

Special Issue

Fisheries

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Special Issue: Climate Change and North American Inland Fishes

SWAPs and AFS

Perspectives on Climate Change and Fisheries from AFS Sections



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425 Barlow Place, Suite 110 • Bethesda, MD 20814-2199
(301) 897-8616 • fax (301) 897-8096 • main@fisheries.org

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Photo caption: A Smallmouth Bass *Micropterus dolomieu* in a Wisconsin lake. Photo credit: Gretchen J. A. Hansen, Minnesota Department of Natural Resources.

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Climate Change: SWAPs and AFS

Ron Essig | AFS President



Climate change is undoubtedly one of the most important threats to aquatic species and habitats in the decades ahead. So it is entirely appropriate that this *Fisheries* issue is devoted to that theme. In this column, I will touch on two main points regarding climate change: (1) how it is being addressed within state wildlife action plans (SWAPs) and (2) how AFS is involved in the issue.

State and territorial fish and wildlife agencies in the United States prepared SWAPs in 2005 to assess the condition of their wildlife and habitats, to identify their threats, and to outline actions for their conservation. Many aquatic species were designated as Species of Greatest Conservation Need (SGCN) in these plans. States recently submitted revisions to their SWAPs, marking their 10-year anniversary. As of this writing, most of these SWAP revisions are available to the public on agency websites but are still being reviewed for approval by the U.S. Fish and Wildlife Service. A major requirement for these SWAP revisions was to address the threat of climate change. States typically characterize the threats from climate change as habitat shifting and alteration, storms and flooding, droughts, and temperature extremes. Aquatic habitat shifting and alteration include such phenomena as sea level rise and ocean acidification, among others.

States propose a variety of actions to address climate change in their SWAP revisions, and I looked at those in the northeast

United States where I work for some aquatic examples. Rhode Island is similar to many states in their identification that a basic need still exists to assess succession of species likely resulting from temperature changes. New York proposes a monitoring program for deep, cold Adirondack lakes that may serve as refuges for sensitive SGCN from the effects of climate change. Virginia identified many heat-tolerant fish SGCN like Blackbanded Sunfish *Enneacanthus chaetodon* and several darter species that occupy small, isolated habitats, preventing them from expanding their range. So species propagation programs and releases into currently unoccupied habitats are proposed. Delaware proposes to restore or improve horseshoe crab spawning habitat affected by sea-level rise through beach replenishment. I suspect that these sample Northeast actions of monitoring, species propagation, species translocation, and improving resiliency to flooding are repeated for other SGCN in SWAPs in other regions of the United States.

Shifting gears to AFS and climate change, the Society has been involved in this issue for many years. Arguably the most comprehensive effort was the development of the climate change position statement approved by AFS members in 2011 (fisheries.org/wp-content/uploads/2015/05/policy_33f.pdf). The bottom line of this 43-page statement is a set of recommendations for greenhouse gas reductions, water use mitigation, integrated

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Drought, Flow, and Aquatic Resources

Thomas E. Bigford | AFS Policy Director

This column has many inspirations, including a drought discussion this past February organized by the Association of Fish and Wildlife Agencies, the March 2016 White House Water Summit, my own worries about how new hydrologic patterns will affect fish, and a talk by Ellen Gilinsky, senior policy advisor in the U.S. Environmental Protection Agency (EPA) Office of Water. Gilinsky represents EPA on the National Fish Habitat Partnership's Board of Directors (where I represent the American Fisheries Society), and she offered a lengthier discourse on this issue to the board on March 9, 2016. For perspective, think "fish" wherever you read "water," "aquatic," or "drought." And for your sanity, be optimistic when you see "resilience."

The Obama Administration has increased collaboration with its state, tribal, and local partners on water quality and quantity issues. In addition, the President informally established the National Drought Resilience Partnership (NDRP) as part of his Climate Action Plan (White House 2013). Recognizing that the nation was facing more frequent and intense droughts, the NDRP focuses on supporting watershed strategies for building long-term resilience and to target scientific and programmatic



resources to help build a more drought-resilient nation. On March 21, 2016, President Obama formally established the NDRP through a Presidential Memorandum on Building National Capabilities for Long-Term Drought Resilience, accompanied by an Action Plan to implement drought-resilience goals.

Pilot efforts are one NDRP priority. The NDRP has created a drought resilience demonstration project in the headwaters of Missouri River, with Montana as a full partner. The Missouri Headwaters Drought Resilience Demonstration Project will deliver drought mitigation tools and resources to watershed stakeholders and gather information from local groups. The goal is a model for information sharing, efficient water use and storage, and community collaboration as people prepare for drought while preserving cultural and ecological values.

The NDRP also emphasizes capacity and tools. Although the EPA's work is mostly with utilities to provide safe drinking water, the aquatic connections are inescapable. In March 2016, the EPA released "Drought Response and Recovery for Water Utilities" (USEPA 2016a) along with a tool to assist small- to medium-sized water utilities. The guide focuses on short-term/emergency actions that build long-term drought resilience. Accompanying the guide is an interactive Case Study Map, a multimedia geo-platform website that documents seven case study utilities across the South and West (USEPA 2016b).

Accompanying the tools is a series of workshops. The EPA conducted two Drought Response and Recovery Workshops for Water Utilities in California's Central Valley, providing an opportunity to share best practices and tools. Look for additional workshops this spring and summer. The EPA is also promoting greater residential and municipal water efficiency through its WaterSense program, an effort that during the past decade has helped consumers save a cumulative 1.1 trillion gallons of water and more than US\$20 billion in water and energy bills.

To highlight fish and fish habitat, the EPA and U.S. Geological Survey (2015) released a draft report this past March on "Protecting Aquatic Life from Effects of Hydrologic Alteration." The report zeroes in on biological integrity, flow targets, seasonal flow disruption, and fluctuating water temperatures, among other variables. For fish, hydrologic alteration can affect spawning, ability to gather nutrients, access to preferred habitat, and more. Hydrologic alteration can impair aquatic water bodies destined to support aquatic life. Stresses on aquatic life from hydrologic alterations may be further exacerbated through climate change. Recent climate trends reveal new frequencies and durations of extreme weather events that can affect flow and aquatic life.

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Effects of Climate Change on North American Inland Fishes: Introduction to the Special Issue

Guest Editors:



Craig P. Paukert | U.S. Geological Survey, Missouri Cooperative Fish and Wildlife Research Unit, Department of Fisheries and Wildlife Science, University of Missouri, Columbia.
E-mail: paukertc@missouri.edu



Abigail J. Lynch | U.S. Geological Survey, National Climate Change and Wildlife Science Center, Reston, VA.
E-mail: ajlynch@usgs.gov

In collaboration with:

James E. Whitney | Missouri Cooperative Fish and Wildlife Research Unit, Department of Fisheries and Wildlife Sciences, University of Missouri, Columbia, MO

*Present address for James E. Whitney: Department of Biology, Pittsburg State University, Pittsburg, Kansas

To sustainably manage North American fishes, understanding how climate change will impact, and is currently impacting, these ecologically, culturally, and economically valuable resources is a critical need. Because the effects of climate change on fishes vary by ecoregion and interact with other anthropogenic stressors, synthesis of available information on the impacts of climate change on inland fishes at a continental scale is useful to their conservation and management.

Therefore, the American Fisheries Society solicited assistance from the U.S. Geological Survey's (USGS) National Climate Change and Wildlife Science Center Chief Doug Beard to develop a special issue on climate change for *Fisheries*. This initial discussion led to a collaboration with the National Climate Change and Wildlife Science Center and the USGS Missouri Cooperative Fish and Wildlife Research Unit to develop the special issue. As team leads, we convened an expert workshop in June 2015 at the USGS Northern Rocky Mountain Science Center in Bozeman, Montana, to examine the effects of global climate change on inland fishes and fisheries in the United States and Canada (see photo). The 30 experts were selected based on their expertise in climate change, fish ecology, and/or human dimensions and were from academia (9), state/provincial governments (8), and federal agencies (13) throughout the United States and Canada. The aim of the workshop was to summarize the current state of knowledge, identify data gaps, and suggest future research directions around four major themes dealing with climate-related impacts on fishes and fisheries:

- Individual-level responses (e.g., physiology, growth)
- Population- and assemblage-level changes (e.g., range shifts, biotic interactions)
- Human dimensions (e.g., recreational fishing)
- Management and adaptation to climate change (e.g., riparian planting, improved connectivity).

Ectothermy in North American inland fishes makes them vulnerable to climate-induced temperature change (see Whitney

et al., this issue). Climate-related deviations from optimal temperatures and salinity may result in chronic stress that challenges the neuroendocrine and osmoregulatory systems of fishes, alters cardiorespiratory performance and aerobic scope, and elicits hyperactive or suppressive immune responses. Temperature and salinity changes will occur in environments with other anthropogenic stressors, but the physiological consequences of interacting stressors are poorly known and are in need of further investigation.

Climate change acts as both a direct and indirect driver of change at the fish population and assemblage levels in inland systems (see Lynch et al., this issue). Thirty-one peer-reviewed research publications between 1985 and 2015 document observed impacts of climate change on North American inland fishes, primarily associated with changes in phenology and distribution. However, more research is necessary to ground-truth projected changes in fish, to provide broader geographic and taxonomic representation, to increase understanding sources of (and enhancers of) resilience to change and interactions among confounding stressors, and to develop accessible decision-support tools.

There are likely three pathways in which climate change may affect inland recreational fisheries in North America (see Hunt et al., this issue). The first pathway suggests that climate change may affect fish populations and habitats, which will indirectly affect fishers. Climate change may also change environmental conditions that directly affect fishers. For example, increased air temperature in northern regions will likely extend the open water fishing season, possibly increasing fishing effort. Lastly, mitigation and adaptation strategies, such as energy policies that may result in higher fuel costs, may affect inland recreational fishers because of increased travel costs to fishing destinations. However, there is limited research on how these three pathways combine to affect fishers.

With possible changes to fish physiology, fish populations and assemblages, and fishers, management agencies have

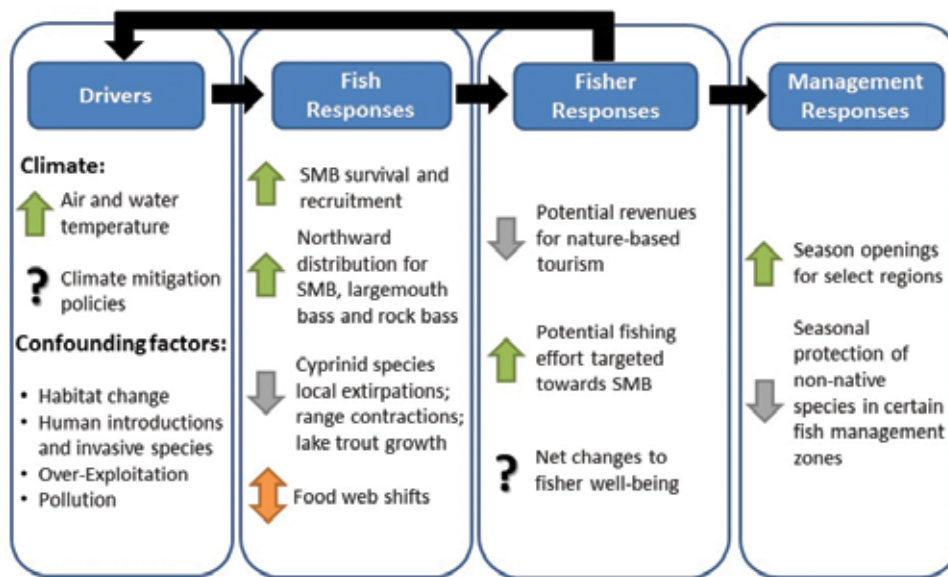


Figure 1. Example of some of the documented fishes, fishers, and management responses to the northward expansion of Smallmouth Bass (SMB) in Ontario's inland lakes facilitated by climate change. Green arrows indicated an increased or earlier seasonal response; gray arrows indicated a decrease or later seasonal response; orange double arrows indicate that responses vary and studies have documented increases, decreases, and/or no change; and question marks indicate an unknown effect. See Hunt et al. (this issue), Lynch et al. (this issue), Whitney et al. (this issue), and Paukert et al. (this issue) for a more comprehensive view of the impact of SMB expansions.



Members of the expert panel that convened in Bozeman, Montana, in June 2015 to determine the effects of climate change on inland fishes and fisheries. Photo credit: USGS.

a challenge to adapt management in the long term to a changing climate while balancing short-term management goals (see Paukert et al., 2016). However, managers can often use traditional approaches (e.g., harvest regulations, habitat management) to tackle novel issues associated with climate change. However, managing for a resilient ecological system may require strategies to increase age structure of populations to minimize possible boom-and-bust recruitment cycles or provide a diversity of species for fishers to use. Paukert et al. (this issue) provide examples of how agencies are using monitoring data to make decisions to create resilient ecological systems and how forward-thinking management structures can increase agency capacity to understand and manage for natural resources in a changing climate.

The range expansion of Smallmouth Bass *Micropterus dolomieu* in Ontario provides an example that links the four themes of this issue (Figure 1). Populations are expanding northward because environmental conditions are more suitable to their physiology. The invasion of Smallmouth Bass in these new areas can disrupt native food webs, impact assemblages of resident fishes, and create new opportunities for recreational fishing. The ecological consequences of Smallmouth Bass expansion into new lakes present opportunities and challenges for fisheries managers in Ontario because many anglers desire to catch Smallmouth Bass, which require new management techniques (e.g., catch-and-release bass fishing negates liberal bag limits as a harvest management tool), but managers still have responsibilities to maintain the native coldwater fish communities. The management process will likely be an exercise in managing expectations of the stakeholders for fisheries changing with climate change.

We hope you enjoy the issue. Please feel free to contact us directly with any questions or comments.

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Physiological Basis of Climate Change Impacts on North American Inland Fishes





James E. Whitney*

Missouri Cooperative Fish and Wildlife Research Unit, Department of Fisheries and Wildlife Sciences, University of Missouri, Columbia, MO

Robert Al-Chokhachy

U.S. Geological Survey (USGS), Northern Rocky Mountain Science Center, Bozeman, MT

David B. Bunnell

USGS, Great Lakes Science Center, Ann Arbor, MI

Colleen A. Caldwell

USGS, New Mexico Cooperative Fish and Wildlife Research Unit, Las Cruces, NM

Steven J. Cooke

Fish Ecology and Conservation Physiology Laboratory, Department of Biology and Institute of Environmental Science, Carleton University, Ottawa, ON, Canada

Erika J. Eliason

Department of Forest and Conservation Sciences, University of British Columbia, Vancouver, BC, Canada

Mark Rogers

USGS, Great Lakes Science Center, Lake Erie Biological Station, Sandusky, OH

Abigail J. Lynch

USGS, National Climate Change and Wildlife Science Center, Reston, VA

Craig P. Paukert

USGS, Missouri Cooperative Fish and Wildlife Research Unit, Department of Fisheries and Wildlife Science, University of Missouri, Columbia, MO

The second through seventh authors are working group members listed alphabetically by last name. The final two authors are workshop organizers.

*Present address for James E. Whitney: Department of Biology, Pittsburg State University, Pittsburg, Kansas.
E-mail: jewhitney@pittstate.edu

Global climate change is altering freshwater ecosystems and affecting fish populations and communities. Underpinning changes in fish distribution and assemblage-level responses to climate change are individual-level physiological constraints. In this review, we synthesize the mechanistic effects of climate change on neuroendocrine, cardiorespiratory, immune, osmoregulatory, and reproductive systems of freshwater and diadromous fishes. Observed climate change effects on physiological systems are varied and numerous, including exceedance of critical thermal tolerances, decreased cardiorespiratory performance, compromised immune function, and altered patterns of individual reproductive investment. However, effects vary widely among and within species because of species, population, and even sex-specific differences in sensitivity and resilience and because of habitat-specific variation in the magnitude of climate-related environmental change. Research on the interactive effects of climate change with other environmental stressors across a broader range of fish diversity is needed to further our understanding of climate change effects on fish physiology.

Bases fisiológicas del impacto del cambio climático en peces de aguas continentales de Norte América

El cambio climático global está alterando los ecosistemas de agua dulce y con ello se afectan las poblaciones y comunidades de peces. El fundamento de los cambios en la distribución de los peces y de las respuestas a nivel de ensamblajes ante el cambio climático tiene que ver con limitaciones fisiológicas individuales. En esta revisión se presenta una síntesis sobre los efectos mecánicos del cambio climático en los sistemas neuro-endócrino, cardio-respiratorio, inmunológico, osmorregulatorio y reproductivo de peces diádomos y de agua dulce. Los efectos observados del cambio climático en los sistemas fisiológicos son numerosos y variados, incluyen la excedencia de los límites de tolerancia térmica, reducción en el desempeño cardiorespiratorio, una función comprometida del sistema inmune y patrones alterados en cuanto a la inversión reproductiva individual. No obstante, los efectos varían ampliamente entre y dentro de las especies a causa de diferencias en cuanto a poblaciones, sensibilidad entre sexos y resiliencia, así como por variaciones en los hábitats particulares como respuesta a la magnitud del cambio ambiental. Con el objeto de entender mejor los efectos del cambio climático en la fisiología de los peces, se requieren investigaciones encaminadas a estudiar los efectos interactivos entre el cambio climático con otros estresores ambientales a lo largo de un rango más amplio de diversidad de peces.

Bases physiologiques des impacts des changements climatiques sur les poissons continentaux d'Amérique du Nord

Le changement climatique mondial modifie les écosystèmes d'eau douce et affecte les populations et les communautés de poissons. Les changements sous-jacents dans la distribution des poissons et les réponses en matière de communautés apportées aux changements climatiques représentent des contraintes physiologiques au niveau individuel. Dans cette revue, nous synthétisons les effets mécanistes du changement climatique sur les systèmes neuroendocriniens, cardiorespiratoires, immunitaires, osmorégulateur et reproductifs des poissons d'eau douce et des diadromes. Les effets du changement climatique observés sur les systèmes physiologiques sont nombreux et variés, y compris le dépassement des tolérances thermiques critiques, une baisse des performances cardiorespiratoires, la fonction immunitaire compromise, et la modification des modes d'investissement dans la reproduction individuelle. Cependant, les effets varient considérablement entre et au sein des espèces en raison des espèces, de la population, et des différences, même selon le sexe, de sensibilité et de résilience, ainsi qu'en raison de la variation spécifique de l'habitat dans l'ampleur des changements environnementaux liés au climat. La recherche sur les effets interactifs des changements climatiques avec d'autres facteurs de stress environnementaux à travers une gamme plus large de la diversité des poissons est nécessaire pour approfondir notre compréhension des effets des changements climatiques sur la physiologie des poissons.

KEY POINTS

- **Neuroendocrine:** Climate change can result in chronically elevated environmental stressors that challenge the neuroendocrine system of some fishes, elevating metabolic costs and decreasing growth and survival.
- **Cardiorespiratory:** Climate change can expose some fishes to thermal conditions outside of their species- or population-specific optimal thermal range for aerobic scope, but for other species or populations thermal conditions will become more suitable and aerobic scope will increase.
- **Immune:** Climate change may elicit hyperactive or suppressive responses from fish immune systems, both of which may result in compromised immune function; these immunocompromised fish have to cope with a climate-altered environment containing altered disease prevalence, pathogenicity, and novelty.
- **Iono- and osmoregulatory:** Rising salinities associated with climate change will disrupt the hydromineral balance of fishes with narrow salinity tolerances, decreasing their abundance in assemblages, while leaving fishes with broader salinity tolerances less affected.
- **Reproduction:** Deviations from optimal temperatures, salinity, and dissolved oxygen will influence reproductive timing and investment of fishes, thus potentially reducing reproductive output and success.

INTRODUCTION

Climate change is altering the physical, chemical, and biological characteristics of freshwater habitats (Hartmann et al. 2013), with concomitant effects on freshwater and diadromous fishes. Climate-induced physical habitat changes include increased mean water temperatures, frequency of extreme temperature events (Austin and Colman 2007; Kaushal et al. 2010), and altered hydrologic regimes of lotic and lentic habitats resulting from changes in precipitation (Magnuson et al. 2000; Leppi et al. 2012). Climate-induced changes in temperature and precipitation may directly affect freshwater habitats (Isaak et al. 2010), or effects may arise indirectly via changes in the terrestrial landscape (Isaak et al. 2010; Davis et al. 2013). Chemical characteristics of water bodies, such as dissolved oxygen (Ito and Momii 2015), salinity (Bonte and Zwolsmen 2010), and nutrient concentrations (Moss et al. 2011), are directly influenced by these climate-induced changes in thermal and hydrologic regimes. Alterations of physicochemical conditions culminate in multiple responses in the biotic environment within which fish need to function, including altered distribution, prevalence, transmission, and pathogenicity of parasites and disease (Britton et al. 2011; Macnab and Barber 2012). These climate-induced environmental changes interact with other anthropogenic alterations (pollution, nonnative species, habitat degradation; Staudt et al. 2013) to directly or indirectly influence the physiological function of fishes.

The physiology of fish is controlled by their internal temperature, which, in the case of most fishes, is regulated by the ambient thermal environment (i.e., ectothermic) and can vary greatly across time and space (i.e., poikilothermic; Box 1). The influence of ambient temperature on the rate of physiological processes (Fry 1947) leaves fishes vulnerable to climate-induced changes in temperature and other environmental factors. The consequence of climate-induced physiological changes are dictated by the severity of environmental change and include no response, behavioral changes (e.g., dispersal), sublethal effects (i.e., on growth or reproductive success), or lethality (Ficke et al. 2007). Climate-induced changes of the physiology of fishes are not uniform; responses depend on a number of factors (eurythermal versus stenothermal; Box 1) that vary among species, creating “winners” and “losers” in a changing climate (Somero 2010). Furthermore, responses to climate change vary within species (sex and life stage) and across geographic regions due to local adaptation of populations (Eliason et al. 2011). Although complex, there is a critical need to synthesize available knowledge on the effects of climate change on fish physiology, which will help identify the most important questions regarding climate change effects on fishes yet to be addressed and thus will help ensure that conservation and management of fishes in a changing climate are well informed (Box 2).

Box 1: Terms

- Acquired immune response:* The immune response that is inducible, temperature dependent, slower, and has more targeted disease specificity.
- Aerobic scope:* The difference between maximum and standard metabolic rate; defines the opportunity for aerobic activity.
- Conservation physiology:* “An integrative scientific discipline applying physiological concepts, tools, and knowledge to characterizing biological diversity and its ecological implications; understanding and predicting how organisms, populations, and ecosystems respond to environmental change and stressors; and solving conservation problems across the broad range of taxa (i.e., including microbes, plants, and animals)” Cooke et al. (2013:2).
- Critical thermal tolerance (T_{crits}):* Organism-specific upper and lower threshold temperatures where aerobic scope is zero and mortality is imminent.
- Ectothermic:* Organisms whose internal temperature is controlled by the ambient environment (antonym = endothermic).
- Endothermic:* Organisms whose internal temperature is controlled by metabolism (antonym = ectothermic).
- Euryhaline:* Aquatic organisms with a broad salinity tolerance of approximately 5 to >40 ppt (antonym = stenohaline).
- Eurythermal:* Organisms with a broad thermal tolerance (antonym = stenothermal).
- Functional thermal tolerance:* The organism-specific range of temperatures where specific aerobic activities are possible; varies across aerobic activities (e.g., locomotion, digestion).
- Homeostasis:* The normal physiological set points in an organism.
- Hyperosmotic:* The ionic concentration of an aquatic organism’s blood serum is greater than the ionic concentration in the ambient aquatic environment (antonym = hypoosmotic).
- Hypoosmotic:* The ionic concentration of an aquatic organism’s blood serum is less than the ionic concentration in the ambient aquatic environment (antonym = hyperosmotic).
- Hypoxia:* Low dissolved oxygen concentrations in the ambient aquatic environment.
- Innate immune response:* The immune response that is preexisting, temperature independent, rapid, and has general disease specificity.
- Iteroparous:* A life history strategy where an organism has multiple reproductive events during its lifetime (antonym = semelparous).
- Maximum metabolic rate:* The maximum rate of oxygen uptake for an organism.
- Optimal temperature (T_{opt}):* Organism-specific temperature where aerobic scope is greatest.
- Osmolality:* The total ionic concentration of an organism’s blood serum.
- Phenology:* The timing of life history events.
- Phenotypic plasticity:* The ability of a single genotype to produce multiple phenotypes depending on environmental conditions.
- Poikilothermic:* Organisms whose internal temperature varies greatly through time (antonym = stenothermal).
- Semelparous:* A life history strategy where an organism has a single reproductive event during its lifetime (antonym = iteroparous).
- Standard metabolic rate:* The minimum rate of oxygen uptake to maintain life in a nonreproducing, nondigesting organism.
- Stenohaline:* Aquatic organisms with a narrow salinity tolerance of approximately 0.0–5.0 ppt (antonym = euryhaline).
- Stenothermal:* Organisms with a narrow thermal tolerance (antonym = eurythermal).

Box 2: Recommendations for Future Research Questions to Advance the Understanding of Climate Change Effects on Fish Physiology

All physiological systems

How do multistressor environments influence the physiological function of freshwater and diadromous fishes?

What are the functional (i.e., values where normal activity ceases) and critical (i.e., values where mortality occurs) physiological tolerances to environmental variables affected by climate change, and how do these tolerances vary across the broad range of fish diversity?

How does physiological tolerance vary within species according to population, sex, and life stage?

What is the adaptive potential of fish to respond to climate change via phenotypic plasticity, acclimatization, and microevolution?

Neuroendocrine

What are the cause–effect relationships among and within levels of the biological hierarchy (i.e., cells, tissues, organs) that influence the stress response in fish?

How do findings concerning the stress response from artificial laboratory conditions translate to real-world field conditions?

Cardiorespiratory

How do climate change–induced reductions in aerobic scope specifically influence physiological performance; for example, digestion, growth, reproduction?

What are the rates of adaptation for aerobic scope?

Immune

What is the relative contribution of compromised immune function, enhanced pathogen performance, novel pathogen presence, and altered host behavior to changes in growth, reproduction, and survival of fishes under a changing climate?

Iono- and osmoregulatory

What are the relative impacts of rising salinity and temperature and decreasing dissolved oxygen for fish hydromineral balance as climate change increases drought prevalence?

Reproduction

Are temperature-driven changes in climate contributing to the adoption of “skipped spawning” strategies (Rideout et al. 2005)?

Does climate change differentially influence species according to their spawning strategy and level of parental care?

Will early-life survival increase in a changed climate to compensate for lower reproductive investment?

Will changes in phenology of spawning events vary across species to an extent where emergence of prey and predators is more commonly a mismatch than a match?

