon responses to climatic variation (and other stressors) have generally been more volatile at lower latitudes where environmental, population, life history, and genetic diversity have been reduced (Moore et al. 2010; Carlson et al. 2011). Unfortunately, the loss of abiotic and biotic diversity at the southern margins of their native ranges is likely to make salmon particularly susceptible to climate change, because the most pronounced climate change effects will occur at those latitudes (Mantua et al. 2015). For instance, Chinook Salmon have already demonstrated consistent, negative responses to changes in hydrologic variability along the Washington coast (Ward et al. 2015). In light of these concerns, conservation of existing environmental and biotic diversity and augmentation of diversity where it has been diminished is prudent for species sustainability.

**Nonnative Smallmouth Bass Range Expansion in Ontario Lakes**

Ontario has an abundance of freshwater lakes (>250,000; OMNRF 2012) that are currently being impacted by climate change. Mean annual air temperatures throughout the region
have increased by 2.3°C, and precipitation, though variable, has decreased by an average of 13% since 1961 (Environment Canada 2013). These lakes support numerous recreational fisheries, with Smallmouth Bass being one of the most important (OMNRF 2010). Smallmouth Bass prefer warmer water and may therefore experience enhanced recruitment, survival, and dispersal if climate change continues to drive increasing temperatures throughout Ontario (Shuter et al. 1980; Chu et al. 2005). Indeed, Alofs et al. (2014) estimate that a northward shift in the distribution of Smallmouth Bass within Ontario lakes has occurred at the rate of approximately 13 km per decade over the past 30 years. This expansion is partially facilitated by human activities (e.g., intentional stocking) and opportunities to move through connected waterbodies (Drake and Mandrak 2010) but is primarily a result of climate-mediated increases in thermal habitat suitability (Table 1; Alofs et al. 2014; Alofs and Jackson 2015).

The increased prevalence of Smallmouth Bass in Ontario lakes has significant potential to disrupt food webs and negatively impact native fish assemblages (Figures 5 and 6). Smallmouth Bass have already caused declines in littoral prey species abundances as well as contractions in cyprinid (prey) species ranges (Vander Zanden et al. 2004; Alofs et al. 2014; Table 1 in Paukert et al., this issue). Smallmouth Bass may also have negative impacts on native top predators, particularly coldwater species such as Brook Trout and Lake Trout *S. namaycush*. Smallmouth Bass prey on young-of-the-year Brook Trout and compete with adult Brook Trout for food resources (Ryder and Kerr 1984; Olver et al. 1991). Similarly, Vander Zanden et al. (1999) documented a reduction in Lake Trout trophic position as Lake Trout shifted their diets from predominantly littoral forage fishes to pelagic forage fishes and zooplankton, following establishment of Smallmouth Bass. This shift in diet translated to decreased somatic growth and growth potential for Lake Trout (Vander Zanden et al. 2004).

Furthermore, concerns regarding climate-mediated expansions of black basses are not limited to Ontario and may, in fact, be realized throughout much of temperate North America. For example, Lawrence et al. (2014) predict that rising stream temperatures in the Columbia River basin may lead to the complete loss of Chinook Salmon stream-rearing habitat with extensive Smallmouth Bass invasions in highly modified streams. In Wisconsin, where black basses are native statewide, Smallmouth Bass and Largemouth Bass *M. salmoides* populations have increased significantly, whereas Walleye populations have declined (Hansen et al. 2015; Rypel et al. 2016). Whether this is a cause-and-effect relationship remains to be investigated, but the shift is consistent with the progression of climate-induced warming.