The objectives of this review are to describe the observed and potential effects of climate change on the physiology of freshwater and diadromous fishes and to illustrate how these physiological responses have implications for parameters of interest to fishery scientists and managers, including survival, behavior, growth, and reproduction. We focus on lentic and lotic freshwater systems throughout North America, although global examples are included when North American examples were rare. Climate change also exerts profound effects on oceans and the marine life history phase of diadromous fishes and, thus, we refer readers to reviews on marine systems to better understand impacts on diadromous fishes (e.g., Roessig et al. 2004; Hoffmann and Todgham 2010). Although manuscripts have previously reviewed the effects of climate change on a single fish physiological system (e.g., see Farrell et al. 2009 for cardiorespiratory and Pankhurst and Munday 2011 for reproduction), we seek to provide a more integrated and comprehensive overview to describe existing information and identify significant knowledge gaps concerning the effects of climate change on five fish physiological systems. By summarizing the effects of climate change on multiple fish physiological systems in a single review, we are able to provide a more complete picture of the overall effects of climate change on fish physiology. Understanding the response of fish physiology to changing climate provides a mechanistic explanation (Pörtner and Farrell 2008; Cahill et al. 2013) for higher-order population and community responses, such as altered phenology, range shifts, and biotic interactions (Lynch et al., this issue). Physiological understanding can also be used

to identify those species or populations most vulnerable to climate change (Williams et al. 2008; Huey et al. 2012), which, in turn, can be used to generate management recommendations to mitigate the effects of climate change (Paukert et al., this issue). Below, we review how climate-induced environmental change can influence the neuroendocrine, cardiorespiratory, immune, iono- and osmoregulatory, and reproductive systems of freshwater and diadromous fishes (Figure 1).

Neuroendocrine Responses

The neuroendocrine system functions in maintaining homeostasis (Box 1) in fishes and thus exerts control over all other physiological systems. Stressful environmental conditions can perturb homeostasis, initiating a neuroendocrine response via the hypothalamic–pituitary–interrenal (HPI) axis (see review by Barton 2002). The ultimate outcome of the HPI response is the release of cortisol and other hormones into the bloodstream, which causes a series of secondary physiological changes that promote adaptation and/or recovery to the stressor (Mommensen et al. 1999). The biochemical reaction rates responsible for the HPI response are regulated by temperature, whereby for every 10°C increase, the speed of reactions approximately doubles (i.e., Q_{10} effect). As such, the most profound effect of climate change on neuroendocrine function in fish occurs through an increase of water temperature outside species- or population-specific optimal temperature ranges. Our understanding of how temperature affects neuroendocrine systems is largely derived from studies of salmonids, with a dearth of information from other families. For instance, Chadwick et al. (2015) found that

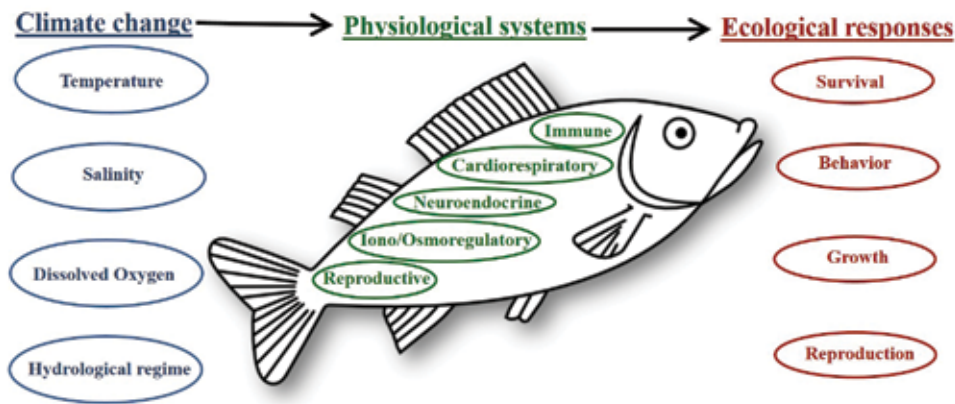


Figure 1. Conceptual model describing the responses of fish physiological systems to climate change. The left column lists abiotic characteristics of freshwater ecosystems that are influenced by climate change, which, in turn, influence five physiological systems within an individual fish. The right column describes how scientists or managers could measure different responses resulting from climate change effects on fish physiology. Fish image is from 4vector.com/free-vector/fish-outline-clip-art-118446.

mean daily water temperatures above the ecological temperature threshold for Brook Trout *Salvelinus fontinalis* (21.0°C) induced an endocrine and cellular stress response by elevating plasma concentrations of cortisol, glucose, and heat shock protein (HSP)-70. Similarly, Meka and McCormick (2005) and Steinhausen et al. (2008) found elevated concentrations of cortisol in Rainbow Trout *Oncorhynchus mykiss* and Sockeye Salmon *O. nerka*, respectively, in response to above-optimum water temperatures.

The consequences of the stress response ultimately depend on whether the stressor initiating the response is acute (temporary) or chronic (long-term). Acute stressors may have positive effects on fish physiological function (e.g., stress-hardening; Schreck 2010), but chronic stressors are energetically costly to fishes and divert energy supplies away from growth and reproduction, and may ultimately result in mortality. For example, Gregory and Wood (1999) found that chronically elevated plasma cortisol concentrations decreased growth, appetite, and condition of Rainbow Trout. Similarly, Peterson and Small (2005) found elevated cortisol decreased growth in Channel Catfish *Ictalurus punctatus* because of inhibitory effects on insulin-like growth factor-I, an important growth-promoting hormone. Negative effects of stress on fish reproduction and survival were found by McConnachie et al. (2012), wherein elevated cortisol concentrations decreased egg output and longevity of Pink Salmon *O. gorbuscha*. The negative effects of stress on growth, reproduction, and survival may ultimately influence the distribution and abundance of fishes. For instance, Chadwick et al. (2015) found that the stress response initiated by above-optimum temperatures limited the distribution and abundance of Brook Trout. Chadwick et al. (2015) highlight how shifting population ranges associated with changing climate can be mechanistically explained by the neuroendocrine stress response in fishes.

Cardiorespiratory Responses

The fish cardiorespiratory system is responsible for the transport of oxygen from the environment to working tissues, thereby playing an essential role for key life functions (e.g., locomotion, digestion, and reproduction). The ability of the cardiorespiratory system to perform key life functions is determined by an individual's aerobic scope, which is defined as the difference between maximum metabolic rate

(MMR) and standard metabolic rate (SMR; Box 1; Figure 2; Pörtner and Farrell 2008; Farrell et al. 2009). Ectothermic fish metabolic and oxygen uptake rates are profoundly influenced by temperature (Fry 1947), which is reflected by the exponential increase in SMR with increasing temperature, and the rapid increase, plateau, and eventual decline of MMR with warming temperatures (Figure 2A). Each individual, population, and species thus has a temperature where aerobic scope is optimal (T_{opt} ; Jonsson and Jonsson 2009), a range of temperatures where specific aerobic activities (e.g., migration, digestion) are possible (i.e., the functional thermal tolerance window), and critical threshold temperatures where aerobic scope is zero and mortality is imminent (T_{crit} ; Box 1; Figure 2B). The general warming trend in freshwater ecosystems as well as the greater intensity and frequency of temperature extremes represent the primary climate-induced changes that affect cardiorespiratory systems in fish. Though brief exposure to temperatures approaching or exceeding an individual's upper or lower T_{crit} can result in immediate or delayed mortality, prolonged exposure to temperatures outside the functional thermal tolerance range can exert negative effects that are subtle and sublethal, such as impaired locomotion, growth, and reproduction (Farrell et al. 2008; Jonsson and Jonsson 2009). For example, in the Fraser River (British Columbia, Canada) temperatures during summer have increased by ~2°C since the 1950s (Patterson et al. 2007) and are projected to continue to increase along the same trajectory (Ferrari et al. 2007). These warm river temperatures have been repeatedly correlated with high mortality in adult Pacific salmon *Oncorhynchus* spp. migrating up the Fraser River (Farrell et al. 2008; Hinch et al. 2012) and at least some of this mortality has been attributed to insufficient aerobic scope to meet the energetic demands of upstream migration. Current peak river temperatures (>22°C) likely exceed the functional thermal tolerance for every Fraser River Sockeye Salmon population examined (Lee et al. 2003; Eliason et al. 2011, 2013). Because Pacific salmon are semelparous (Box 1), they have a single opportunity to reproduce and individuals that are unable to reach their spawning grounds will have zero reproductive success and, as such, these *en route* mortality events can have profound implications for salmonid populations.

Climate change results in a complex range of stressors beyond changes in temperature, which can act additively or synergistically to negatively impact cardiorespiratory

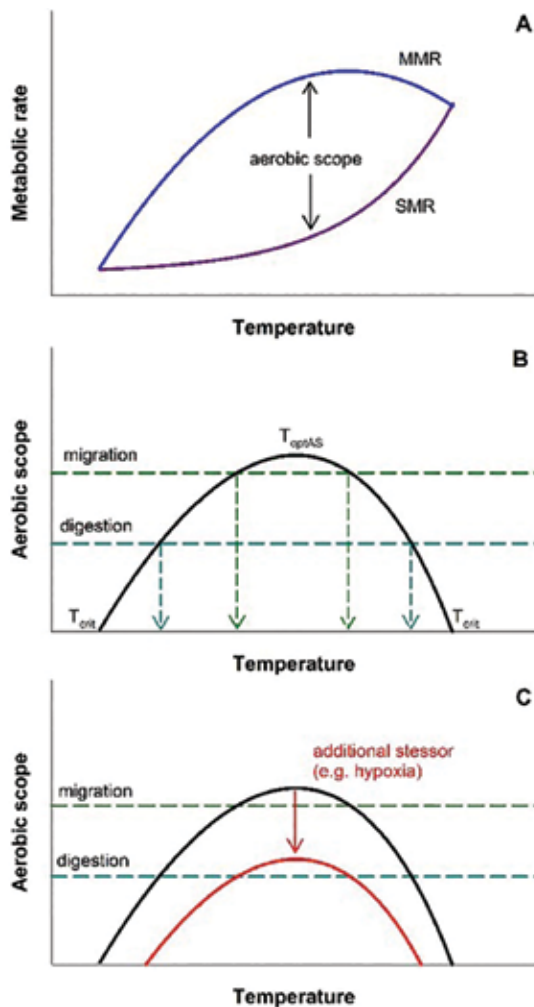


Figure 2. (A) Changes in maximum metabolic rate (MMR; blue) and standard metabolic rate (SMR; purple) with temperature (aerobic scope = MMR – SMR). (B) The aerobic scope curve is indicated in black, with the temperatures corresponding to maximal (T_{optAS}) and zero aerobic scope (T_{crit}) indicated. Some activities (migration) require more aerobic scope than others (digestion); thus, the temperature range for migration is narrower than that for digestion. (C) The decrease in aerobic scope with the addition of an environmental stressor (e.g., hypoxia); migration is no longer possible with the added stressor.

physiology. For example, hypoxia (Box 1) can interact with high temperatures to reduce aerobic scope and the functional thermal tolerance window (see Figure 2C; Pörtner and Farrell 2008; McBryan et al. 2013). In addition, toxicants, metal pollution (Jain et al. 1998; Sokolova and Lannig 2008), and disease (Wagner et al. 2005) impair metabolic rates and swimming performance. Metal exposure coupled with high temperatures can interact to cause a mismatch between oxygen supply and demand, decreasing thermal tolerance and increasing metal toxicity sensitivity (Sokolova and Lannig 2008). Although it is clear that climate change can interact with other anthropogenic stressors to impair aerobic scope, further research is needed to determine how interacting stressors decrease growth, reproduction, and survival (Box 2).

Immune Responses

The fish immune system defends against parasites and pathogens, and is composed of innate and acquired immune

responses (Box 1). These immune responses provide host defense against disease via the activity of proteins, enzymes, and cells located throughout the integument, serum, and gastrointestinal systems of fish (Ellis 2001). The acquired immune function of fish is typically greatest near species- or population-specific optimal temperatures (Dittmar et al. 2014), although innate immunity functions independently of temperature (Ellis 2001). Hence, the influence of climate change on fish immune systems primarily occurs when water temperatures shift beyond optimal temperatures (Bowden 2008). There is little information describing climate change effects on fish immune function in North America, but studies conducted elsewhere inform our understanding. In Germany, Dittmar et al. (2014) revealed an experimental heat wave, mimicking heat waves expected from climate change, compromised the immune system of Threespine Stickleback *Gasterosteus aculeatus*, a species whose native distribution also includes parts of North America. Immunocompetence presumably decreased because thermal stress generated a hyperactive immune response, resulting in damaged tissue and cellular debris that elicited an autoimmune disorder (Dittmar et al. 2014). Temperatures exceeding the optimum can also decrease immune function indirectly via effects on the neuroendocrine system, because immunosuppressive cortisol is released during thermal stress (Weyts et al. 1999). Either of these pathways (autoimmune disorder or immunosuppression) could explain the results of Collazos et al. (1996), who found negative effects of elevated summer temperatures on immunocompetence in Tench *Tinca tinca* when examining seasonal variation in immune function.

Environmental changes other than temperature arising from climate change (e.g., hypoxia; ultraviolet B [UVB] radiation) can also elicit immune responses in fish, resulting in single, additive, or synergistic changes in immune activity with climate-related temperature increases (Bowden 2008). For example, Jokinen et al. (2011) found that elevated temperature and UVB radiation additively decreased immune function in Atlantic Salmon *Salmo salar* juveniles. In contrast, Cramp et al. (2014) observed synergistic impacts of UVB radiation and temperature on disease susceptibility in Eastern Mosquitofish *Gambusia holbrooki*, wherein susceptibility increased when fish were exposed to elevated levels of the stressors in combination. Cramp et al. (2014) suggested that even two stressors can synergistically influence fish immune function, which is concerning for fish conservation given that more than two stressors are present in many aquatic environments (Staudt et al. 2013).

Climate-related alteration of immune function places fishes at greater susceptibility to parasites and pathogens that result in direct mortality to fishes. For instance, Wegner et al. (2008) observed high (>75%) parasite-induced mortality of Threespine Stickleback during a heat wave in Europe in 2003; in the same year, the bacterium *Vibrio anguillarum* caused substantial mortality in migrating adult Atlantic Salmon and Brown Trout *S. trutta* in England (St-Hilaire et al. 2005). Similarly, increasing mortality of Brown Trout over a 25-year warming period in Switzerland was partially explained by increased prevalence of proliferative kidney disease (Hari et al. 2006). Greater disease susceptibility can also result in sublethal negative effects on locomotion (Wagner et al. 2005), growth (Tierney et al. 1996), and reproduction (Rushbrook et al. 2007). These sublethal negative effects can also result in indirect mortality, because diseased fish are more susceptible to predation (Miller et al. 2014).

Climate change will result in interactions among fish immunocompetence and behavior with pathogen performance and emergence to produce feedback responses that could lead to decreases in fish survival, growth, and reproduction. For example, some infectious agents perform better at elevated temperatures (Macnab and Barber 2012) and/or in the drier conditions associated with climate change (Gagne and Blum 2015), exposing potentially immunocompromised fishes to increased prevalence of infectious agents. Further, certain parasites (e.g., *Schistocephalus solidus*) can alter host behavior so that they seek out warmer environments (Macnab and Barber 2012), simultaneously compromising immune function while optimizing parasite performance within the fish. Lastly, within waterbodies the emergence of novel diseases and the disappearance of others will occur as the ranges of pathogens, hosts, and/or vectors shift with changing climate, exposing fishes to infectious agents to which they are not adapted, or eliminating pathogens that were historically problematic (Marcos-López et al. 2010).

Iono- and Osmoregulatory Responses

Freshwater fish are hyperosmotic (Box 1) with respect to their environment and thus face the problem of continuous water uptake and loss of ions (e.g., Na⁺, Cl⁻, K⁺). To combat this environmental challenge, fish use their iono- and osmoregulatory systems to achieve water and salt balance. Water balance is accomplished behaviorally through reduced drinking rates (if at all) and physiologically by producing relatively large volumes of urine, and ion concentrations are regulated by the gills (uptake from surrounding environment) and in the gastrointestinal tract (uptake from food). Most freshwater fishes are stenohaline (Box 1) and are sensitive to changing environmental salinity (Peterson and Meador 1994) and as such are at risk from increased drought frequency and duration resulting from global climate change (Seager et al. 2007, 2013). Drought conditions result in elevated environmental salinity because of evapoconcentration (Mosley 2015), which oftentimes occurs in warmwater or intermittent streams but may be less frequent in coldwater or perennial systems (Datry et al. 2014). Because environmental salinity deviates from species-specific optimal salinity, maintenance of hydromineral balance via iono- and osmoregulatory mechanisms becomes increasingly expensive metabolically. These increased energetic costs associated with elevated environmental salinity decrease a fish's capacity for growth (Morgan and Iwama 1991), reproduction (Hoover et al. 2013), and movement. As environmental salinity increases further, iono- and osmoregulatory mechanisms fail and are no longer capable of maintaining proper osmolality (Box 1), disrupting cellular activity, and ultimately leading to mortality (Barlow 1958; Ostrand and Wilde 2001).

The linkages among climate change, multiyear drought, salinity, and osmoregulation can influence the distribution and abundance of fishes, with several examples from the southern Great Plains in the United States. For example, using historical fishery surveys collected before and after the Dust Bowl era (1930s), Higgins and Wilde (2005) demonstrated that long-term drought shaped prairie stream-fish assemblages through an increased prevalence of euryhaline (Box 1) fishes. Similarly, Miyazono et al. (2015) found abundance of stenohaline fishes in the Rio Grande River of Texas decreased from the 1970s to the 2010s, a result partially explained by a decreasing trend in heavy precipitation events that previously diluted salinity concentrations, thus resulting in increased salinity in the system.

Salinization of another Great Plains river (Pecos River) also resulted in the loss of stenohaline fishes (Hoagstrom 2009; Cheek and Taylor 2015). Similar patterns were found in the Blackwood River of southwestern Australia, where stream salinization contracted the ranges of stenohaline fishes (Beatty et al. 2011).

Diadromous and coastal freshwater fishes are also impacted by changing environmental salinities associated with climate change. For instance, inland coastal habitats are experiencing elevated and more variable salinity levels due to rising sea levels and decreased dilution of saltwater from lower freshwater outflows (Cloern and Jassby 2012). Similar to freshwater habitats affected by more prevalent drought, rising salinity in coastal habitats will disrupt the iono- and osmoregulation of coastal freshwater and diadromous fishes, resulting in reduced growth, reproduction, and survival. For example, the metabolic costs of osmoregulation in juvenile Shortnose Sturgeon *Acipenser brevirostrum* increased with rising salinity, resulting in the fastest growth at 0.0 ppt compared to 5, 10, or 20 ppt (Jarvis et al. 2001). Similarly, augmented salinity decreased the condition factor of Green Sturgeon *A. medirostris* because of increased energetic costs associated with osmoregulation, although the closely related White Sturgeon *A. transmontanus* was unaffected by elevated salinity (Vaz et al. 2015). Rising salinities will interact with changes in other environmental variables in coastal habitats (e.g., food availability; temperature), further influencing the hydromineral balance of coastal fishes (Vaz et al. 2015).

Reproductive Responses

The development of fish reproductive systems is controlled by the temperature-dependent reaction rates of the neuroendocrine hypothalamic–pituitary–gonadal axis (Pankhurst and Munday 2011; Miranda et al. 2013) and thus temperature influences all aspects of fish reproduction. Given the thermal control of fish reproductive systems, alterations in temperature under a changing climate have implications for individual reproductive success. Previous work on the complex interaction between reproductive physiology and temperature-dependent processes suggests four critical areas to consider in a changing climate: (1) cues to commence gamete development and progression, (2) energy allocation for gamete investment, (3) fertilization, and (4) larval hatching and survival (Pankhurst and Munday 2011). First, photothermal cues stimulate the onset of gamete development in both spring and fall spawning fish; the spawning seasons occur within a photoperiod window, but commencement of spawning is controlled by species-specific water temperature thresholds (Bradshaw and Holzapfel 2007). Changing water temperatures proximally altered the onset, progression, and conclusion of reproductive maturation stages in Striped Bass *Morone saxatilis* (Clark et al. 2005). Second, allocation of energy to gametes is controlled by aerobic scope, which, if decreased by climate change as described above, could lead to trade-offs that result in reduced reproductive investment. In Atlantic Salmon, elevated temperature during gametogenesis hindered gonadal steroid synthesis, vitellogenin production, and estrogen receptor dynamics, thus reducing female gonadal investment and gamete viability (reviewed by Pankhurst and King 2010). Third, temperature influences fertilization success, with recent studies outside of North America demonstrating that warmer than optimal temperatures can reduce the percentage of eggs that are externally fertilized by European Whitefish *Coregonus lavaretus* (Cingi et al.

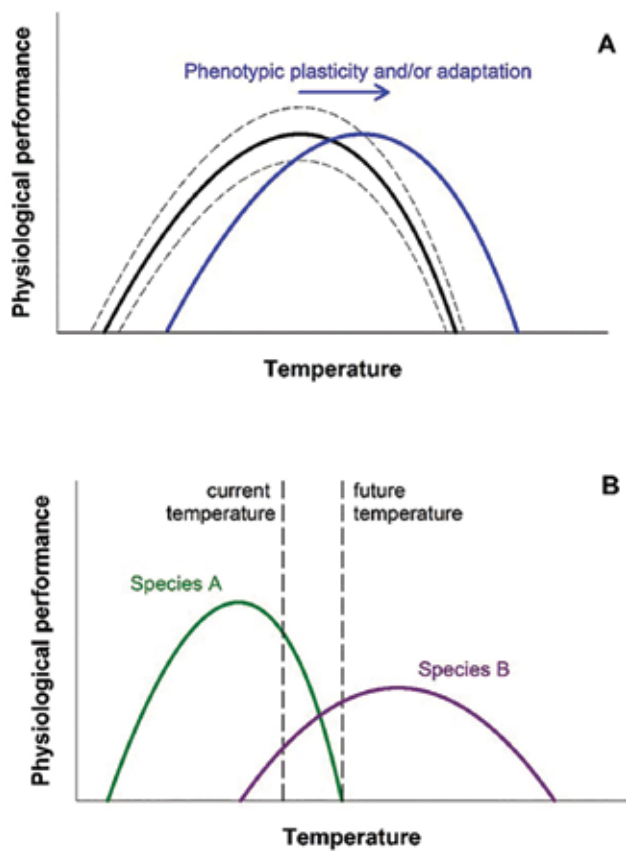


Figure 3. (A) Mean physiological performance (black line) and associated estimate of individual variability (dashed lines) for a hypothetical fish population. The population may be able to respond to elevated temperatures through phenotypic plasticity and/or evolutionary adaptation to right-shift their reaction norm and increase their functional thermal tolerance. (B) Under current climate conditions, species A encounters near-optimal temperatures, whereas species B is operating at the limits of its functional thermal tolerance. Under a warming future scenario, physiological performance (e.g., aerobic scope) collapses to zero for species A, leading to extirpation, whereas species B may thrive under the new conditions.

2010) or Threespine Stickleback (Mehlis and Bakker 2014). Lastly, changing temperatures may influence hatching success and larval survival. For instance, hatching rates for Mountain Whitefish *Prosopium williamsoni* exceeded 90% when temperatures ranged 5°C–8°C (normal range) but declined to 38% when temperatures were 10°C (Brinkman et al. 2013), and Whitney et al. (2013) found that Sockeye Salmon embryonic survival decreased with elevated temperatures. Given that fish eggs and larvae generally have the lowest thermal tolerance of any life stage in a species (Rombough 1997), elevated temperatures resulting from global climate change could result in population bottlenecks from lowered survival and recruitment (Pankhurst and Munday 2011). The mechanistic explanation of elevated temperatures decreasing larval hatching and survival is likely related to pathways discussed above (i.e., collapse of aerobic scope; lowered immune function), but unique pathways associated with reproductive behavior could also explain these patterns. For instance, if climate-induced temperature changes alter reproductive timing such that larval emergence is no longer synchronous with periods of maximum food availability, increases in larval starvation may result (i.e., match/mismatch hypothesis; Cushing 1990). Furthermore, an experiment

involving Threespine Stickleback revealed that warmer temperatures caused males to “fan” fertilized eggs with more intensity to keep them oxygenated, which led to higher mortality for the parent, with the resulting lack of parental care leading to lower embryonic survival (Hopkins et al. 2011).

Although temperature strongly influences the reproductive system and ultimately reproductive success, other environmental variables influenced by climate change can be important. For example, if climate-altered timing and intensity of precipitation events change discharge patterns in rivers, these changes can influence egg production (i.e., higher gonadosomatic indices in higher discharge years for cyprinids in Texas; Munz and Higgins 2013), nest building (i.e., changes in nest structure, building behavior, and gene expression for Threespine Stickleback in response to higher discharge; Rushbrook et al. 2010; Seear et al. 2014), and larval survival (i.e., lower survival of fall-spawning salmonid larvae in New York in years with greater winter and spring discharge; Warren et al. 2009). Salinity in freshwater ecosystems is another variable that is influenced by a changing climate, and Hoover et al. (2013) reported significant reductions in fecundity, fertilization success, and parental care with increasing salinity in experiments with Fathead Minnows *Pimephales promelas* in Canada. Finally, should hypoxic conditions increase in prevalence with elevated temperatures or drought intensity, the egg stage is most vulnerable to hypoxia-induced mortality relative to later life history stages among freshwater fishes (Elshout et al. 2013).

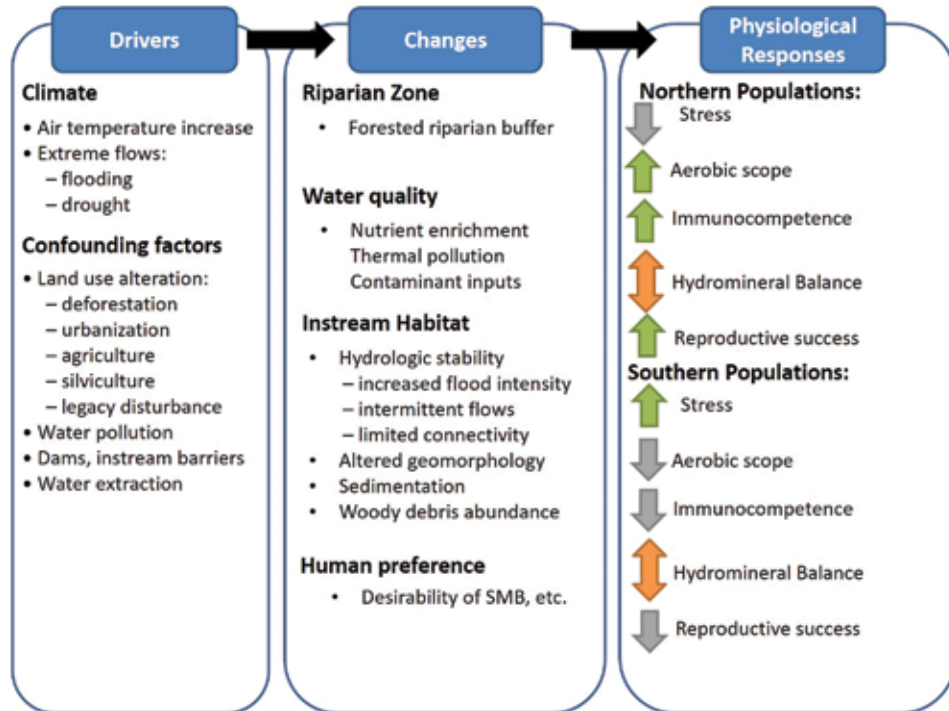
Intra- and Interspecific Variation in Climate Response

The influence of climate change on fish physiology will vary among species according to their exposure, sensitivity, and resilience to climate change (Williams et al. 2008; Comte et al. 2014). Exposure describes the degree that climate change will alter environmental conditions in a species’ habitat; if the multidimensional niche of a species undergoes minimal environmental changes, limited impacts on a species’ physiology should occur. The sensitivity of a species’ physiology to climate change is defined by the range of conditions a species can tolerate, with some species (e.g., eurythermal; euryhaline) naturally less sensitive to climate-induced environmental changes than other species (e.g., stenothermal; stenohaline). A species’ resilience to climate change is their ability to avoid climate-induced environmental change via range shifts, altered phenology, behavior (e.g., seek thermal refugia), phenotypic plasticity, and adaptive microevolution (Figure 3A; Box 1; Lynch et al., this issue). Species that are highly mobile or have labile life history strategies may be able to track their preferred habitat or locate refuge habitats, if present, under a changing climate (i.e., niche tracking; La Sorte and Jetz 2012), whereas more specialized species may be unable to do so. Unfortunately, species or population resilience to climate change is poorly known (Box 2). Furthermore, the potential for phenotypic plasticity varies widely across species and may be minimal (Brook Trout) or dramatic (Sheepshead Minnow *Cyprinodon variegatus*; see Beitinger and Bennett 2000 for a 21-species comparison of thermal tolerance plasticity). The interaction among exposure, sensitivity, and resilience may result in positive effects (i.e., environmental conditions better-suited to their physiology) of climate change on some species’ physiology while having negative effects on others, creating “winners” and “losers” under a changing climate (Figure 3B; Somero 2010).

The effects of climate change on fish physiology will also vary among individuals and populations within a species

Box 3: Effects of Climate Change and Other Anthropogenic Stressors on Smallmouth Bass *Micropterus dolomieu* Physiology

Effects are dictated by the geographic position of a population in the species' overall range, as northern populations may experience increasing frequency of environmental conditions more suitable to their physiology, whereas physiologically inhospitable conditions become more prevalent for southern populations. Green arrows indicated an increased response, gray arrows indicated a decreased response, and orange double arrows indicate that responses vary. This variation may occur among or within populations and watersheds.



because of extrinsic differences arising from geography, as well as from intrinsic differences resulting from age and sex (Seebacher et al. 2012; Stitt et al. 2014). The extrinsic effects of climate change on fish physiology varies according to a population's position within the species' overall range (Box 3); populations near the colder upper latitudinal or elevational limits may expand their ranges poleward or upslope as warming results in thermal conditions becoming more suitable for their physiology, whereas populations residing in the warmer lower latitudes and elevations may contract their ranges as normal physiological function may no longer be feasible or possible in the novel climate (Hampe and Petit 2005; Thomas 2010). Physiology also varies intrinsically with age-dependent (Beer and Anderson 2011; Lawrence et al. 2015) and sex-dependent (Cooke 2004) factors, but few studies have elucidated how species-specific age-classes or sexes are differentially sensitive to climate change (Box 2). Finally, responses of fish physiology to climate change will vary because of individual- and population-specific physiological tolerances; individuals and populations residing in warmer or more variable environments may possess traits with greater resilience to a changing climate. For example, Eliason et al. (2011) determined that Sockeye Salmon populations with warmer migrations had higher functional thermal tolerance compared to populations with colder migrations (Box 4), and Whitney et al. (2013) found that Sockeye Salmon embryos from populations historically exposed to warmer incubation temperatures exhibited higher survival

under elevated temperatures. Lastly, Dittmar et al. (2014) found that Threespine Stickleback collected from a warmer pond had a higher optimum temperature for immune function compared to individuals collected from a cooler stream. Although rare, studies such as these that provide information concerning intraspecific vulnerability to climate change are particularly valuable for conservation and management because they provide the information necessary to identify populations in need of protection.

Implications for Management and Conservation

Physiological knowledge, concepts, and tools are increasingly being applied to identify mechanisms that underlie conservation and management problems and to guide mitigation activities in response to a changing climate or other anthropogenic stressors (i.e., conservation physiology; Box 1; Cooke et al. 2013; Paukert et al., this issue). For instance, understanding fish physiology can help define remediation strategies that could make habitats physiologically suitable in a changing climate (Cooke and Suski 2008). Furthermore, physiological information can be used to identify appropriate source populations to be used in managed translocations (Olden et al. 2011) and select suitable habitats for receiving translocated populations or species (Dunham et al. 2011), although this management strategy remains controversial and could result in unintended negative consequences (Ricciardi and Simberloff 2009). Physiological understanding can also

be used in nonnative control efforts by identifying species with physiologies most likely to promote expansion under novel climatic conditions, which could then be proactively targeted for control efforts to prevent their eventual spread (Lawrence et al. 2014, 2015). Lastly, knowledge of the physiological factors that influence fish survival in catch-and-release (Arlinghaus and Cooke 2009) or commercial fishing (Raby et al. 2011) can be used to instigate fisheries closures during heat waves associated with climate change (Box 4) or incorporated into best handling practices (and associated education and outreach materials) and fishing regulations. These measures may help ensure that anglers modify their behavior during climate extremes such that released fishes are likely to survive (Hunt et al., this issue). Physiological knowledge required to adapt management strategies is complex and requires several important pieces of information for each population or species (Somero 2010; Munday 2015), including the following:

- Physiological tolerance to climate-altered environmental stressors.
- Interactive effects of multiple climate and anthropogenic stressors on physiological tolerance.
- Acclimatization capacity of physiological tolerance.
- Potential for evolutionary adaptation of physiological tolerance and phenology.

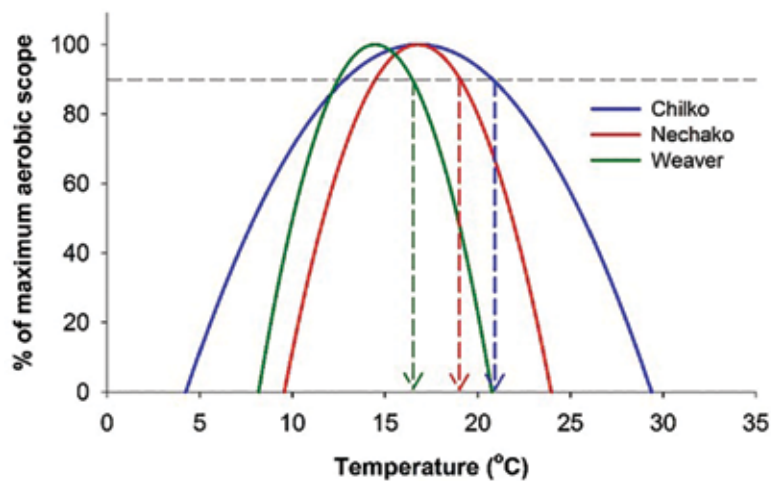
Unfortunately, this information is rarely available for many species, let alone for a given population (Box 2).

CONCLUSION

Global climate change is affecting the physiology of freshwater and diadromous fishes. Climate-related deviations from optimal temperatures are directly influencing fish neuroendocrine function, cardiorespiratory performance, immunocompetence, and reproduction, and climate-induced increases in salinity compromise osmoregulation and reproduction. These climate-induced alterations to fish physiology have concomitant effects on growth and survival, which manifest as higher-order changes in populations and assemblages. Although our understanding of the pathways in which climate change influences fish physiology has increased, it still remains incomplete (Box 2). For example, there is a dearth of physiological information available for North American fishes, because the majority of information concerning the effects of climate change on fish physiology comes from a small number of facultative anadromous species from a subset of families (e.g., Salmonidae, Acipenseridae, and Gasterosteidae) that is likely unrepresentative of freshwater fish diversity. Further, although multistressor environments are the rule in the daily experience of freshwater fishes (Dudgeon et al. 2006), they are the exception in studies examining fish

Box 4: Case Study of How Physiology Is Being Used by Management

The functional thermal tolerance has been determined for seven populations of Sockeye Salmon *Oncorhynchus nerka* in the Fraser River watershed in British Columbia, Canada (Lee et al. 2003; Eliason et al. 2011, 2013). Managers from the Pacific Salmon Commission and Fisheries and Oceans Canada closely monitor river temperatures during the summer and fall months as adult salmon are migrating upstream to their spawning grounds. If temperatures are forecasted to exceed the optimal thermal tolerance of the population, they adjust their escapement predictions and alter commercial and recreational fishing opportunities.



Percentage of maximum aerobic scope (i.e., the functional thermal tolerance) is shown for Chilko, Nechako, and Weaver Sockeye Salmon populations. The dashed line indicates the amount of aerobic scope that is likely required for successful upriver migration. Temperatures exceeding 20.7°C, 19.0°C, and 16.4°C (for Chilko, Nechako, and Weaver populations, respectively) could prevent successful upriver migration. Data are from Eliason et al. (2011). See Eliason et al. (2011) for a map of population spawning locations.

physiological response to changing climate. Quantifying impacts and assigning causality of multiple stressors on fish physiology is a daunting task, but it is one that must be completed if we are to effectively understand, manage, and conserve fishes as the climate changes. This task will be difficult, but we are hopeful that the information synthesized in this review will help guide the way toward accomplishing it.

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Climate Change Effects on North American Inland Fish Populations and Assemblages

Abigail J. Lynch

U. S. Geological Survey (USGS), National Climate Change and Wildlife Science Center, 12201 Sunrise Valley Drive, MS-516, Reston, VA 20192. E-mail: ajlynch@usgs.gov

Bonnie J. E. Myers

USGS, National Climate Change and Wildlife Science Center, Reston, VA

Cindy Chu

Ontario Ministry of Natural Resources and Forestry, Aquatic Research and Monitoring Section, Peterborough, ON, Canada

Lisa A. Eby

Wildlife Biology Program, College of Forestry and Conservation, University of Montana, Missoula, MT

Jeffrey A. Falke

USGS, Alaska Cooperative Fish and Wildlife Research Unit, University of Alaska Fairbanks, Fairbanks, AK

Ryan P. Kovach

USGS, Northern Rocky Mountain Science Center, Glacier National Park, West Glacier, MT

Trevor J. Krabbenhoft

Department of Biological Sciences, Wayne State University, Detroit, MI

Thomas J. Kwak

USGS, North Carolina Cooperative Fish and Wildlife Research Unit, North Carolina State University, Raleigh, NC

John Lyons

Wisconsin Department of Natural Resources, Fish and Aquatic Research Section, Madison, WI

Craig P. Paukert

USGS, Missouri Cooperative Fish and Wildlife Research Unit, University of Missouri, Columbia, MO

James E. Whitney*

Missouri Cooperative Fish and Wildlife Research Unit, Department of Fisheries and Wildlife Sciences, University of Missouri, Columbia, MO

*Present address for James E. Whitney: Department of Biology, Pittsburg State University, Pittsburg, Kansas

The third through seventh coauthors are working group members listed alphabetically by last name. The final two coauthors are workshop organizers.



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.

Efectos del cambio climático en poblaciones y ensamblajes de peces en aguas continentales de Norte América

El clima es un factor forzante clave para muchas poblaciones y ensamblajes de peces y de comunidades acuáticas. Sin embargo, son pocos los estudios observacionales acerca de los impactos del cambio climático en los peces de aguas continentales en Norte América. En esta síntesis (1) se resumen las tendencias climáticas que pueden influir en las poblaciones y ensamblajes de peces de aguas continentales en Norte América, (2) se compilan 31 trabajos arbitrados que documentan los efectos del cambio climático sobre las poblaciones y ensamblajes de peces de aguas continentales en Norte América y (3) se comentan cuatro casos de estudio que representan una variedad de respuestas observadas que van desde los sistemas de aguas cálidas en el suroeste y sureste de Los EE.UU., hasta los sistemas de aguas frías a lo largo de la costa del Pacífico y del escudo canadiense. Finalmente, se identifican huecos de información clave y necesidades de investigación tendientes a proporcionar información para diseñar enfoques ecosistémicos con el fin de manejar a los peces y a las pesquerías de aguas continentales en Norte América de cara a un clima cambiante.

Effets du changement climatique sur les populations et les communautés de poissons continentaux d'Amérique du Nord

Le climat est un facteur critique pour de nombreuses populations de poissons, bancs et communautés aquatiques. Cependant, les études d'observation directe des impacts des changements climatiques sur les poissons continentaux d'Amérique du Nord sont rares. Dans cette synthèse, nous (1) résumons les tendances climatiques qui peuvent influencer les populations et communautés de poissons continentaux d'Amérique du Nord, (2) compilons 31 études examinées par des pairs sur les effets documentés du changement climatique sur les populations et communautés de poissons continentaux d'Amérique du Nord, et (3) mettons l'accent sur quatre études de cas représentant une variété de réponses observées allant des systèmes d'eaux chaudes dans le sud-ouest et sud-est des États-Unis aux systèmes d'eau froide le long de la côte du Pacifique et du Bouclier canadien. Nous concluons en identifiant les lacunes en matière de données clés et les besoins de recherche pour informer sur les approches fondées sur les écosystèmes adaptatifs à la gestion des pêches et des poissons continentaux d'Amérique du Nord face au changement climatique.

KEY POINTS

- Climate change is altering abundance, growth, and recruitment of some North American inland fishes, with particularly strong effects noted on coldwater species.
- Evidence of evolutionary responses to climate change is currently limited but includes earlier migration timing and hybridization in some coldwater species.
- Shifts in species' ranges are changing the structure of some North American fish assemblages, resulting in novel species interactions, such as altered predator–prey dynamics.
- Complex interactions between climate change and other anthropogenic stressors make separating and understanding the relative magnitude of climate effects challenging.
- To sustainably manage North American inland fishes in the face of climate change, research should move beyond distributional studies, ground-truth projected impacts, increase geographic and taxonomic representation, document sources of resilience, implement monitoring frameworks to document changes in assemblage dynamics, and provide better decision-support tools.

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

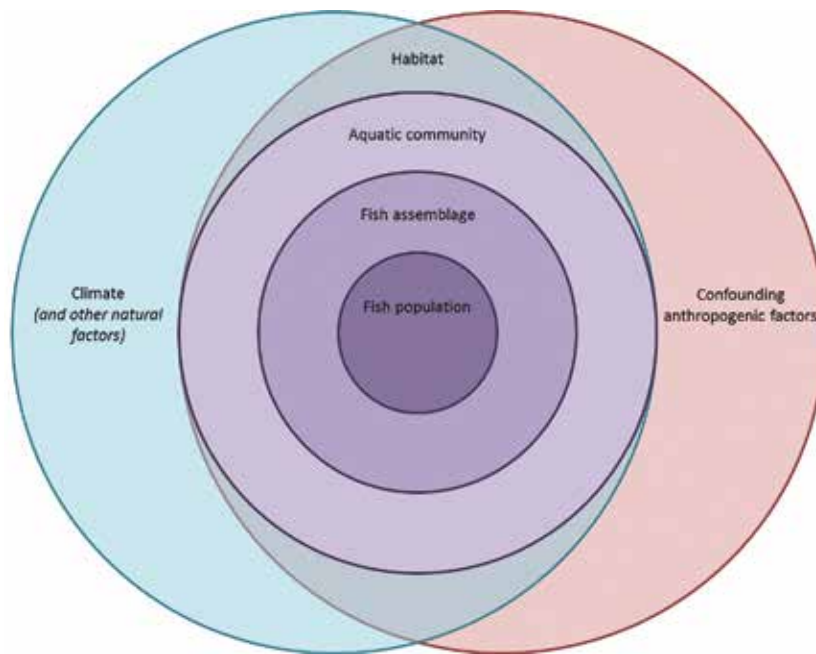


Figure 1. Conceptual model of the impacts of climate change and confounding anthropogenic factors on fish populations, assemblages, and aquatic communities. Climate and confounding factors may be, but are not necessarily, equally influential on fish populations, assemblages, and aquatic communities.

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.

2009; Schneider and Hook 2010), 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). Broad-scale warming trends in lake epilimnetic 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; Boehrer 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 (Kaushal 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; Alofs 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 spring 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 1. Documented climate change effects on North American inland fish populations and assemblages.

Map Data Point	Response	Driver (climate/habitat)	Geographic area and habitat	Response (species or biological variable)	Response (type, direction)	Response level	Reference
1	Assemblage composition change	Warmer air temperatures	Ontario watersheds (n = 137)	Species richness	Increase in species richness	Assemblage	Minns and Moore (1995)
2	Demographic change (growth/biomass)	Warmer water temperatures	Auke Lake, Alaska	Sockeye Salmon, Coho Salmon	Greater size and biomass of Sockeye Salmon smolts	Species	Kovach et al. (2014)
3	Demographic change (recruitment)	Greater flow variability	Washington rivers (n = 21)	Chinook Salmon	Declines in recruitment	Species	Ward et al. (2015)
4	Demographic change (abundance)	Warmer air temperatures	Kawartha Lake, Ontario	Walleye, black basses	Walleye abundance declined, black basses increased	Species	Robillard and Fox (2006)
5	Demographic change (abundance)	Warmer summers, longer growing season	Minnesota lakes (n = 634)	Cisco	Declines in abundance	Species	Jacobson et al. (2012)
6	Demographic change (growth)	Warmer water temperatures, earlier spring	Wood River, Alaska	Sockeye Salmon	Increased zooplankton densities, increased growth of juveniles	Species	Schindler et al. (2005)
7	Demographic change (growth)	Warmer summer temperatures	Nepihjee River, Lake Gamutissait, and Lake Tasiapiik, Québec	Arctic Charr	Growth decreased in one lake	Species	Murdock and Power (2013)
8	Demographic change (population size/survival)	Warmer stream temperatures, lower flows	Massachusetts streams (n = 4)	Brook Trout	Reduced recruitment and population sizes	Species	Bassar et al. (2016)
9	Distributional shift	Warmer air temperatures, less ice cover	Ontario lakes (n = 1,527)	13 game and non-game species	6 gamefishes expanded their range northward, 5 of 7 non-gamefishes had range contractions	Assemblage	Alofs et al. (2014)
10	Distributional shift	Warmer ocean and river conditions in summer	Northwest Territories	Sockeye Salmon, Pink Salmon, Coho Salmon, Chum Salmon	Range expanded northward	Species	Babaluk et al. (2000)
11	Distributional shift	Warmer air and water temperatures	Great Lakes	White Perch	Range expanded in Great Lakes	Species	Johnson and Evans (1990)
12	Distributional shift	Warmer water temperatures	East Fork Bitterroot River, Montana	Bull Trout	Greater site abandonment and shifts in local distributions	Species	Eby et al. (2014)
13	Evolutionary changes (migration timing)	Earlier/warmer spring/summer	Auke Creek, Alaska	Pink Salmon	Natural selection for earlier adult migration	Species	Kovach et al. (2012)
14	Evolutionary changes (migration timing)	Earlier/warmer spring/summer	Columbia River and Snake River, Washington/Oregon	Sockeye Salmon	Natural selection for earlier adult migration	Species	Crozier et al. (2011)
15	Hybridization and Distributional shift	Warmer spring/summer temperatures	Flathead River drainage, Montana	Rainbow Trout, Westslope Cutthroat Trout	Rainbow Trout expanded upstream; greater hybridization	Species	Muhlfeld et al. (2014)
16	Phenological shift	Warmer water temperatures	Auke Creek and Auke Lake, Alaska	Dolly Varden, Pacific salmon	Earlier migrations by all species	Assemblage	Sergeant et al. (2015)
17	Phenological shift	Earlier/warmer spring/summer	Southeastern Alaska streams (n = 21)	Pacific salmon	Sockeye Salmon generally migrated later, Coho, Pink, and Chum salmon migrated earlier	Species	Kovach et al. (2015)
18	Phenological shift	Earlier/warmer spring/summer	Auke Creek, Alaska	5 salmonid species; 14 life histories	Generally earlier fry/juvenile and adult migrations	Species	Kovach et al. (2013)
19	Phenological mismatch	Earlier spring, less snow, lower summer flows	Rio Grande River, New Mexico	8 cyprinid, catosomid, and poeciliid species	Earlier spawning and egg hatching; lentic species increased	Assemblage	Krabbenhoft et al. (2014)
20	Phenological shift	Earlier/warmer spring/summer	Southern New England streams (n = 6)	Alewife	Earlier spawning migrations	Species	Ellis and Vokoun (2009)
21	Phenological shift	Earlier/warmer spring/summer	Columbia River, Washington/Oregon	American Shad	Earlier spawning migrations	Species	Quinn and Adams (1996)

Table 1. (Continued) Documented climate change effects on North American inland fish populations and assemblages.

Map Data Point	Response	Driver (climate/habitat)	Geographic area and habitat	Response (species or biological variable)	Response (type, direction)	Response level	Reference
22	Phenological shift	Earlier/warmer spring/summer	Connecticut, Maine, New Brunswick, Newfoundland rivers (n = 4)	Atlantic Salmon	Earlier spawning migrations	Species	Juanes et al. (2004)
23	Phenological shift	Earlier/warmer spring/summer	European and North American rivers (n = 67 and 16, respectively)	Atlantic Salmon	Earlier smolt outmigration	Species	Otero et al. (2014)
24	Phenological shift	Earlier/warmer spring/summer	European and North American rivers (n = 31)	Atlantic Salmon	Earlier smolt outmigration, reduced marine survival	Species	Russell et al. (2012)
25	Phenological shift	Earlier/warmer spring/summer	Auke Creek, Alaska	Pink Salmon	Earlier fry and adult migrations	Species	Taylor (2008); Kovach et al. (2013)
26	Phenological shift	Earlier/warmer spring/summer	Columbia River, Washington/Orgeon	Sockeye Salmon	Earlier spawning migrations	Species	Quinn and Adams (1996)
27	Phenological shift	Earlier/warmer spring/summer	Fraser River, British Columbia	Sockeye Salmon	Earlier spawning migrations	Species	Cooke et al. (2004)
28	Phenological shift	Earlier/warmer spring/summer	Potomac River and upper Chesapeake Bay, Maryland/Virginia	Striped Bass	Earlier spawning migrations	Species	Peer and Miller (2014)
29	Phenological shift	Earlier/warmer spring/summer	Minnesota lakes (n = 12)	Walleye	Earlier spawning in one-third of lakes	Species	Schneider et al. (2010)
30	Phenological shift	Earlier spring	Lakes Michigan and Superior	Yellow Perch, Lake Trout	Yellow Perch spawned earlier; no change for Lake Trout	Species	Lyons et al. (2015)
31	Demographic change	Shorter, warmer winters	Lake Erie	Yellow Perch	No shift in spawning time, reduced recruitment	Species	Farmer et al. (2015)

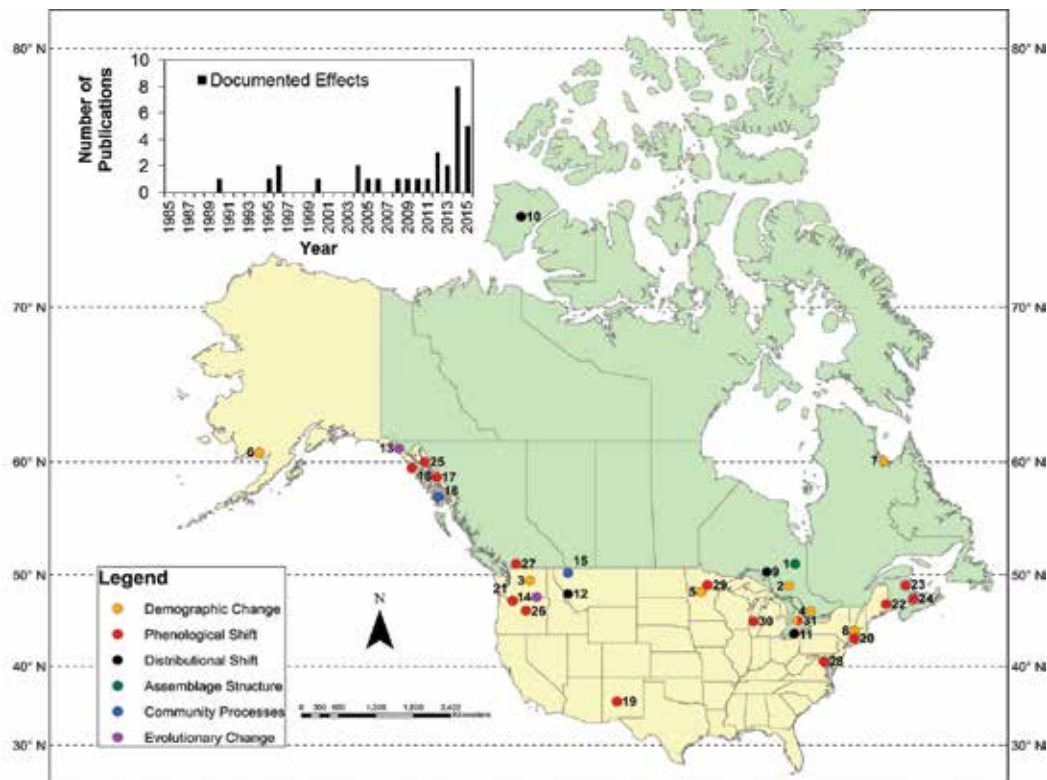


Figure 2. Documented impacts of climate change on inland fishes of Canada (green background) and the United States (tan background) based on a 2015 literature review of 772 peer-reviewed publications (1985–2015). Each circle represents an individual fish species or assemblage response type (i.e., demographic 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 artedii*, 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 (Muhlfeld 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 (Cahill 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).



Figure 3. Sockeye Salmon *Oncorhynchus nerka* migrations are shifting with climate change, though not always in ways that would be expected. Photo credit: Jonny Armstrong, Oregon State University.