**Combined Effects of Climate Change and Alteration of Natural Flow Regimes on Fishes of the Rio Grande**

The Rio Grande is an arid-land river stretching from the southern Rocky Mountains in Colorado to the Gulf of Mexico. Regional air temperatures in the Rio Grande basin have increased 1°C–3°C over the past century (Stewart et al. 2005) with increased evaporation rates and decreased winter snowpack in the headwaters, which result in less surface water and greater aridity (Gutzler 2013). In addition to the direct effects of climate change, the natural flow regime on the Rio Grande has been extensively modified by river regulation, in part to meet greater agricultural, industrial, and municipal water demand in a hotter, drier climate. Climate change has caused warmer summer temperatures, which increase the rate of evapotranspiration and decrease soil moisture content, further intensifying human demand for agricultural and residential water extraction (Hurd and Conrood 2007), exacerbating the direct effects of climate change. The net result of climate change and flow regulation is a reduction in fish habitat size, complexity, and lateral connectivity with floodplain habitats (Hurd and Conrood 2007). Channelization has severed linkages between aquatic and terrestrial communities by reducing riparian or terrestrial subsidies and ultimately decreasing biotic richness (Kennedy and Turner 2011). Changes in flow also affect the reproductive phenology of fishes, leading to earlier spawning across the entire assemblage in years with a weaker, earlier flood pulse (Table 1; Krabbenhoft et al. 2014).
Reduced connectivity to floodplain habitats is also likely to reduce recruitment of floodplain-spawning species, which utilize these lateral habitats as spawning or nursery grounds (Figures 7 and 8). Dry years have promoted crowding among species and life stages that are normally separated in time or space, potentially leading to increased larval competition for food (Turner et al. 2010). Stable isotope data have also revealed an assemblage-level reduction in trophic complexity over the past 70 years (Turner et al. 2015). Though fishes of the Rio Grande have previously been exposed to strong climatic changes (Hurd and Coonrod 2007; Gutzler 2013), the novel conditions created by rapidly changing climate and extensive human disturbances will likely exceed any directional or selective pressures that these fishes have faced in their evolutionary history. A key point is that, in addition to direct effects of climate change (e.g., less precipitation, higher temperature), indirect effects are mediated through human behavior, such as increased river regulation to meet higher water demands in a drier climate.

Despite the negative effects of increasing human water demand under a changing climate, the extensive regulatory infrastructure of the Rio Grande could provide a fortuitous opportunity for minimizing the effects of climate change and other human impacts. Managers can intentionally engineer dam releases to mimic the natural flow regime, which can in turn enhance recruitment of native fishes and suppress nonnative species (Richter and Thomas 2007). These controlled dam releases will likely be insufficient to fully preserve native fish assemblages in arid-land rivers (Propst et al. 2008), but they are nevertheless an important and promising tool to complement other adaptive management and climate change mitigation strategies (Bunn and Arthington 2002; Gido et al. 2013).

Complex Interactions of Stressors in Southeastern U.S. Stream Fish Assemblages

The southeastern United States (Southeast) is a biodiversity hotspot with the highest overall native richness and number of endemic fish species in North America north of Mexico and perhaps of any temperate region (Warren et al. 2000; Scott and Helfman 2001). Many of these fishes, particularly cyprinids, ictalurids, and percids, are imperiled (Jelks et al. 2008). This status is attributed to multiple types of environmental changes, including rapid human population growth, widespread habitat degradation, and the introduction of nonnative species, as well as climate change. However, the Southeast is particularly vulnerable to a number of climate-driven events, including sea-level rise and catastrophic floods, drought, heat waves, winter storms, tropical cyclones, and tornadoes (Ingram et al. 2013). Average air temperatures have been increasing throughout the region since the 1970s, with the most recent decade being the warmest on record (Ingram et al. 2013). Interannual variability in precipitation has also increased, resulting in pronounced wet and dry periods.

Studying the direct effects of climate change on southeastern inland fishes is currently difficult, given the interactive nature of climatic and anthropogenic pressures (Table 1). Because unperturbed reference systems are rare in the Southeast (and elsewhere), direct empirical comparisons are not always possible to assess whether changes in fish assemblages or aquatic ecosystems are due to climatic stressors, human activities (such as landscape alteration), or both (Figures 9 and 10). For example, human alteration of the landscape and riparian zone, like climate change, can result in aquatic habitat homogenization: heavily shaded, coolwater stream reaches with diverse instream physical habitat parameters (e.g., depth, velocity, substrate, and cover) become warmer, open-canopy reaches with lower habitat diversity and higher turbidity, sedimentation, and nutrient and contaminant loads.