Pacific salmon populations: diverse responses to climate change

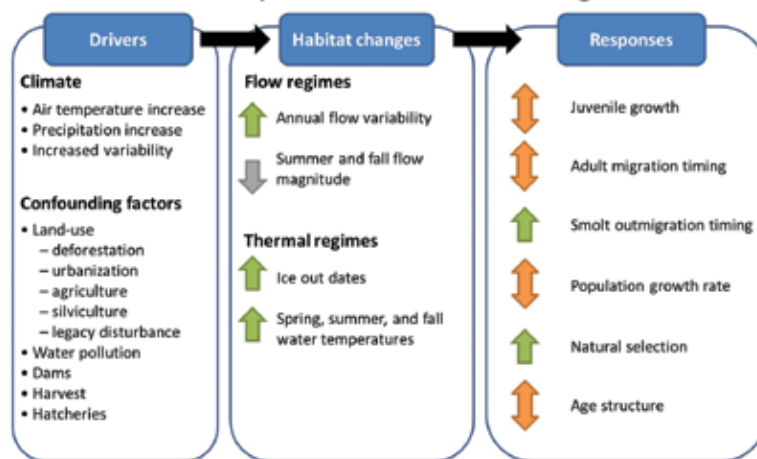


Figure 4. Documented responses of Pacific salmon to climate change. Green arrows indicate an increase or earlier seasonal response, gray arrows indicate a decrease or later seasonal response, and orange double arrows indicate that responses vary and studies have documented increases, decreases, and/or no change. This variation may occur among or within species and watersheds.

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



Figure 5. Smallmouth Bass *Micropterus dolomieu* are finding that Ontario's inland lakes more habitable with climate change. Photo credit: Gretchen J. A. Hansen, Minnesota Department of Natural Resources.

Nonnative Smallmouth Bass range expansion in Ontario's inland lakes

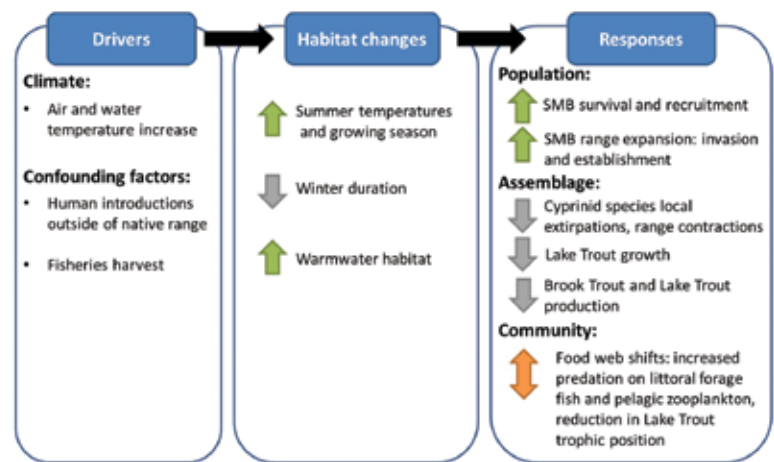


Figure 6. Documented consequences of the northward expansion of nonnative Smallmouth Bass *Micropterus dolomieu* in Ontario's inland lakes facilitated by climate change. All symbols as shown in Figure 4.

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 Coonrod 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 Coonrod 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).



Figure 7. Climate change and flow regulation often leave species in the Rio Grande high and dry. Photo credit: Thomas Turner, University of New Mexico.

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

Effects of climate change and alteration of natural flow regimes on Rio Grande fish

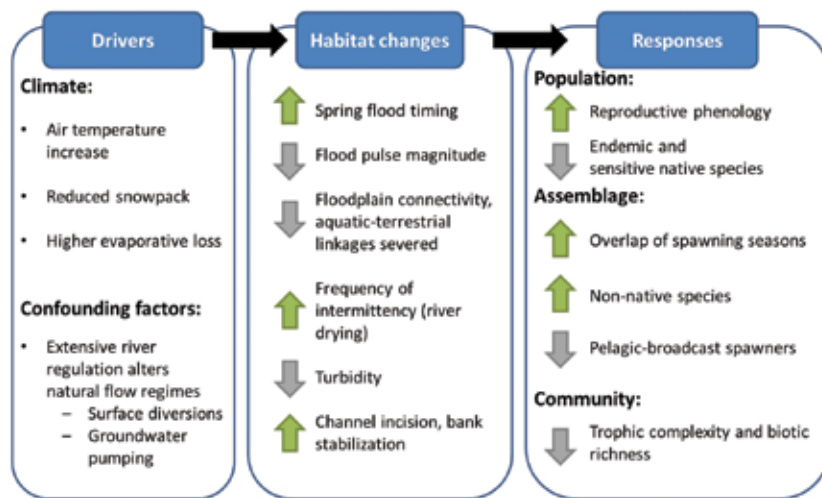


Figure 8. Documented effects of climate change and hydrologic alteration on Rio Grande fishes. All symbols as shown in Figure 4.

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.



Figure 9. Streams and rivers of the southeastern United States support diverse fish assemblages and valuable recreational fisheries, but the environment and biota are changing with land use alterations, water pollution, dams and instream barriers, and water extraction, as well as climate change. Photo credit: Tom Kwak, USGS, NC Cooperative Fish and Wildlife Research Unit.

SE US stream fish assemblages: complex interactions of stressors

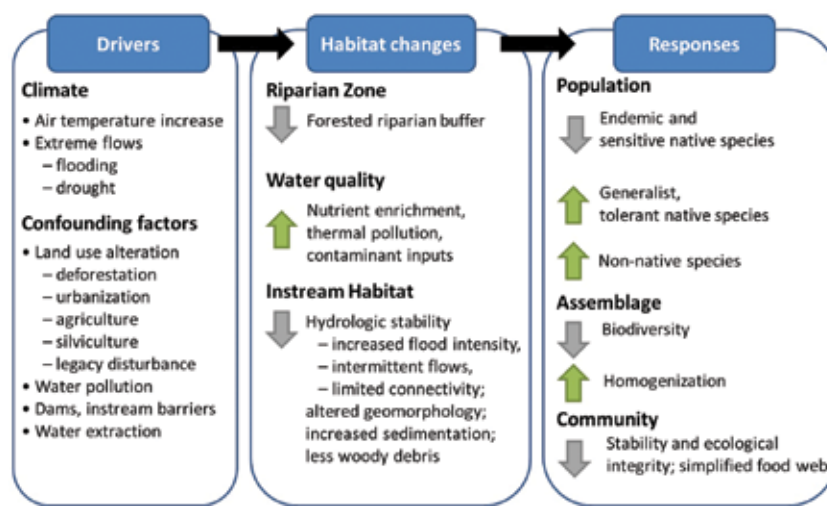


Figure 10. Impacts of climate change on stream assemblages in the southeastern United States are highly confounded by complex interactions with other stressors. All symbols as shown in Figure 4.

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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Identifying Alternate Pathways for Climate Change to Impact Inland Recreational Fishers



Len M. Hunt

Ontario Ministry of Natural Resources and Forestry, Centre for Northern Forest Ecosystem Research, 955 Oliver Road, Thunder Bay, Ontario, P7B 5E1, Canada. E-mail: len.hunt@ontario.ca

Eli P. Fenichel

Yale University, School of Forestry & Environmental Studies, New Haven, CT

David C. Fulton

Minnesota Cooperative Fish and Wildlife Research Unit, Hodson Hall, University of Minnesota, Department of Fish and Wildlife, St. Paul, MN

Robert Mendelsohn

Yale University, School of Forestry & Environmental Studies, New Haven, CT

Jordan W. Smith

Utah State University, Institute of Outdoor Recreation and Tourism and Department of Environment and Society, Logan, UT

Tyler D. Tunney

Center for Limnology, University of Wisconsin–Madison, Madison, WI

Abigail J. Lynch

U.S. Geological Survey (USGS), National Climate Change and Wildlife Science Center, Reston, VA

Craig P. Paukert

USGS, Missouri Cooperative Fish and Wildlife Research Unit, University of Missouri, Columbia, MO

James E. Whitney*

Missouri Cooperative Fish and Wildlife Research Unit, Department of Fisheries and Wildlife Sciences, University of Missouri, Columbia, MO

The fourth through sixth coauthors are listed alphabetically by last name. The final three coauthors are workshop organizers.

*Present address for James E. Whitney: Department of Biology, Pittsburg State University, Pittsburg, KS

Fisheries and human dimensions literature suggests that climate change influences inland recreational fishers in North America through three major pathways. The most widely recognized pathway suggests that climate change impacts habitat and fish populations (e.g., water temperature impacting fish survival) and cascades to impact fishers. Climate change also impacts recreational fishers by influencing environmental conditions that directly affect fishers (e.g., increased temperatures in northern climates resulting in extended open water fishing seasons and increased fishing effort). The final pathway occurs from climate change mitigation and adaptation efforts (e.g., refined energy policies result in higher fuel costs, making distant trips more expensive). To address limitations of past research (e.g., assessing climate change impacts for only one pathway at a time and not accounting for climate variability, extreme weather events, or heterogeneity among fishers), we encourage researchers to refocus their efforts to understand and document climate change impacts to inland fishers.

Identificación de vías alternas de impacto del cambio climático en pescadores de pesca recreativa en aguas continentales

La literatura sobre las dimensiones humana y de las pesquerías sugieren que el cambio climático influencia a los pescadores recreativos en aguas continentales de Norte América de tres formas principales. La forma más ampliamente reconocida es que el cambio climático impacta a las poblaciones de peces y a su hábitat (e.g. la temperatura del agua impacta la supervivencia de los peces) y se transfiere hasta eventualmente afectar a los pescadores. El cambio climático también puede alterar las condiciones ambientales que directamente impactan a los pescadores recreativos (e.g. incremento de temperatura en climas norteros que resultan en una prolongación de las temporadas de pesca y en un aumento en el esfuerzo de pesca). La tercera forma de impacto proviene de los esfuerzos de adaptación y mitigación al cambio climático (e.g. el refinamiento de políticas energéticas se ve reflejado en un aumento en el costo de los combustibles, encareciendo los viajes de pesca). Con el fin de superar las limitaciones de trabajos en el pasado (e.g. evaluar los impactos del cambio climático para una sola vía por vez y no tomar en cuenta la variabilidad climática, eventos meteorológicos extremos o heterogeneidad entre pescadores) en este estudio se invita a los investigadores a enfocar sus esfuerzos para comprender y documentar los impactos del cambio climático en los pescadores de aguas continentales.

Identification of voies alternatives sur l'impact du changement climatique sur les pêcheurs sportifs continentaux

Les pêches et la littérature à dimension humaine suggèrent que le changement climatique influence les pêcheurs sportifs en Amérique du Nord par le biais de trois voies principales. La voie la plus largement reconnue suggère que le changement climatique a un impact sur l'habitat et la population de poissons (par exemple, la température de l'eau ayant une incidence sur la survie des poissons), lequel se répercute sur les pêcheurs. Le changement climatique a également un impact sur les pêcheurs sportifs en influençant les conditions environnementales qui les affectent directement (par exemple, l'augmentation des températures dans les climats nordiques qui induit l'extension des saisons de pêche en eau libre et l'augmentation de l'effort de pêche). L'atténuation du changement climatique et les efforts d'adaptation (par exemple, les politiques énergétiques affinées entraînent des coûts plus élevés en carburant, ce qui rend les voyages lointains plus chers) sont les voies ultimes. Pour faire face aux limitations de recherches antérieures (par exemple, l'évaluation des impacts du changement climatique pour une seule voie à la fois et sans tenir compte de la variabilité du climat, des phénomènes météorologiques extrêmes, ou de l'hétérogénéité entre les pêcheurs), nous encourageons les chercheurs à recentrer leurs efforts de compréhension et à documenter les effets du changement climatique sur les pêcheurs continentaux.

KEY POINTS

- Climate change impacts on fishers arise from changes to fish, changes to other environmental conditions, and possibly from climate change mitigation and adaptation efforts.
- Changes to nonfish pathways can change fishers' behaviors that disrupt existing equilibriums between fish stocks and fishing effort.
- In some U.S. states, fish species targeted by recreational fishers appear to have changed from coldwater to warmwater species since 1991.
- Managing these impacts requires an understanding of connections and feedbacks within and between ecological and social systems.
- Future research should focus on impacts from climate variability including extreme weather events and impacts to subpopulations of fishers (e.g., southern U.S. fishers).

INTRODUCTION

Understanding how climate change might influence fishers remains a major challenge for North American inland fisheries research. This challenge is heightened by the facts that human behavior is complex, and many social and ecological variables influence fishers, leading to changes in a fishery. Though researchers understand some relationships among marine fish communities, fishers, and climate change (Pinsky and Fogarty 2012), such insights about fishers are rare within inland fisheries. In fact, identifying alternate pathways that link climate change to fishers within inland fisheries remain elusive.

Inland fisheries consist of commercial, subsistence, and recreational activities. Among these activities, recreational fishing is a dominant form, especially for industrialized nations such as Canada and the United States (Cooke et al. 2016). In fact, about 28 million individuals participated in freshwater (inland) recreational fishing in the United States in 2011, taking a total of 368 million trips and spending more than US\$25 billion (USDOI et al. 1993, 2011). In 2015, recreational fishers contributed almost \$700 million in revenue to state agencies through a variety of licenses, tags, stamps, and permit options (Figure 1). Given the importance of recreational fishing, we focus on climate change impacts on recreational inland fishers from North America.

Contemporary climate models and scenarios for North America predict widespread increases in annual surface air temperatures ranging from a low of about 1°C on the southern coasts of the United States to greater than 6°C for the Boreal Shield and Canadian Prairies (IPCC 2013). Annual precipitation is expected to increase, especially in far northern areas with an exception in the southwest United States where decline is possible (IPCC 2013). Beyond these average changes, climate change is expected to increase the frequency and severity of drought, flood, and damaging extreme weather events (IPCC 2014). These kinds of climatic changes will impact ecosystems and society; thus, these changes are of concern to inland recreational fisheries and fishers.

Our current understanding of climate change impacts on inland recreational fisheries is largely based on how alterations to aquatic ecosystems affect habitat and fish (see reviews by Lynch et al., this issue; Whitney et al., this issue). However, we focus here on assembling and reviewing the nascent literature on climate change and North American inland fishers to identify the relevant general pathways through which climate change impacts inland fishers. We limit this review to impacts on recreational fishers; a companion paper provides managerial advice including climate change adaptation strategies for inland fisheries (Paukert et al., this issue).

Assessing the impacts of climate change on fishers is complicated. Fishers are embedded in a social–ecological system (SES) where human behaviors and institutions guiding those behaviors are tightly coupled to ecosystems (Post 2013). Inland recreational fisheries consist of feedbacks among fishers, fish, managers, and the broader environment (Fenichel et al. 2013a). These feedbacks suggest that climate change impacts on fishers not only influence the well-being of fishers but that the subsequent (adaptive) responses by fishers will also impact fish and fisheries management (Lewin et al. 2006). Fishers are also highly heterogeneous in terms of their preferences (see reviews by Fenichel et al. 2013a; Hunt et al. 2013), which

complicates attempts to generalize the impacts of climate change on fishers and to identify effective management solutions (Johnston et al. 2010). These issues, combined with the fact that a recreational fisheries SES is nested in a hierarchical societal and environmental context (Hunt et al. 2013), greatly complicate assessments of climate change impacts on fishers.

Assessing impacts of climate change on inland recreational fishers also requires researchers to articulate changes to human well-being given its increasing prominence as a fisheries management objective (Hunt et al. 2013). “Well-being” is defined as net benefits that accrue to fishers from recreational fishing and to nonfishers from fishery-related environmental management (e.g., biodiversity conservation). Researchers have used several disciplinary-specific indicators to quantify aspects of well-being or net benefits including satisfaction (Arlinghaus 2006) and economic welfare (Train 1998), which collectively measure how much people prefer fishing compared to other options (Fenichel et al. 2013b). The value of these net benefits can be thought of as ecosystem services such as food provisioning and cultural services (MEA 2005) and are connected to wealth-based and sustainability metrics (World Bank 2011; Fenichel et al. 2016). However, measuring well-being also provides a model of human behavioral adaptation to environmental and policy change (Abbott and Fenichel 2013) that is critical for planning for climate change.

We illustrate a deliberately simple recreational fishery SES nested within a larger social, political, and environmental context (see the conceptual model; Figure 2) drawing upon concepts from Ostrom (1990). The model highlights general pathways by which climate change impacts fishers. Consequently, the model hides many connections among fisheries habitat and fish communities (see Hansen et al. 2015 for more details), and feedbacks such as the ability of fishers and managers to influence general environmental policy.

The inland fishery SES includes a resource system (e.g., aquatic ecosystems), but we focus here on fish. The social

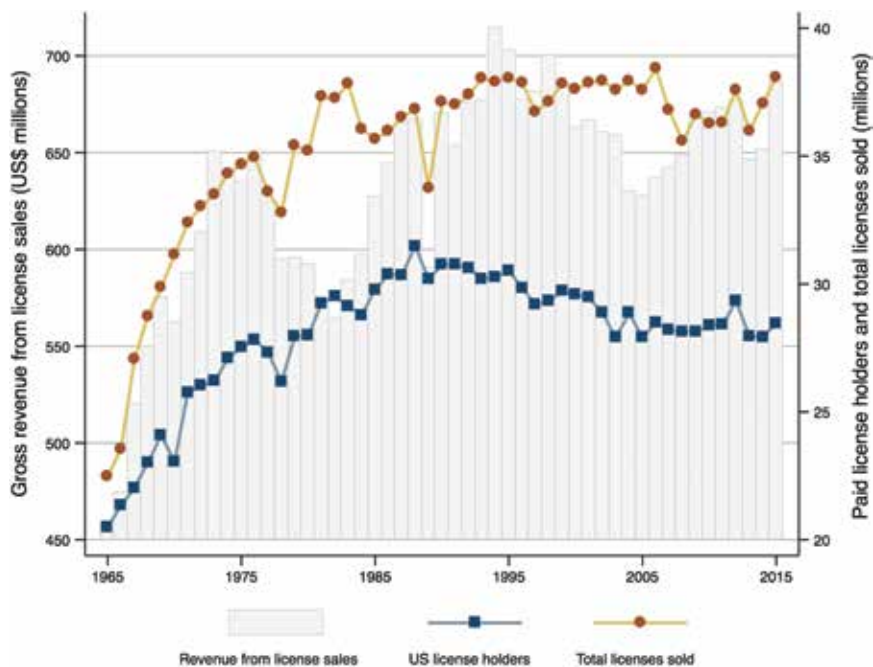


Figure 1. Recreational fishing activity and revenues in the United States, 1965–2015. Revenue from license sales in 2015 US\$.

system includes fishers and managers, although our attention is centered on fishers (see Paukert et al., this issue, for a focus on managers). This fishery SES is nested within a wider context that we highlight only with environmental policy (e.g., climate change mitigation and adaptation) and environmental conditions. Environmental conditions refer to large-scale biogeophysical processes (e.g., hydrologic cycles, air circulation) along with the terrestrial environment that, though related, may operate without much direct influence from a fishery SES. Climate change acts as a catalyst that impacts environmental conditions and possibly anticipatory environmental policy. Connections within the conceptual model illustrate three pathways through which climate change can impact inland recreational fishers:

1. environmental conditions that affect fish and thus, fishers;
2. environmental conditions that directly affect fishers; and
3. general environmental policies that influence fishers.

The first pathway describes how climate change impacts environmental conditions that in turn affect fish (e.g., community, abundance, and behavior) and sequentially fishers. Within this pathway, we describe the strength of connections that link fishers to fish, and we describe the few studies that estimate changes to well-being from climate change.

Second, we consider how changing environmental conditions can influence recreational fishers independent of changes to fish. There is strong evidence that recreational fishers' choices of whether, when, where, and how much to fish are in part based on non-catch-related attributes of a potential fishing location (Hunt 2005). Many of these non-catch attributes are susceptible to climate change impacts independent of fish.

Third, we consider how climate change mitigation and adaptation through environmental policy could influence recreational fishers. For example, mitigation attempts (e.g., carbon tax policies) can result in increases to fishers' travel

costs, reducing well-being, and effort. We also include adaptations within the pathway from environmental policy through environmental conditions (e.g., water allocation policies) here because environmental policy is the catalyst for impacts to fishers through pathways 1 and 2.

This review identifies an important, but relatively untouched, research agenda focused on the critical role that fishers and even environmental policymakers play in fisheries ecology and management. The strength of each pathway influences the ability of fishers and fisheries managers to mitigate and adapt to climate change impacts on fishers and fish.

PATHWAY 1: FISH-MEDIATED IMPACTS OF CLIMATE CHANGE ON RECREATIONAL FISHERS

Climate change impacts mediated by fish (see pathway 1 in Figure 2) are implicitly believed to dominate fishers' behaviors especially for commercial marine fisheries (Fenichel et al. 2016). Though there is little doubt that fish affect fishers' well-being and behaviors, the strength of these effects are debatable and likely variable (see Box 1). We review the handful of studies that predict well-being impacts to fishers from this pathway and point interested readers to Lynch et al. (this issue) and Whitney et al. (this issue) for information about how climate change impacts fish. We also summarize existing data to describe how the target species of North American inland fishers have changed from 1991 to 2011.

Fishers' well-being is affected through cultural and food provisioning ecological services (MEA 2005). Though there are several ways to measure well-being, here we describe three studies that use economic nonmarket valuation techniques to link climatic changes through fish to inland fishers' well-being. The results of these studies suggest that climate change potentially can result in large negative impacts to well-being primarily through reduced distribution and abundance of coldwater fish species, but there is also the potential for positive impacts to well-being in some regions.

Pendleton and Mendelsohn (1998) examined the effects of a doubling of greenhouse gas emissions on Rainbow Trout *Oncorhynchus mykiss*, other trout, and panfish in the northeastern United States. They combined an ecological model that predicted changes to catch rates for different species with an economic model from fishers' behaviors to establish changes to net benefits. Their estimates of welfare change ranged from a net loss of US\$8.4 million to a net benefit of \$37.3 million based on fiscal year (FY) 2015 dollars for a doubling of CO₂ and depended heavily on which climate circulation model was employed (i.e., Goddard Institute of Space Science and Oregon State University). Within the region, Maine and New Hampshire were predicted to benefit from climate change, though the outcomes for New York and Vermont were less certain.

Ahn et al. (2000) investigated the effects of climate change scenarios on coldwater fish in the southern Appalachian Mountains of North Carolina through changes to habitat (area available for fishing) and abundance of fish. Through a variety of scenarios with different assumptions about habitat and abundance, Ahn and his colleagues (2000) estimated large potential economic welfare losses ranging from US\$95 to \$911 million per year in FY2015 dollars for licensed North Carolina fishers.

Jones et al. (2013) examined how changes to fish habitat in streams throughout the coterminous United States might impact the economic value of recreational fishers. Using an existing

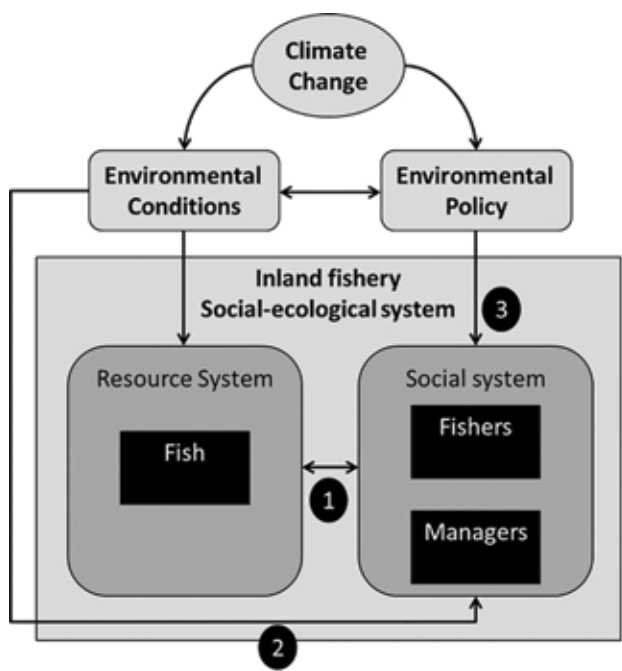


Figure 2. Pathways for climate change impacts on fishers within a social-ecological system of inland recreational fisheries. (The numbers correspond to climate change pathways that impact fishers).

Box 1: Potential for Climate Change to Impact Fishers through Fish

Little information exists that establishes links between climate change impacts to fishers from fish. Therefore, we assessed the potential for climate change to impact fishers through this fish-mediated pathway by summarizing literature that connects fish to fishers. Though it is commonly assumed that there is a strong relationship between fish and fishers, evidence for this relationship is less clear. In fact, there is increasing evidence suggesting that catch rates decline at a much slower rate than fish stock abundance (e.g., Post et al. 2002; Ward et al. 2013). There is a growing belief that this hyperstability of catch for inland fisheries results from effort sorting; where a population of fishers with different skill levels mobilize their effort differently, with more skilled fishers remaining at water bodies with depressed fish stocks (see Ward et al. 2013). If true, effort sorting implies that changes to fish abundance will impact recreational fishers' catch rates and behaviors, albeit in potentially nonintuitive ways (e.g., skilled fishers will be overrepresented at sites with low fish abundance).

The amount and location of fishing effort can also be influenced by fish. Evidence that catch-related fishing quality influences fishing participation decisions is mixed (see Dabrowska et al. 2014 for some support and Loomis and Fix 1998 for little support). However, there is evidence that catch-related fishing quality is related to effort. For example, Abbott and Fenichel (2013) demonstrated strong links between total effort and catch rates for Chinook Salmon *Oncorhynchus tshawytscha* and Lake Trout *Salvelinus namaycush* on Lake Superior and Lake Michigan. This importance of catch and fishers' behaviors are supported by others (e.g., Johnson and Carpenter 1994; Post et al. 2008), including a large set of literature focusing on fishing site choices (Hunt 2005). However, these studies also reveal that non-catch-related factors (travel costs, environmental quality, facility quality, congestion, and regulations) combined with heterogeneous preferences among fishers for catch- and non-catch-related factors influence fishers' behaviors (Hunt 2005; Fenichel et al. 2013a). Thus, climate change impacts on fishers through fish are moderated by resource and social conditions including the type of fisher.

Climate change can also influence fishers through fish by altering decisions about voluntary harvest decisions. Inland fisheries in North America have a strong tradition of voluntary catch-and-release fishing, where decisions to release fish are influenced by situational (catch) and personal (fisher) factors (Arlinghaus et al. 2007). Consequently, catch-related factors such as the target species, catch rates for target and substitute species, and size of fish influence fishers' decisions to retain caught fish (Hunt et al. 2002; Cooke and Suski 2005). Therefore, as fish stock abundance and fish communities change, the behaviors of fishers will change.

model of fishing effort, transfers of benefits from different types of fishing trips, different discount rates, and climate change scenarios, the authors estimated that climate change could negatively impact recreational fishers by between US\$101 million and \$7.1 billion in FY2015 dollars over the period 2009–2100.

We assessed changes to target fish species by inland recreational fishers in Canada and the United States from existing data sources and reports based on large-scale survey data from recreational fishers (DFO 1990, 2010; USDOJ et al. 1993, 2011). We used these data sources to summarize the target species of resident inland fishers by state, province, and territory since 1990. Target species were based on estimated targeted effort in the United States and from estimates of catch reported in Canada. United States data were collected in species aggregates with the most targeted species being either a warmwater (black bass, panfish [excluding crappie], and catfish), a coolwater (Walleye *Sander vitreus*), or a coldwater (trout and salmon) guild.

Given the coarse resolution of target species from the reports and our interest to explore the role of climate change at influencing these patterns, we grouped species by their thermal preference with coldwater (10°C–18°C), coolwater, (19°C–25°C), and warmwater ($\geq 26^\circ\text{C}$) guilds (Coker et al. 2001). In the early 1990s, fishers in western, mountainous, and northeastern states and all Atlantic provinces mostly targeted coldwater species (Figure 3). Fishers from the remaining Canadian provinces and territories, along with Minnesota and the Dakotas, mostly targeted coolwater species. However, between 1991 and 2011, the thermal guild of the primary target species was estimated to have changed in seven U.S. states. Six of these seven changes (Connecticut, New Hampshire, New Jersey, New York, Vermont, and Washington) were from a cold- to warmwater species. These changes are consistent with documented and suspected impacts of climate change on the distribution of fish species (Lynch et al., this issue). In fact, if we assume that seven changes in target species occurred by chance, there would only be a 6.3% chance that at least six of the seven changes in target species would be from colder to warmer water guilds. Therefore, it is plausible that these changes arose instead because fishers are responding to environmental signals associated with greater prevalence of species from warmer thermal guilds. Of course, we cannot definitively say that climate change caused these changes as other factors, such as state/province specific management actions and policies as well as overexploitation could have influenced fish communities and fishers' behaviors.

PATHWAY 2: NON-FISH (ENVIRONMENTAL CONDITION) MEDIATED IMPACTS ON RECREATIONAL FISHERS

Fisheries scientists often focus on climate change impacts on fishers mediated through fish. However, as illustrated by pathway 2 in Figure 2, changing environmental conditions can directly impact fishers through changes to the quality and/or availability of recreational fishing experiences (Hunt 2005). In fact, de Freitas (1990) suggested that thermal (e.g., temperature, humidity), physical (e.g., precipitation, wind), and esthetic (e.g., clear skies) conditions of climate and weather affect the behaviors of tourists and recreationists. Though researchers have developed indices from these conditions to identify potential climate change impacts to tourists (Scott et al. 2015), such indices have not been applied to recreational fishers.

Fishers from northern latitudes appear to respond positively to warmer thermal conditions measured crudely through change to air temperatures (e.g., Hunt and Dyck 2011) partly because ice fishing is far less popular relative to open water fishing (USDOJ et al. 2011). However, climate change is likely to reduce participation

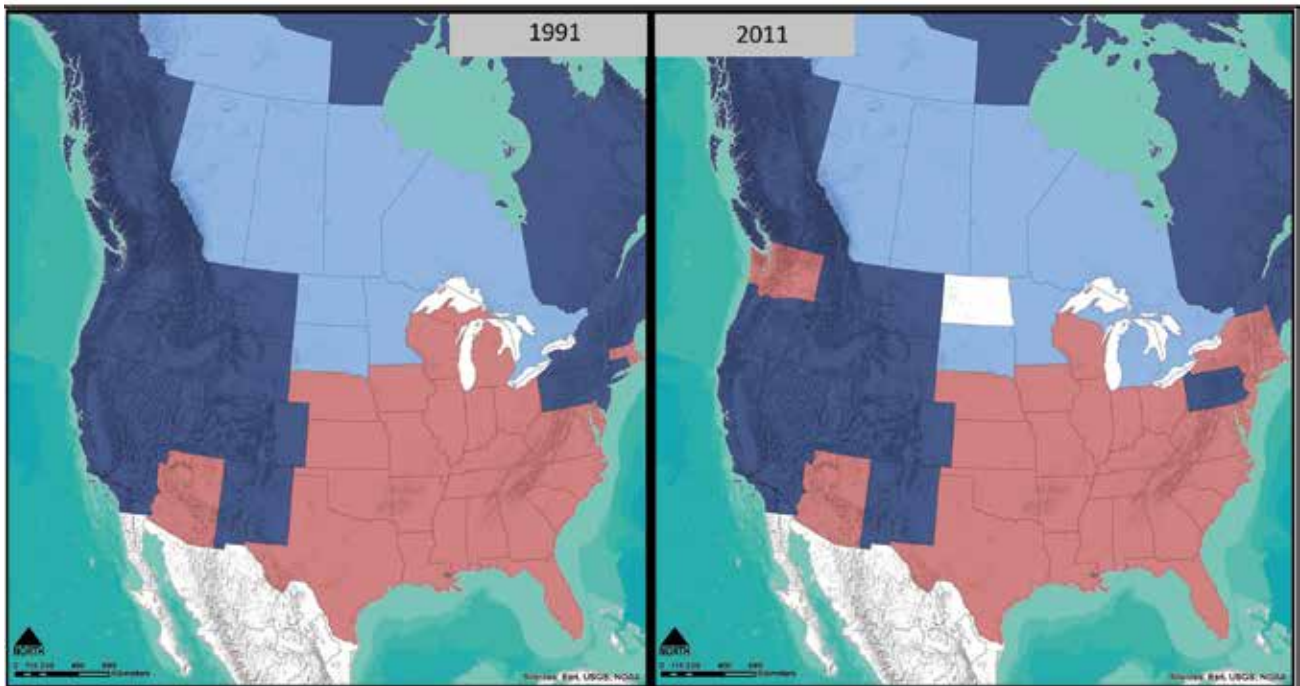


Figure 3. Thermal guild of most targeted species by inland recreational fishers in Canada and the United States. (Dark blue, light blue, and pink shading refer to cold (10-18°C), cool (19-25°C), and warm ($\geq 26^\circ\text{C}$) water species guilds; 2011 North Dakota data were unavailable; for Canadian data primary target defined as species with greatest reported catch).

in ice fishing through reduced ice formation (i.e., season, timing, depth) across Northern Hemisphere lakes (Benson et al. 2012). These changes in ice phenology already have led to the cancellation of an ice fishing championship in Ontario (Scott et al. 2015) and are projected by 2100 to reduce the ice fishing season in northeastern Ontario by between 6% and 15% (Hunt and Kolman 2012). Even if fishers concentrate their existing ice fishing effort into this smaller season length, the increased congestion at these fishing sites is expected to negatively impact fishing quality and the well-being of fishers (see Hunt 2005 for a review).

Mendelsohn and Markowski (1999) attempted to predict the impacts of changing thermal conditions from climate change on a variety of activities including recreational fishing for the United States. The authors developed models to predict the number of days that individuals participated in each activity using demographic and January and July temperatures as explanatory variables. The authors predicted positive impacts, and by 2060 climate change impacts on recreational fishing (including inland and marine) were estimated to be US\$3.1 and \$8.7 billion (FY2015 dollars) from temperature increases of 1.5°C and 2.5°C, respectively. These large estimates arose because of longer open water fishing seasons and more desirable temperatures for fishing and not from any consideration of pathway 1 impacts. Though consistent with other beliefs (Morris and Walls 2009), the conclusions are limited by only considering thermal conditions from this one pathway and assuming homogeneous effects from temperature on all fishers. Yet, they highlight important trade-offs and forces and suggest that climate change-driven effects may move in opposite directions.

Physical conditions of weather also impact fishers. In northern latitudes, trip timing for recreational fishers is negatively impacted by precipitation and, for trips to large-sized lakes, strong wind speeds (Hunt and Dyck 2011). Climate change is expected to increase the frequency of these extreme

weather events (heavy precipitation and strong wind events), likely resulting in changes to the timing and/or amount of fishing activity. Anecdotal evidence suggests that these extreme events are already more common. For example, between 2008 and 2012, weather and wind damage aside from hurricanes represented the third most common factor inducing insurance claims among members of the Boat Owners Association of the United States (Fusco 2013). In 2005, these damage claims ranked fifth (Fusco 2013), suggesting that these events are occurring more often and that climate change can impact fishers through increased costs for insuring fishing-related equipment against these events.

Increased climate variability can also impact fishers through increased occurrences of drought and flood. For example, decreased fishing activity was observed at Lake Mead on the Arizona–Nevada border through closure of several boat launches and marinas because water levels decreased 40 m from 1999 to 2010 in part due to drought (Holdren and Turner 2010). Lower water levels can represent a limiting factor for boat-based recreational activities. For example, over a quarter of marina operators on the Canadian side of the Laurentian Great Lakes closed slips for boats and over one-half had conducted dredging activities to combat low water levels at some point since owning a marina (Bergmann-Baker et al. 1995). Though fishers can adapt to changes in low water levels in marinas and boat launching facilities by choosing other sites, these fishers will likely incur well-being losses (e.g., increased travel costs).

Esthetics such as forested settings and water quality influence recreational fishers' choices of fishing sites (Hunt 2005). Climate change is likely to impact these setting and water quality attributes through changing patterns of natural disturbance and changes to land use activities (Mendelsohn and Dinar 2009; IPCC 2014). Consequently, climate change can impact fishers' behaviors and well-being through this esthetic factor.

PATHWAY 3: ENVIRONMENTAL POLICY-MEDIATED IMPACTS OF CLIMATE CHANGE ON RECREATIONAL FISHERS

The third climate-related pathway that could affect inland recreational fisheries is through environmental policy that is designed to mitigate or adapt to impacts from climate change (see pathway 3 in Figure 2). We are unaware of any studies that have explicitly investigated this pathway. Given the lack of information about this pathway on recreational fishers, we speculate about two potential cases whereby environmental policies may impact inland recreational fishers and fisheries.

Mitigation efforts to reduce greenhouse gas emissions are already underway. In fact, almost 40 countries and a number of states and provinces such as California, British Columbia, and Quebec are actively engaged in emission trading or carbon tax policies (Kossov et al. 2015). These and other efforts to reduce dependence on fossil fuels make energy more expensive (IPCC 2014). The higher cost of transport will affect fishers' choices of the location and number of fishing trips (e.g., Morey et al. 1993; Hunt 2005). For example, a 10 cent (CDN) increase per liter of fuel was predicted to reduce trip taking by between 4% and 7% among fishers in northern Ontario, Canada (Hunt and Dyck 2011).

Higher transportation costs will likely reduce fishing effort in remote locations while fishing effort near heavily populated regions could increase. This change would lead to increased exploitation impacts on fisheries near urban centers, thus placing an increased burden on fisheries managers to maintain or to increase fishing opportunities near cities, many of which are already supported through stocking efforts. Likewise, the increased costs for fuel could result in fishers reducing their travels by boat or shifting modes from gas-powered outboard motors to shore-based or paddle-based fishing trips, resulting in fishing effort concentrated near locations where fishers access a water body (e.g., boat launch).

Another possible impact of climate change policy on fishers occurs when policy impacts environmental conditions that in turn flow through pathway 1 from Figure 2. We include this pathway here because its genesis is from external environmental policy change that is rarely considered when discussing climate change impacts on inland fisheries.

Climate models predict more punctuated precipitation events across most of North America and increased precipitation has occurred in North America's temperate latitudes since the 1950s (IPCC 2014). However, demands for water will likely increase because of human population growth, reduced snowmelt, and possibly increasing needs for food production. In arid regions, riverine systems are expected to be negatively affected by decreased stream flow and increased water removal (USCCSP 2008). Reservoir and dam managers will need to respond to this list of demands for water in response to climate change. Cases like the Klamath River where conflicts emerged between allocating water for agriculture and stream flow for endangered fish species (Jaeger 2004) could become more common. We suggest that it is probable that maintaining water flow for recreational fisheries is low on the list of concerns when paired with residential, commercial, and agricultural demands for water. Consequently, water allocation decisions can compromise water quality (e.g., temperature) and levels necessary to support fish. These influences on fish habitat will work back to fishers through the first pathway.

CONCLUSION

Climate change is likely to impact inland recreational fishers through three primary pathways (Figure 2). There is a lack of published data and information that describe the potential strength of influence of each pathway on fishers. Where such publications exist, there is no documentation of impacts and instead the information is extracted from models based on associations that only considered one possible pathway. It is also not clear that the three pathways will necessarily lead to shifts in fishing behavior and well-being in the same direction (e.g., longer summers on their own might lead to increases in effort, whereas warm waters could make fishing itself less desirable through impacts on fishes). Furthermore, past research results are presented at very coarse scales (e.g., the United States), and well-being assessments have lacked appreciation for climate impacts arising from climate variability and increased prevalence of extreme weather events. Therefore, the overall impact of climate change on the well-being of inland recreational fishers is uncertain (Box 2) and is likely heterogeneous given the variability in recreational fisher populations. Though specific groups will be negatively impacted (e.g., ice fishers and fishers who target coldwater species at current southern range limits), research findings are too limited to develop lists of "winners" and "losers" in terms of well-being. Such lists can only be assembled once researchers develop a more comprehensive understanding of how each pathway individually and jointly impacts the behaviors and well-being of fishers (see Box 3).

The potential for climate change to impact fishers through the three pathways is poorly understood. Even for the most studied pathway of fish impacts on fishers, the relationships are likely less straightforward and weaker than is typically assumed when viewing fishers as a predator within a predator-prey system (see Box 1). Additional research is also needed to understand better the complex network of direct and indirect feedbacks between fishes and fishers (see Box 3).

Climate change has and will continue to impact fishers as well as fish. Part of what makes addressing climate change challenging is the fact that climate change and climate change adaptation and mitigation are likely to alter the social and economic landscape in which people, including recreational fishers, live. The managers of recreational fisheries already need to account for societal shifts in attitudes and preferences. Climate change and the broader societal response to climate change (e.g., water, energy, and transportation policy) are likely to create new challenges on the social dimensions of fisheries research. Though these social dynamics may be seen as external pressures from the standpoint of some fishery managers, savvy managers will anticipate these changes, particularly when evaluating the benefits and costs of attempting to preserve a stressed fishery or to replace it with a new "climate change-adapted" system.

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Box 2: Smallmouth Bass and Profitability of Ontario Tourism Operators Catering to Recreational Fishers

Climate change–induced expansion of Smallmouth Bass *Micropterus dolomieu* population distributions may affect the revenues generated by fishing-oriented nature-based tourism operators in northeastern Ontario, Canada (see Hunt and Kolman 2012 for details). Throughout North America, many individuals offer accommodation to recreational fishers in the form of fishing lodges and camps. In some instances, individuals offer guests a unique experience whereby fishers travel by float plane to access lodges and camps on remote lakes. For northern Ontario, the 770 lodges and camps that were accessible only by float plane and were operating in 2000 served a single market (Hunt and Kolman 2012). Consequently, the prices that these individuals charged recreational fishers include the market value of the characteristics that encompass a fishing package (e.g., fishing quality and lodge amenities).

Revenues were estimated from a proxy of the market price that tourism operators charged for a weeklong fishing trip at tourism establishments that were primarily accessed by floatplane. A (hedonic) model was developed to explain variations in these market prices by site and setting characteristics at these establishments and associated water bodies from across northern Ontario. Catch-related fishing quality characteristics were measured by operator-reported catch rates and expected size for the primary species that guests targeted such as Walleye *Sander vitreus* along with the presence of Smallmouth Bass. Combined with projections of changes to Walleye abundance from climate change scenarios (Chu and Fischer 2012), a potential modest decrease of revenues (~8.5%) was estimated for establishments situated on lakes with Smallmouth Bass (Hunt and Kolman 2012). Though this decrease was driven by the presence of Smallmouth Bass and not changes to Walleye catch rates, the exact reason why Smallmouth Bass presence was negatively associated with revenues remained unexplained. Nevertheless, the result implies that introductions of bass might result in losses to revenues generated by the nature-based tourism industry in northern Ontario. Therefore, as the range of Smallmouth Bass in Ontario increases northward (Alofs et al. 2014) and management agencies respond by removing seasonal restrictions on harvest of nonnative species (Paukert et al., this issue), climate change can exacerbate this negative impact on nature-based tourism operators in Ontario. Of course, the overall impact of range expansion on the well-being of Ontario fishers is uncertain partly because fishers and tourist operators will respond to these changes in Smallmouth Bass abundance in ways that will impact different drivers, resulting in further changes and responses (see Figure 4).

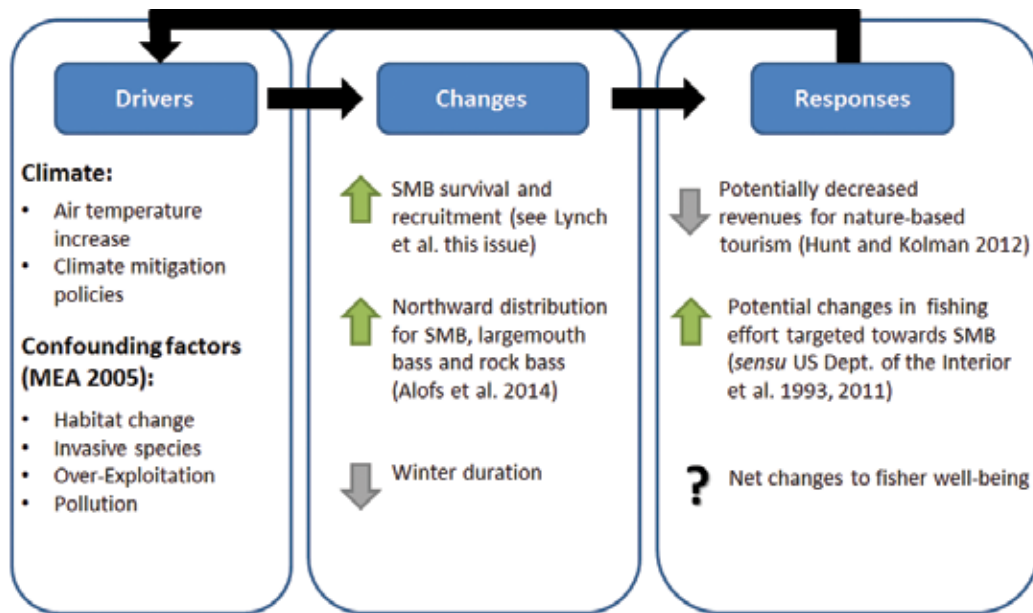


Figure 4. Possible climate change impacts to fishers from northward range expansion of nonnative Smallmouth Bass (SMB) in Ontario's lakes facilitated by climate change. (Changes to SMB from Lynch et al. this issue, green arrows indicated an increased or earlier seasonal response, gray arrows indicated a decrease or later seasonal response, while the question mark represents an unsure response).

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Box 3: Suggestions for Future Research and Management of Climate Change Impacts on Recreational Fishers

- **Integrating considerations of all three pathways into management:** Fisheries managers should be mindful of the potential of all three pathways to impact inland fishers from climate change across space and time. It is important for fishers and fisheries managers to work with others who develop environmental policy to try and ensure that fisheries concerns are adequately considered and to give ample warning for fishers to adapt to changing social and resource conditions that arise from such policy.
- **Developing long-term monitoring data about fishers:** These data should focus on more than effort and instead provide opportunities to understand the diversity of preferences and fishing behaviors and the wide array of well-being benefits that accrue to fishers. The monitoring should also provide data about lapsed and potential fishers (i.e., people who do not fish but might under different conditions) that would help researchers to understand and predict how climate change and other environmental stressors could impact fishing participation (Abbott and Fenichel 2013; Fenichel et al. 2013a). For example, one can use repeated cross-sectional or panel surveys of fishers to measure changes in behaviors such as location, timing, and intensity of effort and changes to satisfaction with recreational fishing opportunities.
- **Extending efforts focused on integrative and interdisciplinary models:** These models are needed to help understand the consequences of climate change and other drivers (stressors) on fishers' behaviors and well-being. Such model predictions should be validated through active experimentation or at least from associations with long term monitoring data. For example, by modeling both the ecological and social systems, researchers can assess the consequences of climate change scenarios jointly on aquatic ecosystems and fishers.
- **Exploring new methods, impacts, and study areas:** Thermal, physical, and esthetic conditions of weather and climate influence the behaviors of tourists and recreationists (de Freitas 1990; de Freitas et al. 2008). Research is needed to assess the reliability of these conclusions in the context of recreational fishing. Research is also needed to move beyond average impacts to account for increased climate variability including extreme weather events and to focus on southern U.S. recreational fishers who are likely to be most negatively impacted through changing climate.
- **Evaluating the strength of responses between fish abundance and fishing behaviors (effort):** This research is critical to understand the relative strength of the three pathways. This understanding is also important to assess how fishers' behaviors might serve to moderate the impacts of climate change on fishes. For example, if fishers respond strongly to change in fish stock abundance, fishers could adapt by reducing fishing effort on species that become less abundant and shifting time allocation to other activities.
- **Communicating climate science effectively to audiences:** The impacts of climate change on fishers should be communicated in ways that resonate with the audience. For example, DeWeber and Wagner (2015) communicate the extirpation of Brook Trout *Salvelinus fontinalis* in the northeastern United States through messages of how much further residents will need to travel to pursue their trips. Such communications can serve to highlight the importance of climate change to fishing and other human activities.

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ADAPTING INLAND FISHERIES MANAGEMENT TO A CHANGING CLIMATE

Craig P. Paukert

U.S. Geological Survey (USGS), Missouri Cooperative Fish and Wildlife Research Unit, Department of Fisheries and Wildlife Sciences, University of Missouri, 302 ABNR Building, Columbia, MO 65211. E-mail: paukerc@missouri.edu

Bob A. Glazer

Florida Fish and Wildlife Conservation Commission, Fish and Wildlife Research Institute, Marathon, FL

Gretchen J. A. Hansen*

Wisconsin Department of Natural Resources, Science Services, Madison, WI

Brian J. Irwin

USGS, Georgia Cooperative Fish and Wildlife Research Unit, Warnell School of Forestry and Natural Resources, University of Georgia, Athens, GA

Peter C. Jacobson

Minnesota Department of Natural Resources, Park Rapids, MN

Jeffrey L. Kershner

Emeritus, USGS, Northern Rocky Mountain Science Center, Bozeman, MT

Brian J. Shuter

Department of Ecology and Evolutionary Biology, University of Toronto, Toronto, ON, Canada

James E. Whitney**

Missouri Cooperative Fish and Wildlife Research Unit, Department of Fisheries and Wildlife Sciences, University of Missouri, Columbia, MO

Abigail J. Lynch

USGS, National Climate Change and Wildlife Science Center, Reston, VA

*Present address for Gretchen J. A. Hansen: Minnesota Department of Natural Resources, St. Paul, MN

**Present address for James E. Whitney: Department of Biology, Pittsburg State University, Pittsburg, KS



Natural resource decision makers are challenged to adapt management to a changing climate while balancing short-term management goals with long-term changes in aquatic systems. Adaptation will require developing resilient ecosystems and resilient management systems. Decision makers already have tools to develop or ensure resilient aquatic systems and fisheries such as managing harvest and riparian zones. Because fisheries management often interacts with multiple stakeholders, adaptation strategies involving fisheries managers and other partners focused on land use, policy, and human systems, coupled with long-term monitoring, are necessary for resilient systems. We show how agencies and organizations are adapting to a changing climate in Minnesota and Ontario lakes and Montana streams. We also present how the Florida Fish and Wildlife Commission created a management structure to develop adaptation strategies. These examples demonstrate how organizations and agencies can cope with climate change effects on fishes and fisheries through creating resilient management and ecological systems.

Adaptación del manejo de pesquerías continentales a un clima cambiante

Los tomadores de decisiones en materia de recursos naturales tienen la tarea de adaptar el manejo a un clima cambiante, y al mismo tiempo sopesar entre los objetivos de corto plazo y los cambios de largo plazo en ecosistemas acuáticos. Esta adaptación requerirá desarrollar tanto ecosistemas como sistemas de manejo resilientes. Los tomadores de decisiones ya cuentan con herramientas para desarrollar o asegurar sistemas acuáticos y pesquerías resilientes, tales como manejo por cuotas y por zonas riparias. En virtud de que el manejo de pesquerías a menudo implica la interacción entre varias partes interesadas, las estrategias de adaptación que involucran a manejadores de pesquerías y otros participantes con intereses en el uso de la tierra, en la política y en sistemas humanos, en conjunto con un monitoreo de largo plazo, son elementos indispensables para constituir sistemas resilientes. Se muestra cómo organizaciones y agencias de los lagos de Minnesota y Ontario y en los ríos de Montana, ya se están adaptando a un clima cambiante. También se muestra cómo la Comisión de Pesca y Vida Silvestre de Florida creó una estructura de manejo con el objeto de desarrollar estrategias de adaptación. Estos ejemplos demuestran cómo las organizaciones y agencias pueden responder a los efectos del cambio climático en materia de peces y pesquerías, a través de la creación de sistemas ecológicos y de manejo resilientes.

Adapter la gestion des pêches continentales à un climat changeant

Les décideurs des ressources naturelles sont mis au défi d'adapter sa gestion aux changements climatiques tout en équilibrant les objectifs de gestion à court terme avec des changements à long terme dans les systèmes aquatiques. L'adaptation exigera de développer la résilience des écosystèmes et de créer des systèmes de gestion souples. Les décideurs disposent déjà d'outils pour développer ou assurer la résilience des systèmes aquatiques et de pêche, tels que la gestion des prises et des zones lacustres. Parce que la gestion de la pêche interagit souvent avec de multiples parties prenantes, des stratégies d'adaptation impliquant les gestionnaires des pêches et d'autres partenaires, qui se concentrent sur l'utilisation des terres, les politiques et les systèmes humains, associés à la surveillance à long terme, sont nécessaires pour les systèmes souples. Nous montrons comment les agences et les organisations s'adaptent aux changements climatiques dans les lacs du Minnesota et de l'Ontario, ainsi qu'au niveau des ruisseaux du Montana. Nous présentons également la façon dont la Commission des poissons et de la faune de la Floride a créé une structure de gestion pour élaborer des stratégies d'adaptation. Ces exemples montrent comment les organisations et les agences peuvent faire face aux effets des changements climatiques sur les poissons et la pêche en créant une gestion et des systèmes écologiques souples.

KEY POINTS

- Adapting to climate change requires managing habitats, landscapes, and ecosystems to develop resilient fisheries.
- Resilient management is as important as resilient ecosystems.
- Managing for resilient systems requires collaboration between fisheries management and a wide range of partners focused on land use, policy, and human systems.
- Monitoring and managing for long-term change is needed.
- Uncertainty is certain, and decision makers can cope with the uncertainty.

INTRODUCTION

Fisheries managers have a long history of adapting management strategies to changing environmental and social conditions. Climate change is adding to the suite of uncertainties influencing fish populations and their response to management (Hansen et al. 2015). Managers have the ability to affect the ecological resilience, which is the capacity of a system to absorb or recover from disturbance while retaining its essential structure and function (Box 1; Holling 1973), and sustainability of fisheries resources by acknowledging uncertainty, employing decision-making strategies robust to uncertainty (e.g., scenario planning, Peterson et al. 2003; structured decision making, Irwin et al. 2011), and conducting the pre- and post-monitoring necessary to understand actual outcomes (Lempert et al. 2013). Some uncertainties bear strongly upon decisions, whereas others may be beyond managers' control. By understanding the difference, managers may be able to initiate management actions that reduce uncertainty (Irwin and Conroy 2013).