In general, these changes tend to favor tolerant, generalist species over more sensitive specialist species (Scott and Helfman 2001; Radwell and Kwak 2005; Roy et al. 2006; Wenger et al. 2008). Temperature sensitive stenothermic species are replaced by more tolerant eurytherms, food specialists are replaced by generalist feeders, lithophilic spawners are replaced by species that do not require specific substrates, and species that are...
relatively insensitive to degraded water quality replace less-tolerant species. In light of these unknowns, minimizing the impacts of more well-known anthropogenic stressors, such as land use change, can serve to create a “buffer” against less understood climate change impacts.

CONCLUSIONS AND FUTURE RESEARCH NEEDS

Climate change impacts on inland fishes are complex and variable, and the current literature does not yet adequately represent the diversity of North American inland fishes that are being impacted (Table 1; Figure 2). By synthesizing current knowledge on this broad, important issue, we attempt to identify and focus attention on key unknowns in this rapidly emerging field of study. Additional research is now needed to address these knowledge gaps, inform adaptive ecosystem-based management of North American inland fishes, and ensure a sustainable future for these important natural resources. We conclude this synthesis with a summary of key research areas that may confer maximal benefits in this larger effort.

Move beyond Distribution Studies

Most climate change research so far has focused on species’ phenologies and distributions (Table 1; Figure 2). Though this is an important first step, greater emphasis should be placed on population dynamics, evolution, and interspecific interactions. Research on these topics is being pursued in other regions (e.g., Thackeray et al. 2013; Jonsson and Setzer 2015), but relatively little work has been done in North America.

Ground-Truth Projected Impacts

Most explicit climate change studies have projected future effects on North American inland fishes. As more long-term data sets become available (e.g., the National Ecological Observatory Network), an important task will be to assess whether model-predicted impacts are consistent with observed change through time (Figure 2; see Cisco case study in Paukert et al., this issue). Observed and projected changes should be carefully analyzed to allow enhanced understanding of fundamental processes and to facilitate improved predictive capabilities.

Increase Geographic and Taxonomic Representation

Efforts to document climate change impacts on inland fishes have been disproportionately concentrated along the East Coast, West Coast, and the Great Lakes regions of Canada and the United States (Figure 2). They have also focused primarily on game species. These studies are not representative of the geographic and taxonomic diversity of North American inland fishes, and new research is now needed to examine climate change effects on non-game species as well as fishes from other regions of North America. Geographic underrepresentation is particularly acute in Mexico, much of Alaska, the North American Great Plains, the North American deserts, and the Northern Forests and Territories of Canada. Taxonomic representation is poor in families beyond Salmonidae, Percidae, and Centrarchidae.
Document Sources of Resilience

As climate change continues to alter freshwater habitats and pressure inland fishes to move or adapt, research should seek out and document instances of resilience. Failing to identify processes that buffer fishes from climate change, such as physical environmental heterogeneity (e.g., groundwater upwelling), phenotypic plasticity, and adaptive microevolution, may lead to biased and unduly pessimistic predictions regarding future population dynamics or range shifts (e.g., Reed et al. 2011; Seebacher et al. 2014; Snyder et al. 2015). Empirical reports of resilience and the processes that sustain it are currently lacking for most North American inland fishes, highlighting an urgent priority for future research.

Implement Monitoring Frameworks to Document Changes in Assemblage Dynamics

The diverse impacts of climate change include shifts in species’ production rates, accelerated rates of nonnative species invasions, native species extirpations, and the creation of novel habitats and assemblages (Thackeray et al. 2010; Jeppesen et al. 2012; Chester and Robson 2013). Strategic monitoring programs that implement systematic sampling designs to cover broad spatial and temporal scales (e.g., dense monitoring networks such as the U.S. Environmental Protection Agency’s National Rivers and Streams Assessment) are needed to track and model potential changes and help tease climate change apart from confounding stressors (Parmesan et al. 2013).

Provide Better Decision-Support Tools

Natural resource managers are integral to fish conservation efforts, and they will need better decision-support tools, inclusive of uncertainty estimates, to make informed decisions (Harwood and Stokes 2003). To ensure that these tools will meet their needs, managers should be consulted and included during the design stages. Collaborative and transparent coproduction of science will lead to better tools, such as scenario planning and interactive vulnerability maps (Peterson et al. 2003), and will ultimately maximize opportunities for inland fishes to continue to thrive in the face of climate change.

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