Although we have learned from documented fish responses to climate, to date these assessments are relatively limited (Lynch et al. this issue). Adaptation can be facilitated by forecasting future climate conditions, but such predictions are fraught with uncertainty (Lourenco et al. 2015), which is compounded by uncertainty in how natural resources respond to these changes (Wenger et al. 2013). Thus, decision makers are faced with a number of important questions in the context of climate change, such as, How will aquatic communities respond to changing water temperatures and flow regimes in five years? Ten years? A century from now? How reliable are downscaled climate models in predicting future conditions on the local to regional scale?

Our capacity to manage fisheries under a changing climate depends on reasonably accurate future predictions of ecological conditions but, more important, it depends on our ability to manage ecosystems in a way that buffers against some of these predicted changes by using a management structure

Box 1: Terms

Ecological resilience: The capacity of a system to absorb or recover from disturbance while retaining its essential structure and function (Holling 1973).

Resilient management: Management designed to adapt to rapidly changing ecological and social conditions.

Social resilience: The ability of human groups or communities to cope with external stresses and disturbances as a result of social, political, and environmental change (Adger 2000).

Adaptation: Minimizing the impact of climate change on ecological and social systems while exploiting beneficial opportunities (IPCC 2007).

General resilience: Does not focus on a specific attribute of a system or type of disturbance; focuses on maintaining core system attributes under a variety of unknown conditions and unforeseeable events (Carpenter et al. 2012).

Specified resilience: Answers the question “resilience of what, to what?” and is useful for minimizing the impact of well-defined potential stressors (Carpenter et al. 2012).

Adaptive management: An iterative process of using management decisions as experiments designed to learn about system responses and eventually reduce uncertainty.

designed to adapt to rapidly changing ecological and social systems (management resilience; Box 1) and environmental flexibility. Much like Aldo Leopold’s first rule of “intelligent tinkering” (make sure that you keep all the pieces; Leopold 1949), adapting to climate change means that fisheries and resource managers will need to consider how to maintain the key natural resource components required to sustain fisheries over the long term. Ecosystems that have already been degraded by anthropogenic activities will make climate adaptation even more challenging. Ensuring that managed systems operate within acceptable boundaries (Scheffer et al. 2015) to maintain certain characteristics or a diverse portfolio of fish populations in the face of climate change and other interacting stressors (MEA 2005; Haak and Williams 2012; Staudt et al. 2013) is challenging because interactions may be unforeseen, complex, and dynamic. Managers need to apply the best available science on how fish and habitats are responding to climate change (Lynch et al., this issue; Whitney et al., this issue), coupled with a strong focus on how resource users may respond to these actions (Hunt et al., this issue). In addition, fisheries managers will need to consider the context of both ecological and social systems (Figure 1). Adaptation strategies that incorporate partnerships across sociopolitical boundaries and other organizational structures (e.g., state/provincial agencies, federal

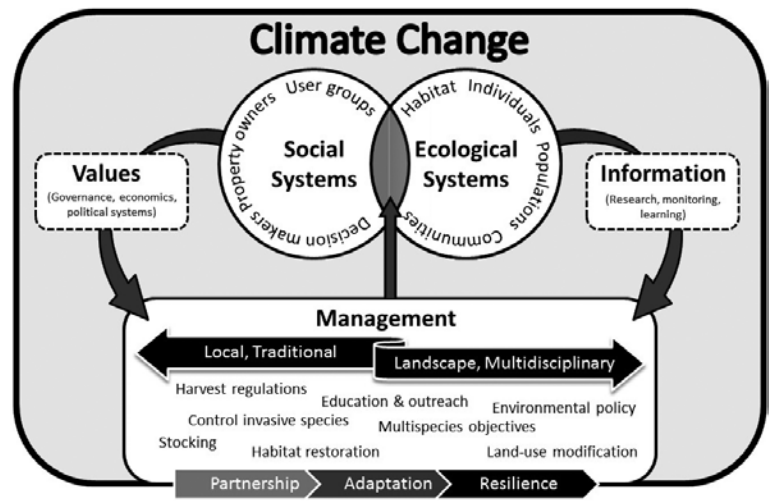


Figure 1. Conceptual models of how climate change may overlay upon development of management strategies, including how individual fish (Whitney et al., this issue), populations and communities (Lynch et al., this issue), and human behavior (Hunt et al., this issue) influence or respond to management decisions. Information is gathered from both management and social systems; thus, fisheries management is influenced by both empirical observations of aquatic ecosystems and value-based objectives of user groups, such that implemented policies are intended to buffer the interactions within socioecological systems. Adapting management for more resilient ecological and social systems will require increased partnerships and implementation across broader spatiotemporal scales.

agencies, nongovernmental organizations [NGOs], public interest groups) will be required for efficiency because of limited staffing, budgets, and expertise within any individual agency or organization.

The objectives of this article are to identify key components to the successful management of fisheries resources in a changing climate. We review adaptation strategies that agencies and organizations have developed to manage both ecological systems and their own administrative structures. We present case histories to demonstrate how agencies can adapt locally to manage systems in the face of climate change and discuss the importance of monitoring to detect change and adapt to new situations. Finally, we review challenges that organizations and agencies face in making decisions when uncertainty remains about how fish and fisheries will be affected by a changing climate.

MANAGING FOR ECOLOGICAL RESILIENCE

Fisheries management activities are unlikely to reverse the course of climate change; therefore, successful management will require adaptation. Because biological responses to climate hold uncertainty, adapting to climate change requires enacting strategies that are robust to unpredictable future conditions and their impacts and preparing for surprises and extreme events (Wilby et al. 2010). These strategies are varied but can include protection of watersheds (e.g., forest conservation easements) to minimize nutrients entering lakes, which reduces dissolved oxygen levels (Jacobson et al. 2013), to ensuring a diversity of population age classes through harvest regulations to buffer against year-class failure due to extreme events (Hansen et al. 2015). The capacity of a fisheries system to adapt to climate change will depend on its ecological resilience. Managing for ecological resilience requires a focus on processes and feedbacks that maintain or transform a system into a desirable state (Walker and Salt 2012). Acknowledging the interdependence of social and ecological systems is a critical component of

managing for ecological resilience (Berkes and Folke 1998; Biggs et al. 2012; Walker and Salt 2012), and we call attention to managing for the resilience of both ecological and social systems for fisheries management (Figure 1).

Managing for resilient ecological systems requires protecting the mechanisms that maintain a desired structure or function, such as sustainable recreational fisheries, rather than managing for stability of a single population or yield (Holling and Meffe 1996; Chapin et al. 2010). Resilient ecosystems maintain critical functions under the novel, unknown conditions and extreme events associated with climate change (Folke et al. 2010). Multiple recommendations for resilient fisheries management strategies have been proposed (e.g., Biggs et al. 2012; FAO 2012; Pope et al. 2014), and these strategies may fall (in part) within the current purview of most inland fisheries management agencies. For example, managing freshwater systems to maintain a diversity of species and heterogeneous age structure can be achieved through harvest regulations and can increase a system's resilience to extreme events (Hansen et al. 2015). Non-harvest-based regulations can also improve resilience, including nutrient management and land-use regulations (e.g., Walsh and Fletcher 2015) and protected areas or refuges (Bengtsson et al. 2003). Applying heterogeneous management tools buffers against fallible management (Elmqvist et al. 2003); if one approach fails due to incomplete understanding or unanticipated events, other approaches may be more effective. In contrast, a focus on single-species management with highly specific goals (e.g., maximizing yield) may erode ecological resilience and increase the likelihood of collapse (Holling and Meffe 1996).

Managing for ecological resilience frequently requires confronting trade-offs, such as sacrificing fishery harvest or development opportunities in the present day, to ensure the long-term stability of the system as a whole (Holling 1996; Rist and Moen 2013). In the Minnesota Cisco *Coregonus artedii* example (Box 2), the persistence of Cisco and other native coldwater fish species in a warming climate requires protecting forests in the watersheds of important refuge lakes with conservation easements that forego near-term economic benefits of those lands being converted to agriculture or development (agricultural and developed land values are typically 50%–400% higher than forested lands). In other cases, trade-offs exist between managing for specified vs. general resilience (Folke et al. 2010; Walker and Salt 2012), which may be conflicting; that is, managing a fishery to withstand a specified disturbance may erode its capacity to withstand other types of unknown disturbances (Walker and Salt 2012). For example, managing for general resilience means maintaining some degree of separation among system components, such that harmful effects are not transmitted throughout the entire system (Carpenter et al. 2012). Specifically, decreasing connectivity among inland fish stocks may reduce the vulnerability of the entire system to a disease outbreak or exposure to invasive species. However, connectivity among populations or stocks is critical for the ecological resilience of a species to regional disturbances (Hilborn et al. 2003). Thus, managing for general resilience requires some level of suboptimal outcomes to specified events to maintain system functionality in an uncertain future (Rist and Moen 2013). Resilient management systems recognize such trade-offs and set priorities for both the short and long term in order to optimize management outcomes over the temporal scales most relevant to the resources they manage.

Ecological resilience may require reestablishing ecological

processes that enable systems to respond to both human and environmental disturbances. We recognize that in most cases it is impossible to reset systems to early historical conditions prior to disturbance by increased human settlement several hundred years ago, but resilience requires maintaining processes and functions within the constraints set by current social and ecological systems. Partnerships can allow management actions that achieve ecological resilience where multiple objectives are balanced by a single resilience strategy. These activities often are beyond the exclusive purview of traditional fisheries management; thus, partnerships and collaborations will be necessary (Pierce et al. 2013; Box 3). For example, landowners, agencies, and NGOs worked together in the Blackfoot River, Montana, to change livestock grazing practices and plant riparian vegetation to promote stream shading and decrease water temperature. These practices have been effective at reducing summer water temperatures in tributary streams where threatened Bull Trout *Salvelinus confluentus* exist (Williams et al. 2015). This is a good example of a partnership restoring ecological function that will ultimately help the system buffer increasing temperatures that will result as climate warms.

DEVELOPING RESILIENT MANAGEMENT SYSTEMS

In addition to managing for ecological resilience, adaptation to climate change will require that agencies and organizations build the capacity to act proactively, identify and respond to change, evaluate and refine actions, and manage social systems in addition to ecological systems; that is, fisheries management agencies must themselves be resilient (Arlinghaus et al. 2013). In this framework, human actions are viewed as part of a social–ecological system, whereby ecological and social dynamics are linked (Figure 1; Folke et al. 2010). One component of resilient systems is the capacity to learn about and adjust to changing conditions and drivers while also evaluating the outcome of past management actions (Folke et al. 2010; Pope et al. 2014). Monitoring (see next section) and adaptive management will allow fisheries management agencies to better identify the impacts of climate change and adjust to new environmental and social conditions (Allen et al. 2011; Hansen et al. 2015). Resilient management systems acknowledge and emphasize uncertainty, but uncertainty should not prevent a management action (Berkes and Folke 1998; Walker and Salt 2012); an absence of action is itself a management decision, which can potentially come at a high cost. Therefore, management entities should be structured to allow responses to unforeseen events to minimize and contain potential impacts (see Box 4). In some cases, management actions that anticipate possible changes may be warranted, whereby management strives to minimize projected impacts of climate change in high-priority locations. For example, planting trees in the riparian zones of streams where temperatures are projected to become unsuitable for high priority species can reduce the magnitude of temperature increases and maintain coldwater habitat longer than would be possible in the absence of such proactive strategies (e.g., Wilby et al. 2010; Box 3).

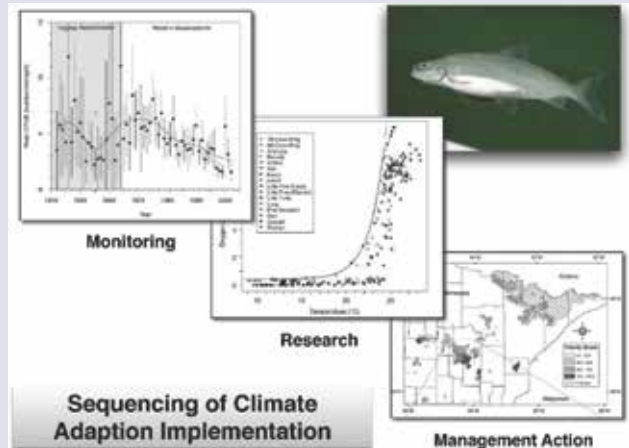
Social resilience also requires flexibility in stakeholder expectations and management objectives. That is, rather than a narrow definition of angler satisfaction hinging on the provision of a single species, social resilience may require an expansion of species preferences and the value of ecosystem services other than fishing (Berkes and Folke 1998; Hunt et al., this issue). Such a shift in focus from extraction of a single species to a

Box 2: Protecting Cisco Refuge Lakes in Minnesota Using a Landscape Approach

Fisheries scientists with the Minnesota Department of Natural Resources (MNDNR) analyzed long-term monitoring data, available starting in the 1940s, for an important forage fish Cisco *Coregonus artedii* and identified a declining trend in abundance (see figure). These trends led to a research program to identify causes of the declines and potential management solutions. Although Cisco are a coldwater fish sensitive to multiple ecological stressors including eutrophication, MNDNR researchers uncovered evidence that the decline was climate related (Jacobson et al. 2012). Cisco populations have apparently suffered from longer durations of stratification due to lake temperatures warming earlier and cooling down later that have allowed hypolimnetic oxygen levels to be depleted to critically low concentrations in some lakes.

A large Cisco summer kill during the unusually warm summer of 2006 allowed MNDNR scientists to accurately map the thermal niche of Cisco by measuring lethal temperature and oxygen concentrations in the field (Jacobson et al. 2008; see figure). Other deep, clear lakes in the region maintained excellent coldwater habitat conditions that were well below lethal levels. Based on that observation, a research collaboration with lake modeling colleagues at the University of Minnesota identified 176 lakes that were resilient (sufficiently deep and clear to provide suitable habitat for coldwater fish), even in a climate-warmed Minnesota (Fang et al. 2012).

Research results led to management action to protect Cisco habitat in these important refuge lakes. Protecting water quality in these coldwater fish refuge lakes has become the focus of a significant landscape conservation effort among a diverse coalition of partners that include local, state, and national resource and water quality agencies, and a number of nongovernmental organizations (NGOs; Jacobson et al. 2013). Extensive forests are being protected in the watersheds of these resilient systems that offer multiple benefits beyond coldwater fish habitat (e.g., protection of water quality and reduction of forest fragmentation) that allow funding from a number of nontraditional sources; i.e., forest protection and water quality initiatives; dnr.state.mn.us/tullibeelake.html; MNDNR 2016). Approximately US\$4 million has been expended by local, state, and NGO partners working with landowners in prioritized Cisco refuge lake watersheds to develop private land forest protection plans and conservation easements (e.g., leechlakewatershed.org/index.cfm/pageid/14; Leech Lake Area Watershed Foundation 2016).



Schematic diagram of sequence of steps used to develop and implement a climate adaptation strategy to protect Cisco in Minnesota lakes. The sequence including a monitoring program sufficiently long enough to detect a trend, research that directly described the thermal niche and predicted subsequent population responses, and then specific management actions that protected the resilience of important refuge lakes identified by the research.

Box 3: The Blackfoot Challenge

The Blackfoot River is one of the most famous rivers in Montana and gained national recognition in the book and movie *A River Runs through It* (McLean 1976). By the late 1980s and the early 1990s, the people in the Blackfoot Valley recognized that they and the river system were facing mounting stressors. Mining, land-use change, and an expanding human population were colliding with the listing of grizzly bears and Bull Trout *Salvelinus confluentus* under the Endangered Species Act. Local residents banded together with state, federal, and local governments to build the “Blackfoot Challenge.” The challenge recognizes the unique values of the watershed to better address the management issues facing them (blackfootchallenge.org).

The challenge has spent the last two decades identifying the critical resource, economic, and social issues facing the watershed and built a blueprint for watershed restoration. Included in this plan is a recognition that climate change is occurring and that any plan will need to address emerging issues. Rather than develop specific climate-related actions, the goals of the plan are to develop resilient aquatic and terrestrial ecosystems. For example, one of the needs identified in the plan was to increase the resilience of stream temperatures to increasing air temperatures. This involved restoring functioning riparian areas in grazed lands by planting willows and riparian vegetation along stream banks to shade stream reaches and reduce local water temperature. Private landowners, state and federal managers, and nongovernmental groups like Trout Unlimited have worked together to implement these actions, in addition to other restoration activities such as channel reconstruction, improving fish passage, and restoration of stream flows. These actions have increased wild trout abundance in middle to upper watershed reaches, particularly in areas where partners have continued to minimize human activities such as riparian grazing (Pierce et al. 2013).

more holistic view of ecological services is no small challenge. Management agencies can foster social resilience through outreach and education designed to promote a shift in species preferences and broader participation in resource management (e.g., Biggs et al. 2012), but human behaviors are themselves resistant to change and thus may require an unforeseen crisis to adapt and even transform into a new set of values that promotes resilience (Gunderson 1999; Walker and Meyers 2004; Folke et al. 2010). Managing for resilient ecosystems, coupled with a management framework that provides administrative and social resilience, will allow agencies and organizations to better cope with a changing climate.

MONITORING AND MAKING DECISIONS

Fishery managers routinely rely on monitoring programs to assess spatial and temporal differences in resource status metrics, such as fish abundance or angler satisfaction. Monitoring is particularly important for tracking the impacts of climate change in freshwater systems, since projected impacts are uncertain (e.g., Jimenez Cisneros et al. 2014). However, empirical evidence demonstrating current effects of climate change on freshwater systems is beginning to emerge (Eby et al. 2014; Lynch et al., this issue). These outcomes can only be measured by monitoring programs designed to detect and track the primary signals expected from changes in climate. That is, to document change on the ground, there needs to be effort on the ground aimed at detecting change. Monitoring programs will likely continue to focus on detecting the emergence of expected changes, but they may increasingly need to adapt to new knowledge that will inevitably develop as potential individual, population, ecosystem, and social responses to climate changes become better understood. An effective climate change monitoring program can be a vehicle for both hypothesis development and testing. This is best done through a dual structure, consisting of (1) a core data collection program, designed to detect both expected trends (e.g., shifts in spawning phenology of benchmark species groups) and critical events and (2) a research program (linked to the core data collection program) that has an explicit mandate to develop and test new hypotheses around ecosystem responses to climate change, thus ensuring that the core program adapts and continues to generate knowledge regarding realized changes in climate and their impacts on freshwater ecosystems (e.g., Box 5).

Monitoring programs may produce information relevant to decisions, thereby allowing for evidence-based management (Wagner et al. 2013). These programs should monitor not just biophysical changes but also the attitudes and actions of the human users of inland aquatic systems (Hunt et al., this issue). The direct responses of stakeholders to changing climatic conditions and their responses to the ecosystem consequences of climate change will influence how best to manage for sustainable human use of these systems.

Monitoring can also produce the data needed to assess the consequences of management decisions, address uncertainty in the response, determine whether objectives were met, and possibly alter the management

if the objectives were not met. Over time, monitoring programs can also distinguish among alternative hypotheses about system structure and function and improve understanding of how systems respond to management actions (Irwin et al. 2011; Irwin and Conroy 2013).

Comparable data on populations of managed species, spread across a broad climatic range, will help improve our understanding of how such populations respond to changes in climate. Monitoring at this broad spatial scale will likely cross jurisdictional boundaries, which further highlights the need to develop multi-agency collaboration to generate large, systematic landscape-level data sets. Data comparability will demand adoption of standard sampling protocols (e.g., Bonar et al. 2009) or completion of cross-calibration studies (Petersen and Paukert 2009) to generate comparable indices of system status from data collected using different methodologies.

Successful examples exist of freshwater monitoring programs capable of detecting the trends and abrupt shifts expected from systematic changes in climate. For instance, long-term monitoring identified declines of Cisco in northern Minnesota lakes caused by climate change, and this finding led to management actions to help restore this native species (see Box 2). In Ontario, monitoring has identified shifts in both the spawning dates and distributions of centrarchids, and thus led to changes in recreational fishing regulations (Figure 2).

CHALLENGES TO ADAPTATION STRATEGIES

The spatial and temporal scales of climate change will require rethinking some traditional management approaches. Many traditional fisheries management actions, such as stocking and angling regulations, are designed to influence single populations of species in local water bodies. Protecting and restoring the resilience necessary to sustain valuable fisheries in the face of climate warming will require expanding the scope of fisheries management beyond such approaches. Joining forces with other agencies and partners will be required to achieve the broad-scale conservation objectives necessary for managing

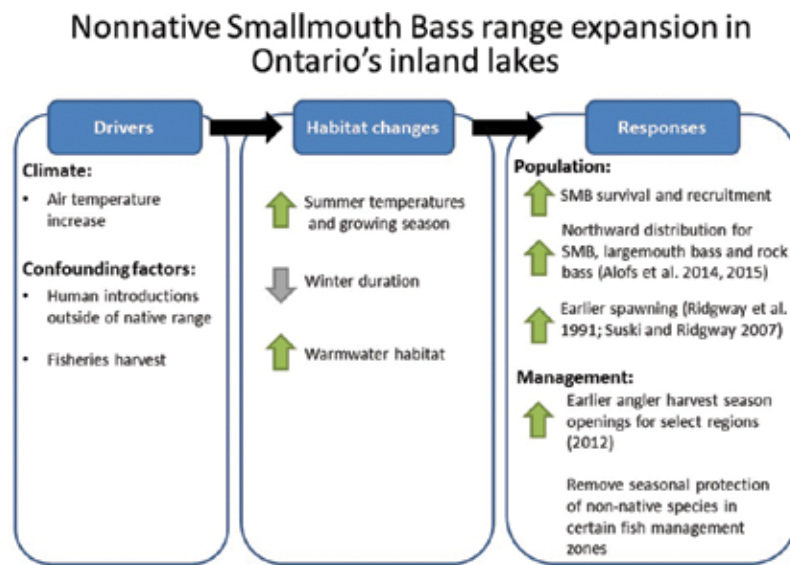


Figure 2. Documented consequences of the northward expansion and changes in spawning phenology of nonnative Smallmouth Bass (SMB) in Ontario's inland lakes facilitated by climate change and the adjustment in harvest regulations by agencies to adapt to these changes. Green arrows indicate an increase or earlier seasonal response; gray arrows indicate a decrease or later seasonal response.

Box 4: An Agency Adapts to a Changing Climate: The Florida Fish and Wildlife Commission Example

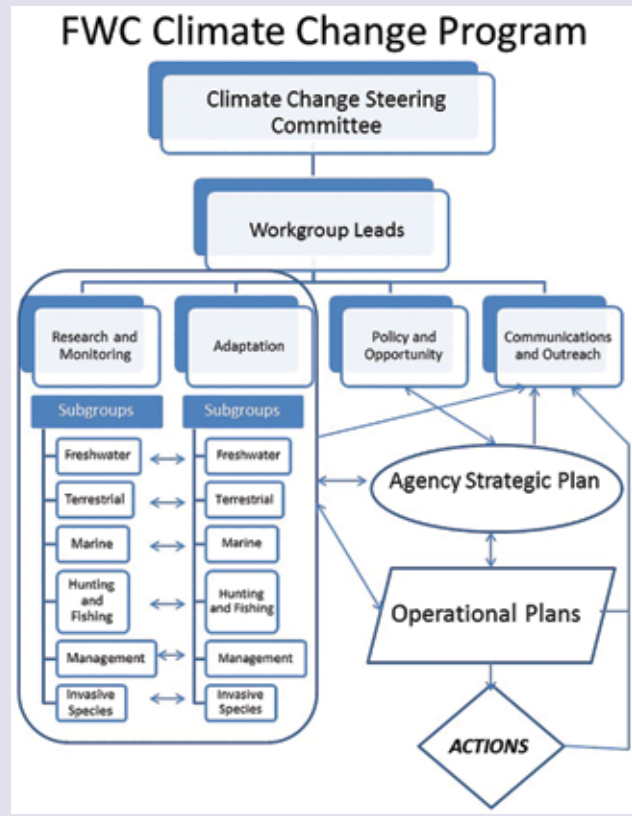
The State of Florida is largely a low-lying peninsula with approximately 1,900 km of coastline. Of the 4,368 species of plants and animals (invertebrate and vertebrate species) identified in the state in 2002, 269 of them were endemic (Stein 2002). Both species and habitats are under threats from a changing climate including impacts associated with rising sea levels, changes in precipitation patterns, increasing ocean acidity, and land-use conflicts arising from development and urbanization. The Florida Fish and Wildlife Conservation Commission (FWC) is charged with “managing fish and wildlife resources for their long-term well-being and the benefit of people” (myfwc.com/about/overview/programs/mission-benefits). Given this mission, the FWC is responding to threats related to a changing climate by developing resources, processes, and projects that can (1) anticipate changes to landscapes and seascapes, (2) identify species and systems that are most vulnerable, and (3) devise adaptation strategies that increase the adaptive capacity of the resources the FWC is mandated to conserve.

In 2008, the FWC developed a program designed to add internal capacity within the agency, thereby facilitating the development and incorporation of adaptation options within the agency’s planning and operations. The structure of that program addresses priorities of a natural resources management agency focusing on species and habitat conservation and management, invasive species control, and providing recreational opportunities for stakeholders. More specifically, the FWC created workgroups focused on climate adaptation, research and monitoring, communications and outreach, and planning and policy. The work groups are overseen by a steering committee of senior managers and administrators (see figure). Given the focus on internal capacity building, a nine-month internal “climate change certification course” was launched. This course consisted of monthly lectures by nationally renowned climate scientists and practitioners. The course included lectures and readings focused on climate science, climate change effects, vulnerability analyses, adaptation development, communications, and policy; a follow-up course addressed more Florida-specific issues. These courses have served as the basis for the National Conservation Training Center’s “Climate Academy” and the California Department of Fish and Wildlife’s “Climate College.”

To build on these activities, the work groups are developing an adaptation guide to provide baseline information that will support incorporating climate change into planning and management processes and actions. The guide will present the current state of the science and predicted changes in the state, the ecological consequences of those changes, and guidance on possible adaptation strategies that could be incorporated into management actions under the emerging threats.

The FWC has also funded a number of projects through existing funding mechanisms including the State Wildlife Grants Program to help understand plausible future impacts. These projects focused on assessing the vulnerabilities of Florida’s species and natural communities, developing information that will influence and guide inclusion of climate change into planning processes, and implementing and assessing adaptation strategies. In some cases, projects focused on possible social and economic futures that could guide planning. The projects are designed to build upon each other so that ultimately a comprehensive roadmap for conservation under a changing climate can be developed. In some cases, on-the-ground projects have tested concepts that have emerged from this process including bank stabilization, developing living shorelines, and removing barriers to connectivity.

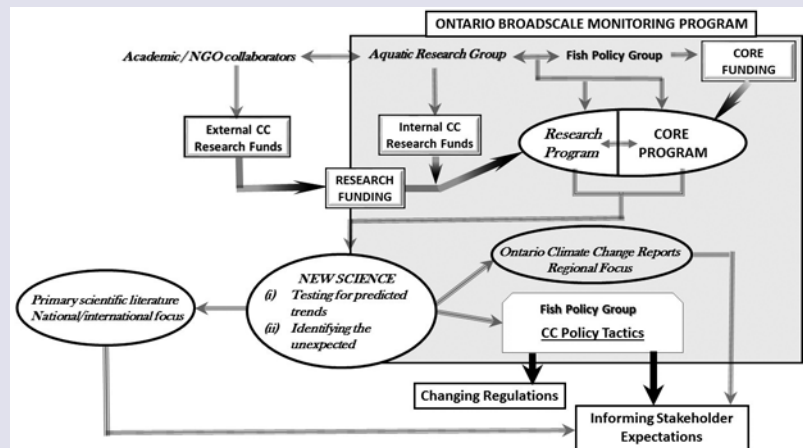
To date, several FWC planning processes have integrated climate impacts, including a dedicated chapter in the 2015 revised version of the State Wildlife Action Plan, Imperiled Species Management plans and associated Integrated Conservation Strategy, and Wildlife Management Area plans as they cycle through the scheduled revision process. “Climate-smart” approaches have been introduced to managers of two of the FWC’s wildlife management areas as a pilot, and the feedback is informing a more comprehensive project that will address the management plans of several of the state’s wildlife management areas and U.S. Fish and Wildlife Service refuges under threats from rising seas and land use change. All of the activities of the FWC climate change program are designed to build internal capacity, develop partnerships, and reduce uncertainty. Importantly, the FWC climate activities are designed to develop a more adaptive agency, increase the resilience of the resources under their stewardship in the face of emerging threats, and instill a culture of considering a changing climate in the agency’s plans.



The Florida Fish and Wildlife Conservation Commission (FWC) Climate Program’s structure including the linkages to operational plans and actions. The Adaptation and Research and Monitoring workgroups are composed of subgroups of both managers and scientists who work together to develop adaptation strategies to incorporate into the agency-wide plans (e.g., Agency Strategic Plan). Operational plans include for example the State Wildlife Action Plan, the Imperiled Species Management plans, and Wildlife Management Area plans. Some examples of actions may include changes in prescribed burning practices to account for changing climatology, adjusting water-release schedules from impoundments to ensure suitable estuarine salinity for aquatic “species of greatest conservation need,” and changes in fishing seasons to preserve fish reproductive output.

Box 5: The Broadscale Monitoring Program by the Ontario Ministry of Natural Resources and Forestry

The Ontario Ministry of Natural Resources and Forestry Broadscale Monitoring Program (2008–present) is an example of a resilient monitoring program that is capable of detecting the trends and abrupt shifts expected from systematic changes in climate (see figure). Its dual structure of research and core components (see figure) ensures that (1) the research program develops new knowledge about the likely impacts of climate change on Ontario’s freshwater resources and (2) the core monitoring program efficiently incorporates that new knowledge in order to maintain its ability to detect the realized impacts of climate change. The program is designed to operate over successive five-year cycles. In each cycle, a representative sample of approximately 700 lakes is randomly selected from the approximately 11,000 lakes greater than 500 ha in Ontario. These lakes are surveyed within a two-month window using identical survey protocols. Data from the core survey program characterize: (1) lake water chemistry and temperature, (2) zooplankton abundance, (3) fish community composition, (4) relative abundance and life history characteristics of sport fishes (e.g., Lake Trout *Salvelinus namaycush* and Walleye *Sander vitreus*), and (5) fishing intensity and other indices of human use. Data from the core program and related Ontario Ministry of Natural Resources and Forestry surveys have been used to detect trends toward earlier spawning dates in Ontario centrarchid populations and to identify northward shifts in centrarchid zoogeographic distributions across the province (Alofs et al. 2014; Alofs and Jackson 2015). These findings have led to changes in recreational fishing seasons in different regions of the province (Figure 2). Results from the research program have extended earlier work (e.g., VanderZanden et al. 1999; Venturelli et al. 2010) to show how changes in climate may affect sustainable harvests of Walleye and Lake Trout (Lester et al. 2014; Tunney et al. 2014).



Schematic diagram of the management and outputs of the Ontario Broadscale Monitoring Program. Arrows indicate connections between groups involved in running the program, and generating and using its products. Relevance of its data products to climate change (CC) is highlighted. Compound arrows are science information pathways; gradient arrows are funding pathways; solid black arrows are policy and stakeholder pathways.

resilience in aquatic systems. For example, protecting coldwater fishes that are particularly susceptible to warming temperatures requires coordinated efforts from local, regional, national, and sometimes international management groups. These efforts will also require coordinated efforts from local communities and private landowners, tribal entities, and state/provincial and federal governments (see Box 3). Though there are several examples of successful partnerships to address fisheries issues, the scale of coordination, the recognition of the roles of the various parties, and the development of meaningful actions can be a challenging process. Frameworks that explicitly incorporate climate adaptation into broad-scale conservation will be valuable (Schmitz et al. 2015). In addition, governmental policies and decisions often work at different purposes and administrative levels in the development and implementation of conservation goals. Negotiating the balance between resource sustainability and the economic and social consequences of implemented actions will require difficult decisions and in some cases lost opportunities. Government actions coordinated across all scales are necessary and will require us to take the “long” view for resource sustainability.

Adequate funding and valuation by the public for fisheries conservation and management has always been a challenge, and adding climate change to the myriad of issues facing agencies and organizations will make funding prioritization even more challenging. New partnerships among government, private, and nongovernmental organizations will be needed to expand the resources available to address climate-induced challenges. In

some cases, these partnerships have already been formed and have recognized the need to address climate change in current management (see Box 3). Funding developed from multiple sources, including the private sector, will be needed to meet management needs moving forward.

One challenge is that many conservation partnerships have been developed to conserve and manage species of concern or charismatic species. We typically have more information on the life history and basic biology of these charismatic or economically important species than the thousands of other species that exist on the landscape. Though cool/coldwater game fishes have received much of the attention, other species may provide important information on thermal tolerances and resistance to changing temperatures and how rapidly organisms can respond and adapt to changing conditions (Whitney et al., this issue). In a recent assessment of Missouri stream fishes’ vulnerability to climate and land use change, 25% of the species could not be assessed because of limited information on thermal and flow tolerances of those species (Sievert et al. 2016). In addition, nonnative species are sometimes habitat generalists that are more tolerant of changing environmental conditions and thus represent a threat to aquatic systems where desired native recreational, commercial, and subsistence fisheries may exist (e.g., Common Carp *Cyprinus carpio*). Understanding how climate affects these relationships will be important to sustain these opportunities or, in some cases, realize where we need to reprioritize our management actions.

CONCLUSIONS

Decision makers can cope with climate change and its effects on fish and fisheries by developing resilient ecological and management systems and monitoring the ecological systems to detect changes. Our knowledge of how climate change affects individual fish, populations, and communities is certainly incomplete but is growing (Lynch et al., this issue; Whitney et al., this issue). Managers may consider prioritizing monitoring for the production and use of information to enable defensible, evidence-based decision making. Currently, some on-the-ground monitoring programs are producing decision-relevant information, and agencies are adapting in response to changing socioecological influences (Hunt et al., this issue). System monitoring can help increase the quality and quantity of information available to policy makers (e.g., question-driven monitoring) and also help assess whether outcomes match expectations (e.g., metric-driven monitoring). Furthermore, we believe that managing for resilience will require expanding the definition of fisheries management beyond traditional boundaries. Such efforts will require broad-reaching partnerships and will be critical for adaptation on a scale that produces meaningful results.

Climate change and its associated effects will be one of the grand challenges facing fisheries management in the future. We suggest that managers and their partners are making substantial strides in developing resilient systems. Continued adaptation and decision making based on long-term monitoring will help us learn more about the effects of climate change on fish and fisheries, aquatic communities, and the users of these resources. This growing knowledge base will allow managers to mobilize the best available science in making the decisions needed to sustain, enhance, and restore fish populations.

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CANADIAN AQUATIC RESOURCES SECTION

Climate Change Impacts on Freshwater Fishes: A Canadian Perspective

Mark S. Poesch

Department of Renewable Resources, University of Alberta, 751 General Services Building, Edmonton, AB, Canada T6G 2H1. E-mail: poesch@ualberta.ca

Louise Chavarie

Center for Systems Integration and Sustainability, Michigan State University, East Lansing, MI

Cindy Chu

Ontario Ministry of Natural Resources and Forestry, Peterborough, ON, Canada

Shubha N. Pandit

Terrestrial and Aquatic Applied Research and Management, Terraqua Inc., Entiat, WA

William Tonn

Department of Biological Sciences, University of Alberta, Edmonton, AB, Canada

Current and projected patterns of global climate change are a major concern to freshwater fisheries in Canada. The magnitude of the impacts of climate change vary among species and ecoregions. The latest climate change scenario projections for Canada suggest that by 2050 temperatures will increase between about $4.9^{\circ}\text{C} \pm 1.7^{\circ}\text{C}$ (average mean \pm standard deviation) and $6.6^{\circ}\text{C} \pm 2.3^{\circ}\text{C}$ under the Representative Concentration Pathways (RCPs) 2.6 and 8.5 emission scenarios, respectively. These changes will have an important influence on the physiology, distribution, and survival of freshwater fishes, as well as other ecological processes in direct, indirect, and complex ways. Here we provide a perspective from the Canadian Aquatic Resources Section on the impacts of climate change to freshwater fishes. Given the geographic size and diversity of landscapes within Canada, we have divided our perspective into three regions: eastern, western, and northern Canada. We outline the impacts of climate change to these regions and outline challenges for fisheries managers. Because climate change does not operate in isolation of other environmental threats, nor does it impact species in isolation, we suggest improved interjurisdictional integration and the use of an adaptive and ecosystem-based approach to management of these threats.

INTRODUCTION

The Canadian Aquatic Resources Section (CARS) has a mandate to promote the conservation, development, and wise management of aquatic resources in Canada, within the context of sound ecological principles and sustainability. Inland recreational fisheries in Canada encompasses over 3.6 million anglers and represents CDN\$2.5 billion in direct expenditures and \$8.7 billion in other purchases annually (DFO 2013). Current and projected patterns of global climate change are a major concern to freshwater fisheries in Canada. The magnitude of the impacts of climate change vary among species and ecoregions, but it has been predicted to be higher particularly in northern freshwater ecosystems as water temperature is predicted to rise faster in northern regions due to reduced ice cover and decreased albedo effects (Hansen et al. 2006; Karl et al. 2009). A study has already shown that in the experiment lake areas (Ontario), mean annual air temperatures have risen by 2°C and evaporation rates have increased by 30% within a 20-year period (1960s to mid-1980s; Schindler et al. 1990), and the latest climate change scenario projections for Canada suggest that by 2050 temperatures will increase between about $4.9^{\circ}\text{C} \pm 1.7^{\circ}\text{C}$ (average mean \pm standard deviation) and $6.6^{\circ}\text{C} \pm 2.3^{\circ}\text{C}$ under the Intergovernmental Panel on Climate Change (IPCC) Representative Concentration Pathways (RCPs) 2.6 and 8.5

emission scenarios, respectively (Figure 1). Because temperature affects ectothermic species such as freshwater fishes (Whitney et al., this issue), changes in water temperature, snowpack, and permafrost will have an important influence on the physiology, distribution, and survival of freshwater fishes, as well as other ecological processes in direct, indirect, and complex ways (Table 1).

EASTERN CANADA

Eastern Canada, defined here as the region spanning the provinces of Ontario, Quebec, New Brunswick, Nova Scotia, Prince Edward Island, and Newfoundland and Labrador, encompasses an area of 2.7 million km^2 . The region includes hundreds of thousands of freshwater lakes, thousands of kilometers of natural and regulated rivers, and some of the largest tracks of pristine wetlands and boreal forests in the world (NRCan 2010). These aquatic ecosystems drain into the St. Lawrence River, Hudson Bay, and Atlantic Ocean (NRCan 2010) and include eight freshwater ecoregions of the world (Abell et al. 2008). The latest IPCC RCP projections indicate that by the 2070s, air temperatures will increase throughout eastern Canada by 2°C – 11°C , with greater warming in the north (Figure 1). Precipitation will generally increase throughout the region, but northern Quebec and Labrador will have the greatest

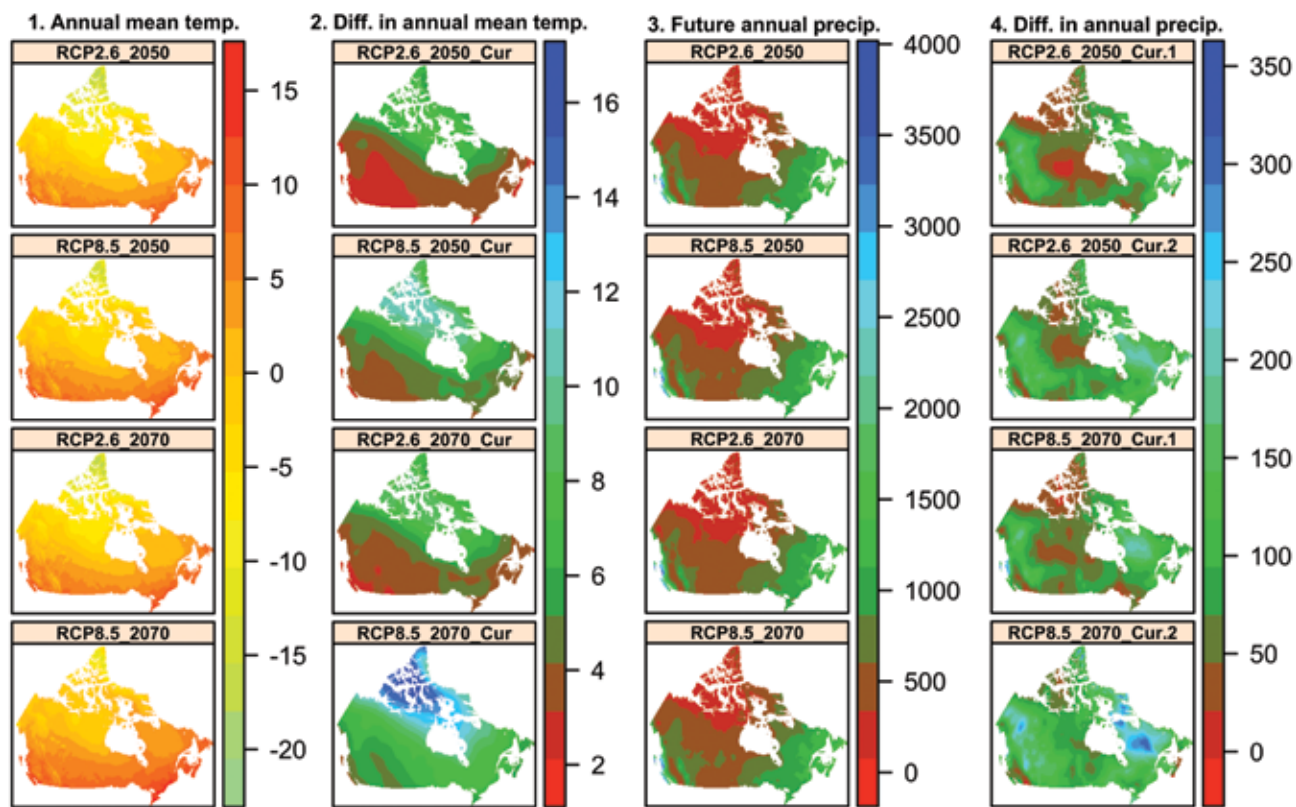


Figure 1. Projected (A)–(D) temperature (°C) and (E)–(H) precipitation (mm) in Canada for 2050s and 2070s under two Representative Concentration Pathways (RCP 2.6 and RCP 8.5 of Geophysical Fluid Dynamics Laboratory’s [GFDL] CM3). A1 and B1 are the difference in annual mean air temperature of 2050s from the current air temperature under RCP 2.6 and 8.5, respectively, whereas C1 and C2 are the difference in air temperature between 2070s and current under RCP 2.6 and 8.5, respectively. E1, F1, G1, and H1 are the difference in annual total precipitation between 2050s and current and 2070s and current under scenarios RCP 2.6 and 8.5, respectively. Note: This figure was generated using the data of 2013 generation General Circulation Model (GFDL CM3 at five-minute spatial resolution) projections with two greenhouse gas emission concentration scenarios (RCP 2.6 and 8.5) from the 5th Assessment Report of the IPCC. The data were accessed from Worldclim.org on February 20, 2016.

increases of 150–350 mm by the 2070s. In addition to these general regional patterns, the water budgets of the lakes, rivers, and wetlands will be affected by variations in the seasonal timing and magnitude of temperature and precipitation.

The highest biodiversity of freshwater fishes in Canada is found in the Laurentian Great Lakes Ecoregion (approximately 120 species) and decreases with latitude (Abell et al. 2008). Fish assemblages in southern watersheds are dominated by warmwater and coolwater species, such as centrarchids and percids, whereas more northern watersheds are dominated by coldwater salmonids (Chu et al. 2014). Several studies have projected the impacts of climate change on aquatic ecosystems in different regions of eastern Canada. These include increases in lake and stream temperatures in Ontario and New Brunswick (Kurylyk et al. 2013; Chu 2015); increases in winter discharges, earlier spring freshets, and decreases in spring discharges in tributaries of the St. Lawrence River in Quebec (Boyer et al. 2010); decreases in winter stream surface temperatures due to snow melt in east–central New Brunswick (Kurylyk et al. 2013); and degradation of perennially frozen peatlands and severe drying of peatlands in the northern region of eastern Canada (Tarnocai 2009). Documented effects of climate change on freshwater habitats in eastern Canada are rare, but a handful of studies suggest that lake temperatures have increased (Dobiesz and Lester 2009), and winter flows in some rivers have increased due to snowmelt (Beauchamp et al. 2015). These changes will

likely be amplified into the next century under the temperature and precipitation changes. Evidence of the impacts of climate change on freshwater fish species distributions, phenology, and population and assemblage dynamics is mounting (Casselman 2002; Robillard and Fox 2006; Alofs et al. 2014; Lynch et al., this issue). The northern range limits of centrarchids that prefer warm waters are moving poleward at the rate of 13 km/decade (Alofs et al. 2014); earlier spawning runs and smolt outmigration in Atlantic Salmon *Salmo salar* (Russell et al. 2012); mismatch between the timing of smolting (Friedland et al. 2003); biogeochemical conditions in the marine environment; and the proportion of coolwater and warmwater species in fish assemblages are shifting from coldwater and coolwater assemblages to those dominated by coolwater and warmwater species (Robillard and Fox 2006). These observations are consistent with the forecasted changes in species distributions, phenology, and assemblages in eastern Canada (Power 1990; Chu et al. 2005; Jonsson and Jonsson 2009).

In eastern Canada, inland commercial fisheries support a \$37.5 million industry, whereas recreational fisheries support a \$3.39 billion industry (DFO 2013). The most harvested commercial species are Yellow Perch *Perca flavescens* and Walleye *Sander vitreus*. Recreational harvest varies by region, but the most sought after species are Brook Trout *Salvelinus fontinalis* (Russell et al. 2012) and Walleye (DFO 2013). The potential decline or increase in habitat availability and

Table 1. Summary of some key environmental changes (ongoing and anticipated) in Canadian freshwater ecosystems and potential consequences to their fish communities resulting from climate change. The table is not meant to be read across; that is, changes and effects in the same “row” do not imply direct links; rather, effects are likely the result of interactions among several environmental changes. Also listed are anticipated effects of increased human population and development activities. This table is a synthesis of the following sources: Schindler et al. (1990); Minns and Moore (1992, 1995); Prowse et al. (2011); Reist et al. (2006, 2013, 2015); Schindler and Donahue (2006); Ficke et al. (2007); Angers et al. (2010); Vincent et al. (2011); Culp et al. (2012); Linnansaari et al. (2012); Shuter et al. (2012); CAFF (2013); Nielsen et al. (2013); Salinas et al. (2013). ↑ = increase; Δ = change.

Expected changes	Environmental effects	Biotic effects
↑ frequency of extreme climate events	↑ permafrost degradation and Δ thermokarst processes	Δ quantity and access to critical habitat
Δ seasonal phenology	Δ drainage patterns	↑ mismatch of phenology and life history
↑ air temperature (especially winter)	Δ ice breakup processes and timing	Δ contaminant bioaccumulation
↑ water temperature	Δ freshet timing, duration, and magnitude	Δ population structure (e.g., age and size classes)
Δ precipitation (amount and form)	Δ groundwater levels	Δ demographic parameters
Δ ice cover duration	Δ evaporation, surface water levels, and habitat connectivity	Δ phenotype and genotypes
Δ ice thickness	Δ timing and magnitude of nutrient and dissolved organic carbon (DOC)	Δ ecosystem productivity and relative contributions from terrestrial, pelagic and benthic sources
Δ wind patterns	Δ ecosystem productivity	Δ geographical range limits of northern and southern species
Δ atmospheric pressure	Δ turbidity and light regime	Δ community composition and relative abundance (predators, prey, competitors, parasites)
↑ human population and activities	Δ sedimentation	
Δ drainage patterns	Δ carbon source/sinks/availability	
Δ ice breakup processes and timing	Δ mixing/stratification patterns, oxygen, and thermal profiles	
Δ freshet timing, duration, and magnitude	↑ mobilization and toxicity of contaminants	
Δ groundwater levels	Δ contaminant catchments (air and water)	
Δ evaporation, surface water levels, and habitat connectivity	↑ industrial activities and infrastructure	
Δ timing and magnitude of nutrient and DOC	↑ resource exploitation (commercial, recreational)	
Δ ecosystem productivity	↑ contaminant export from the south via long-range atmospheric transport	
Δ turbidity and light regime		
Δ sedimentation		
Δ carbon source/sinks/availability		
Δ mixing/stratification patterns, oxygen, and thermal profiles		
↑ mobilization and toxicity of contaminants		
Δ contaminant catchments (air and water)		
↑ industrial activities and infrastructure		
↑ resource exploitation (commercial, recreational)		
↑ contaminant export from the south via long-range atmospheric transport		
↑ mismatch of phenology and life history		
Δ contaminant bioaccumulation		
Δ population structure (e.g., age and size classes)		
Δ demographic parameters		
Δ phenotype and genotypes		
Δ ecosystem productivity and relative contributions from terrestrial, pelagic and benthic sources		
Δ geographical range limits of northern and southern species		
Δ community composition and relative abundance (predators, prey, competitors, parasites)		

productivity of coldwater versus warmwater species will bring a variety of social and economic challenges as novel fishing opportunities for warmwater species may not offset declines in the coldwater or coolwater fisheries. Therefore, adaptive management is required throughout eastern Canada with the known and potential effects of climate change incorporated into fisheries management plans (Dove-Thompson et al. 2011). Climate change adaptation plans have been developed for several jurisdictions within eastern Canada (Gleeson et al. 2011; Government of Quebec 2012). All outline policy, potential adaptation options, research and monitoring needs, and implementation plans to address climate change impacts. These plans provide guidelines that, if realized, should assist in the conservation and sustainability of fishes and fisheries in eastern Canada in the future.

WESTERN CANADA

Western Canada defined here is the region spanning the provinces of Manitoba, Saskatchewan, Alberta, and British Columbia. This area includes a diversity of ecoregions: the Pacific coastal range, Okanagan interior plateau, foothills, the Rocky Mountains, open prairie, and northern boreal forest. Freshwater systems and species composition are similarly diverse and include the Pacific Coast, Glaciated Columbia, Upper Missouri, Upper and Middle Saskatchewan, Winnipeg Lakes, Southern Hudson Bay, and the Upper Mackenzie (Abell et al. 2008). Impacts of climate change varies across western Canada from drought in the prairies (Schindler and Donahue 2006), to reduced snow pack in the Rocky Mountains (Stewart et al. 2004; Milner et al. 2009), to changes in precipitation and fire in the boreal forest (Flannigan and Van Wagner 1991). Because the freshwater systems in this region primarily drain from the Rocky Mountains to outlets across the continent such as the Pacific Ocean, Arctic Ocean, and Hudson Bay, issues related to reductions in snowpack and drought remain of high concern throughout the region (Hauer et al. 1997; Stewart et al. 2004; Schindler and Donahue 2006), although understanding the interconnectedness between climatic, environmental, and biotic interactions remains complex (Table 1).

Each ecoregion in western Canada supports important recreational fisheries, representing approximately CDN\$1 billion in direct expenditures and \$2.5 billion in additional purchases (DFO 2013). The Pacific coast and interior plateau are composed of 46 species, most as postglacial migrants, with large runs of anadromous salmon. The Rocky Mountains and foothill natural regions support numerous trout species, including pure Westslope Cutthroat Trout *Oncorhynchus clarkia lewisi* and Bull Trout *Salvelinus confluentus* populations, as well as Lake Whitefish *Coregonus clupeaformis* and Arctic Grayling *Thymallus arcticus*. The prairies have popular game species such as Yellow Perch, Northern Pike *Esox lucius*, and Lake Whitefish. The boreal forest ecoregion supports common game fish species including Arctic Grayling, Mooneye *Hiodon tergisus*, Goldeye *Hiodon alosoides*, Lake Trout *S. namaycush*, Mountain Whitefish *Prosopium williamsoni*, Lake Whitefish, Northern Pike, Walleye, and Yellow Perch. Many of the freshwater species found throughout western Canada are already undergoing dramatic declines that are predicted to be amplified with climate change. For example, Arctic Grayling have declined by over 40% from their historical range in Alberta (AESRD 2005), and 78% of Bull Trout core areas are considered to be at high risk (AESRD 2012). Athabasca Rainbow Trout *O. mykiss* are a subform in the Rainbow Trout complex that remain east of

the Continental Divide (Carl et al. 1994) that are susceptible to impacts from climate change through shifting distributions and competition with nonnative species (AESRD 2009). Coho Salmon *O. kisutch* spawning has declined substantially in the Pacific region (Bradford and Irvine 2011).

Mitigation of climate change impacts to fisheries in western Canada will require concerted effort from management agencies and is complicated by other large drivers such overfishing, invasive species, land-use change, resource development, and habitat alteration (Bradford and Irvine 2011; Maitland et al. 2016). Knowledge gaps include understanding changing ocean conditions on returning anadromous salmon (Bradford and Irvine 2011), the influence of snowpack on water availability (Stewart et al. 2004; Milner et al. 2009), and how water quantity will influence fisheries productivity (Schindler and Donahue 2006). Given the diversity of landscapes in western Canada, the challenges faced by climate change will vary across the region and will require adaptive management approaches. Management plans for many declining species have been developed across jurisdictions in western Canada (AESRD 2005, 2009, 2012) and include mitigating impacts of climate change. However, these plans are often species specific and are therefore not ecosystem based. Future management will require integrated interjurisdiction coordination and ecosystem-based approaches to help mitigate the impacts of climate change.

NORTHERN CANADA

Northern Canada defined here includes all Canada territories: Nunavut, Northwest Territories, and the Yukon. Freshwater ecoregions found in northern Canada are the Upper MacKenzie basin, central Arctic coasts, western Hudson Bay, the Upper Yukon, and the Canadian Arctic archipelago (Abell et al. 2008). Climate change represents the most serious anthropogenic challenge to northern, and especially arctic, ecosystems, not only threatening biodiversity directly but also by contributing to other significant threats; for example, increases in industrial activity, pollution, and overharvest, and the spread of nonnative species (CAFF 2013). The Arctic is warming at a rate twice the rest of the planet (Solomon 2007); a trend that is expected to continue throughout the 21st century. Arctic lake and river ecosystems in Canada will be affected by climate change through changes in the annual thermal and hydrological regimes (Figure 1), changes that will significantly impact the systems' hydrological and limnological properties and contaminant burdens. These environmental changes will, in turn, affect freshwater biodiversity, including potential new species moving northward (Table 2). To develop management plans for the fisheries (and other biotic resources) of these ecosystems, we need to understand and anticipate how northern Canada's freshwater fauna will respond to such dramatic and rapid changes.

Canadian Arctic and Subarctic freshwaters support 13 families of fishes, with Salmonidae being the most diverse, many of which are important in various fisheries. Many fishes of northern Canada, including many of the important salmonids, are winter specialists, exhibiting adaptations for extended periods of low temperature, light, and food levels (Shuter and Meisner 1992; Minns and Moore 1995). These cold-climate adaptations, however, will likely leave many Arctic fishes vulnerable to climate change, because they bring decreasing winter duration and increasing summer surface-water temperatures, as well as other cumulative, cascading, and synergetic effects (Table 1). Given the extent of their adaptations to the harsh Arctic environment and the speed of the predicted

Table 2. List of species that have potential to extend their range and/or abundance northward into the Arctic, with some biological characteristics related to expansion of their existing ranges. Temperatures are for adult individuals; values in parentheses capture spatial variation across populations found in the literature.

Species	Optimum temperature (growth; °C)	Lower/upper range for survival	Salinity tolerance	Colonization potential	Current/projected status	References
Atlantic Salmon	16-19	0-(23.3-26.7)	Euryhaline	Populations in Ungava Bay (QC) but never colonized habitat outside of their native range to date	Large range of temperature tolerance but least tolerant to low temperatures of <i>Salmo</i> species, northern tip of Québec may be a migration barrier	Scott and Crossman (1973); ACIA (2010); Elliott and Elliott (2010); Hasnain et al. (2010); Nielsen et al. (2013)
Chinook Salmon	14.8-20	0.8-(24.7-26.2)	Euryhaline	Pacific salmon have been documented in the Arctic for over 100 years	Since 2003, only seven observations reported	Brett (1952); Scott and Crossman (1973); Jobling (1981); Raleigh et al. (1986); Wismer and Christie (1987); McCullough (1999); Sullivan et al. (2000); ACIA (2010); Hasnain et al. (2010); Dunmall et al. (2013); Nielsen et al. (2013)
Coho Salmon	15-17	1.7-(25.8-28)	Euryhaline	Pacific salmon have been documented in the Arctic for over 100 years	Since 2003, only one observation reported	Brett (1952); Scott and Crossman (1973); Jobling (1981); Wismer and Christie (1987); Sullivan et al. (2000); ACIA (2010); Hasnain et al. (2010); Dunmall et al. (2013); Nielsen et al. (2013)
Chum Salmon	12-14	-0.5 to (23.2-25.8)	Euryhaline	Chum Salmon juveniles are presumed relatively tolerant of low freshwater temperatures, spend less time postemergence in freshwater, and grow rapidly in marine habitats	Chum Salmon have been harvested annually since 1997 and abundant harvests are becoming more frequent. Spawning populations are reported in the Upper Mackenzie	Brett (1952); Scott and Crossman (1973); Jobling (1981); ACIA (2010); Hasnain et al. (2010); Sullivan et al. (2000); Dunmall et al. (2013); Nielsen et al. (2013)
Pink Salmon	15.5	0-23.9	Euryhaline	Pink Salmon juveniles are presumed tolerant of the low freshwater temperatures, spend less time postemergence in freshwater, and grow rapidly in marine habitats	Pink Salmon has the broadest distribution of all Pacific salmon in the Arctic, and harvests have increased, but spawning populations in Canadian Arctic remain elusive	Brett (1952); Scott and Crossman (1973); Wismer and Christie (1987); Jobling (1981); Sullivan et al. (2000); ACIA (2010); Hasnain et al. (2010); Dunmall et al. (2013); Nielsen et al. (2013)
Sockeye Salmon	15	3.1-(23.5-25.8)	Euryhaline	Pacific salmon have been documented in the Arctic for over 100 years	Since 2003, only 10 observations reported	Brett (1952); Scott and Crossman (1973); Jobling (1981); Wismer and Christie (1987); Sullivan et al. (2000); ACIA (2010); Hasnain et al. (2010); Dunmall et al. (2013); Nielsen et al. (2013)
Lake Whitefish	12-16.8	0.1-26.6	Stenohaline	Whitefish have expanded northward into to the low Arctic, up to Cambridge Bay (NU)	Whitefish yields are projected to increase threefold	Scott and Crossman (1973); Jobling (1981); Christie and Regier (1988); Wismer and Christie (1987); Minns and Moore (1992); Reist et al. (2006); ACIA (2010); Hasnain et al. (2010)
Small-mouth Bass	25-29	(1.6-10.1)-35	Stenohaline	Not present currently in Arctic	Lakes in the Arctic are predicted to be thermally suitable by 2100	Horning and Pearson (1973); Scott and Crossman (1973); Jobling (1981); Wismer and Christie (1987); Jackson and Mandrak (2002); Chu et al. (2005); Reist et al. (2006); Sharma et al. (2007, 2009); Hasnain et al. (2010)
Northern Pike	23	0.1-(28.4-34)	Stenohaline	Temperate center of distribution but ranges widely into the Arctic, up to coastal area of Arctic Ocean	Northern Pike yields in Arctic/Subarctic are projected to increase threefold	Scott and Crossman (1973); Jobling (1981); Wismer and Christie (1987); Christie and Regier (1988); Minns and Moore (1992); Casselman (1996); Hillman et al. (1999); Reist et al. (2006); ACIA (2010); Hasnain et al. (2010)
Walleye	18-22	<4-(29-35)	Stenohaline	Temperate center of distribution but ranges into southern Arctic, extending to the Mackenzie River delta	Walleye yields in Subarctic are projected to increase tenfold	Scott and Crossman (1973); Kitchell et al. (1977); Jobling (1981); Wismer and Christie (1987); Christie and Regier (1988); Minns and Moore (1992); Armour (1993); Hillman et al. (1999); Chu et al. (2005); Reist et al. (2006); Zhao et al. (2008); ACIA (2010); Hasnain et al. (2010)
Yellow Perch	21-24	1.1-(29.2-32.3)	Stenohaline	Temperate center of distribution but ranges into Subarctic (Great Slave Lake)	Northward range extensions of 2° to 8° latitude are projected	Scott and Crossman (1973); Kitchell et al. (1977); Jobling (1981); Wismer and Christie (1987); Hillman et al. (1999); Reist et al. (2006); ACIA (2010); Hasnain et al. (2010)

changes in their environment, coldwater specialists may be unable to respond sufficiently (Reist et al. 2006, 2013, 2015; Shuter et al. 2012). Impacts from climate change, therefore, may directly and indirectly affect abundances of local populations and cause range reductions along southern distributional boundaries, just as more eurythermal species become increasingly better suited and extend their ranges northward (CAFF 2013). First-order responses of fish populations—for example, changes in growth and survival—are expected to be followed by mostly negative second-order effects, including loss of coldwater refugia, mismatches between environmental phenology and life history, and increased competition from eurythermal species (Table 1; Reist et al. 2006; Prowse et al. 2011). These effects would alter community composition and diversity, likely to the detriment of northern specialists.

In face of climate change, fisheries management will need to mitigate effects on fish populations at different timescales, because increases in extreme climatic events can induce short-term variability (i.e., 1–5 years), whereas longer timescales should bring about more consistent climatic change impacts (Brander 2010). However, our limited knowledge about the biology of Arctic fishes and their ecosystems, combined with uncertainty regarding the specifics of climate projections, limits our ability to prepare for the predicted changes. Nevertheless, a number of general response recommendations have been put forward by Heller and Zavaleta (2009). Because climate change does not operate in isolation of other environmental threats, nor does it impact species in isolation, we need to (a) develop and implement integrated techniques for monitoring (early detection), reporting, and management of these anthropogenic biodiversity threats (climate change, invasive species, pollution, overharvesting) across large spatial scales; and (b) take an ecosystem-based approach to management of these threats at local scales; (c) establish a connected network of protected areas to safeguard Arctic ecosystem resilience and better enable species to adapt to climate change; (d) identify and protect refugial areas for Arctic specialists; and (e) increase research efforts aimed at addressing knowledge gaps for Arctic taxa; for example, advance our understanding of physiological, behavioral, and demographic responses to drivers of climate change and the responses of the freshwater ecosystems that support Arctic specialists.

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Round-the-Coast: Snapshots of Estuarine Climate Change Effects

Karin Limburg

Department of Environmental and Forest Biology, SUNY College of Environmental Science and Forestry, Syracuse, NY. E-mail: klimburg@esf.edu

Randy Brown

U.S. Fish and Wildlife Service, Fairbanks, AK

Rachel Johnson

Southwest Fisheries Science Center, National Marine Fisheries Service & Department of Animal Sciences, UC Davis, Davis, CA

Bill Pine

Department of Wildlife Ecology and Conservation, University of Florida, Gainesville, FL

Roger Rulifson

Institute for Coastal Science and Policy, and Department of Biology, East Carolina University, Greenville, NC

David Secor

Chesapeake Biological Laboratory, University of Maryland Center for Environmental Science, Solomons, MD

Kelly Timchak

Lower Rogue Watershed Council Coordinator, Gold Beach, OR

Ben Walther

Department of Life Sciences, Texas A&M University, Corpus Christi, TX

Karen Wilson

Department of Environmental Science and Policy, University of Southern Maine, Portland, ME

ALASKA

Recent declines in Arctic Ocean summer sea ice constitute one of the most tangible effects of climate change anywhere. Notable environmental effects are increased water temperature, solar exposure, and freshwater inputs, which have led to enhanced primary production and a distributional shift north for many marine organisms including fish. Adult Pacific salmon *Oncorhynchus* spp. are occasionally captured along the north coast of Alaska and northwest Canada, and there is a widespread public expectation that they will become an abundant resource over time. However, winter still falls on the land and sea, and few northern rivers maintain adequate flow and temperature for successful spawning and egg incubation. If young are produced in northern rivers, they would smolt into the Beaufort Sea, where they would face a long migration against prevailing currents into the southern Bering Sea before winter sea ice covers the ocean. Temperature under sea ice drops to about -1.7°C , which is too cold for salmonids. Eventually, the Arctic region may warm enough that the entire Pacific salmon life cycle will work and colonization will be successful. In the meantime, small numbers of Pacific salmon will continue to probe the northern limits of available habitat.

—R. Brown

ROGUE RIVER, OREGON

The city of Gold Beach and much of Curry County, Oregon, depend economically on the lower Rogue River and its estuary and the fish, wildlife, and recreation values they impart. The estuary is the vital interface between ocean and freshwater that is critical to the health and survival of threatened anadromous species such as Coho Salmon *O. kisutch* and Chinook Salmon *O. tshawytscha*, Green Sturgeon *Acipenser medirostris* and White Sturgeon *A. transmontanus*, steelhead *O. mykiss*, and Pacific Lamprey *Lampetra tridentata*. Climate change affects salmon throughout their life stages and poses an additional stress. As more winter precipitation falls as rain rather than snow, higher winter streamflows scour streambeds, damaging spawning nests and washing away incubating eggs. Earlier peak streamflows flush young salmon from rivers to estuaries before they are

physically competent for the transition, increasing a variety of stresses including the risk of being eaten by predators. Lower summer streamflows and warmer water temperatures create less favorable summer stream conditions for salmon and other coldwater fish species in many parts of the Northwest. To help brace against the effects of climate change, the Lower Rogue Watershed Council is working to restore freshwater and tidal wetlands, floodplain connectivity, and streamflow regimes to increase habitat diversity and population resilience.

—K. Timchak

SAN FRANCISCO ESTUARY

San Francisco's estuary, the largest on the U.S. West Coast, provides habitat to 14 imperiled migratory or estuary-resident fishes (e.g., Delta Smelt *Hypomesus transpacificus*, Chinook Salmon) and marine species supporting fisheries (e.g., dungeness crab *Metacarcinus magister*). The freshwater region of the estuary supplies water to 25 million people and irrigates economically important farmland. Floods and droughts are part of the historical ecology of the estuary and its 163,000 km² watershed. Yet, there is growing concern that large-scale loss and degradation of diverse aquatic habitats due to land- and water-use practices will compromise the ability of species to respond/adapt to climate change. Projections suggest that the region will become warmer and drier with increased environmental variability, placing the ecosystem into novel regimes. California's current four-year drought, exhibiting low freshwater outflow and record air and water temperatures, together with anomalously warm ocean conditions, foreshadows these conditions. Record low abundances of native pelagic fishes and poor survival of endangered juvenile salmon appear to have been exacerbated by the drought. Warm, dry conditions likely favored nonnative resident fishes (e.g., centrarchids), nonnative aquatic vegetation, and harmful algal blooms. Threats of sea level rise and armored shorelines further reduce shallow marsh habitats, already in short supply. Managing fish populations in a highly degraded and diminished natural habitat and changing climate will likely further constrain California's limited water supply, providing daunting challenges for resource managers.

—R. Johnson

TEXAS GULF COAST

In Texas estuaries, the watchword is “drought.” The region has a long history of interannual aperiodic cycles of freshwater inflow, but rising average temperatures coupled with intensifying droughts drive estuarine dynamics in worrying directions. Reduced inflows lead to hypersalinity in systems enclosed by barrier islands, a characteristic of many Texas estuaries. The most recent statewide drought in 2015 exceeded the intensity and duration of the record drought in the 1950s. The effects of aperiodic inflow variation on estuarine-dependent organisms are of great concern, although clear relationships between inflow dynamics and biotic responses are elusive. A central question is whether Texas populations of estuarine-dependent species have sufficient tolerance to withstand hypersaline regimes given the historical propensity for drought in the region or whether inherent tolerance thresholds will be exceeded if droughts intensify. These dynamics will be further shaped by range expansions of tropical species (e.g., black mangrove *Avicennia germinans*) that may alter nursery habitats for important fishery species. Understanding these altered biotic interactions along with threshold tolerance responses to hypersalinity will be crucial for unraveling the multifaceted effects of climate change.

—B. Walther

FLORIDA

Estuaries in Florida provide key economic and ecological benefit to a state highly dependent on natural resources to drive the tourism, agriculture, and development segments of the economy. With more than 2,100 km of coastline and a human population of over 20 million people (and growing by about 1,000 people a day), climate change is important to every citizen and visitor to the Sunshine State. In the highly developed southeastern corner of Florida, climate change–related sea level rise is contributing to increases in coastal flooding of metropolitan areas, such as Miami Beach during spring and fall high tides. Lesser known, yet equally dramatic, impacts to marshes and estuaries are also occurring throughout the state including the sparsely developed “Big Bend” region in the northeastern Gulf of Mexico, where estuaries are squeezed by rising sea levels and changes in freshwater inputs contribute to die offs in coastal vegetation and loss of oyster reefs. Between 60% and 90% of the key commercial and recreational fisheries in Florida are dependent on estuaries for some part of their life history necessitating protection of these habitats for these resources to remain viable. Addressing climate change and the related impacts to coastal Florida is likely one of the biggest challenges ever faced by the state.

—B. Pine

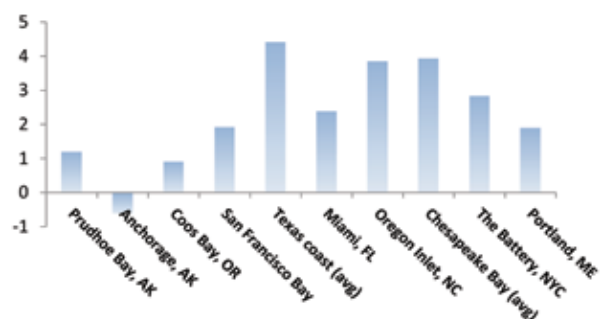
Concerns in estuaries include the rates of sea level rise and temperature warming. We examined data sets for trends in our geographic areas. Sea level rise is variable; highest rates occur mostly in the central Gulf of Mexico coast, but even off the Atlantic coast, there are hot spots of rise. West Coast rates tend to be lower, and in southern Alaska they are negative because of isostatic rebound. On the other hand, increases in temperature show a latitudinal gradient. To make this comparison, we restricted our data sets to be as consistent as possible; that is, from 1995 to 2015. In this case, highest rates are observed in Alaska and lowest rates at more southerly latitudes. This is in accordance with climatological predictions. Knowledge of such trends provides managers with broad guidance for planning.

Sources

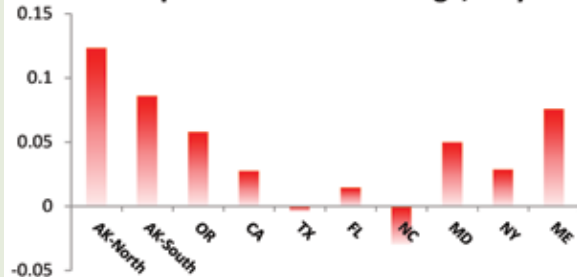
Sea level rise: Data are from the National Oceanic and Atmospheric Administration (NOAA) Center for Operational Oceanographic Products and Services (CO-OPS) Sea Level Trends display (co-ops.nos.noaa.gov/sltrends/sltrends.html; see also NOAA 2001, 2009). These are based upon observations of a minimum 30 years from the National Water Level Observation Network.

Water temperature: Annual temperature trends (1995–2015) were gathered from a variety of sources. National Estuarine Research Reserve (NERR) data were summarized for Maine (Wells), Florida (Apalachicola), and Oregon (South Slough) NERRs (NERR Centralized Data Management Office, cdmo.baruch.sc.edu). Data for the Hudson River were collected at Poughkeepsie, New York, by the U.S. Geological Survey (monitoring station 01372058) and the Chesapeake Biological Laboratory Pier and for the Neuse River basin by the Albemarle–Pamlico National Estuary Program (compiled by M. Chad Smith, received from Roger Rulifson via personal communication). The NOAA CO-OPS' PORTS data product (tidesandcurrents.noaa.gov/ports.html) was used to obtain water temperature data for Galveston Channel (station 8771450) and Sabine Pass North (station 8770570) in Texas, Port Chicago (station 9415144), Suisun Bay, California, and Port of Anchorage, Alaska (station 9455920). Finally, data were used from the Kuparuk River on the Alaskan North Slope; these were collected by the Arctic Long Term Ecological Research program and are described in Kane and Hinzman (2013). Data for each site mentioned may be found at catalog.ioos.us/datasets/filter and entering corresponding the station number.

Relative Sea Level Rise, mm yr⁻¹



Temperature rates of change, °C yr⁻¹



NORTH CAROLINA

The largest barrier island system in North America provides North Carolina with large expanses of lagoonal estuaries and estuarine habitats and offers important habitats for spawning and nursery for many commercially and recreationally important finfish and shellfish species. Alewife *Alosa pseudoharengus* is at the southern limit of its range and appears to be losing ground as temperatures warm. Striped Bass *Morone saxatilis*, which historically overwinter off the Outer Banks and provide a popular winter surf fishery, have moved northward over the past decade to waters off Chesapeake Bay. The Bull Shark *Carcharhinus leucas* is now using habitats in Pamlico Sound as pupping grounds since about 2010; the previous known northern habitat for pupping was in northern Florida. Sea level rise over the next 100 years will cover large expanses of coastal counties that currently flood routinely; saltwater intrusion has poisoned significant expanses of agricultural lands, which are extensively ditched for freshwater runoff. Tough regulations regarding bulkheading and beach hardening may allow marsh systems to migrate landward more easily than in other states with minimal hardening regulations.

—R. Rulifson

CHESAPEAKE BAY

“America’s estuary” serves as the dominant source of recruits for Atlantic Menhaden *Brevoortia tyrannus*, blue crabs *Callinectes sapidus*, and Striped Bass. Winter weather sets the clock for nursery conditions of these and other living resource species within the Chesapeake. Cold, wet conditions favor Striped Bass and other anadromous species; warm winters favor blue crab, Bluefish *Pomatomus saltatrix*, and other coastal spawning fishes. Recent, modest declines in Striped Bass recruitment coincide with a period of warm winters. Striped Bass now spawn earlier in the Potomac River, which may affect the foraging and thermal environments that offspring encounter. Resident Striped Bass avoid summertime hypoxic conditions by occupying warmer surface habitats in which they grow poorly. Anglers now encounter sickly or diseased stripers. Warmer conditions could broaden the window of successful recruitment by menhaden, which move from the shelf into the Bay’s tributaries. Warming will allow blue crab juveniles a longer growing season before hunkering down for the winter, yet this applies also to their cannibalistic larger siblings. Increasingly, drums (Sciaenidae) are making a toe-hold in both the lower and upper Chesapeake Bay segments, including Atlantic Croaker *Micropogonias undulatus* and Red Drum *Sciaenops ocellatus*, consistent with poleward range expansion for this warmwater family.

—D. Secor

NEW YORK

In the 250-km Hudson River estuary, we began to notice warming in the 1980s, when Rainbow Smelt *Osmerus eperlanus*, at its southern range limit, began to get scarce. The last individual was observed in 1998, and Rainbow Smelt

became the first known climate-based extirpation. Since then, Atlantic Tomcod *Microgadus tomcod* are barely holding their own, whereas tropical marine strays are increasingly observed. Additionally, earlier onset and shorter duration in spawning phenology appear to be the case for anadromous American Shad *Alosa sapidissima* and river herring (*A. aestivalis* and *A. pseudoharengus*). One of the biggest impacts of the more energetic climate is the increased frequency of powerful storms. The Hudson River estuary witnessed three within a 14-month period: Hurricane Irene followed by Tropical Storm Lee in 2011 and Superstorm Sandy in 2012. Irene and Lee deposited several centimeters of fine sediments, burying submersed macrophytes; five years on, recovery of this critical habitat is just beginning. Sandy rearranged habitats lower in the system, but the main impacts were likely financial rather than ecological, given the heavy urbanization. With rising sea levels, managers are concerned for wetlands that have little space to move in this largely rock-bound estuary.

—K. Limburg

MAINE

Almost all of Maine’s estuaries are long “drowned river valleys” stretching many kilometers inland and, as in most estuaries, the position and extent of the mixing zone are highly dependent on both tides (ranging from 9 to 11 ft) and freshwater input. Changes in the intensity and timing of storms and spring meltwaters are expected to affect these already dynamic patterns. Warming Gulf of Maine waters are bringing new species north and allowing “old” invasives, such as the European green crab *Carcinus maenas*, to flourish. At the same time, Maine’s warmer interior estuaries harbor warmwater organisms such as the horseshoe crab *Limulus polyphemus* and the eastern oyster *Crassostrea virginica*; these species may find expanded habitat with warmer marine temperatures. Although species such as smelt are still hanging on in Maine, populations are declining. In contrast, river herring are increasing in numbers, particularly in the Kennebec and Penobscot rivers, where dam removals increased access to spawning grounds and stocking have resulted in millions of returning spawners. The use of the Penobscot estuary by juvenile river herring has increased dramatically since dams were removed in 2012 and 2013, and Shortnose Sturgeon *A. brevirostrum* were documented moving upstream into potential spawning habitat this fall for the first time in over 100 years.

—K. Wilson

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Providing Safe Haven for Sensitive Aquatic Species in a Changing Climate

Michael Dege

California Department of Fish and Wildlife, Redding, CA

Eric Jones

California Department of Fish and Wildlife, Mt. Shasta, CA

Mark Clifford

California Department of Fish and Wildlife, #3 North Old Stage Road, Mt. Shasta, CA 96067.

E-mail: mark.clifford@wildlife.ca.gov

Carl Kittel

Texas Parks and Wildlife Department, San Marcos, TX

FISH CULTURE IN A CHANGING CLIMATE

Fish culture will be affected by climate change, but many aspects of the fish husbandry environment can be controlled through the use of modern technology and engineering. The ability to control the culture environment provides the option to engineer around climate change as it occurs and additionally allows fish culture to be used as a tool to address issues of climate change and associated impacts on native or wild fishes. Aquaculture for coldwater fish species, such as salmon and trout, will likely require modern technologies to supply conditions suitable for fish husbandry in a changing climate. Recirculating aquaculture systems (RAS) have proven effective for production hatcheries and also as an emergency tool to address issues of climate change and mitigate impacts on native or wild fishes. Such work was recently demonstrated by the California Department of Fish and Wildlife (CDFW) to provide drought safe haven for wild fishes that were otherwise jeopardized by unprecedented drought. Other recovery efforts have been planned or implemented recently in Texas, North Carolina, New Mexico, and other locations to protect imperiled fish and mussel populations by bringing populations into culture facilities. These and other efforts worldwide demonstrate innovative approaches to address potential or realized impacts of climate change. These fish culture techniques should be considered part of the available toolbox for all fisheries professionals as they face impacts of climate change.

CASE STUDY: McCLLOUD RIVER REDBAND TROUT

McCloud River Redband Trout *Oncorhynchus mykiss stonei* is one of several sensitive and unique fish species in California that required fish rescue during recent extreme drought to prevent excess fish loss and alleviate population-level effects. McCloud River Redband Trout streams (tributaries of the upper McCloud River) were monitored from late 2013 through mid-2015 for drought-related impacts. Stream monitoring during this period indicated drought effects during two separate seasonal periods—winter and summer. The winter period consisted of reduced stream flows and episodic events of cooler than normal air temperatures, freezing solid significant portions of Redband Trout habitat. Summer period impacts included reduced streamflows sooner and more extensively than long-term averages. These conditions suggested that genetically distinct



McCloud River Redband Trout *Oncorhynchus mykiss stonei*. Photo credit: California Department of Fish and Wildlife.

subpopulations of McCloud River Redband Trout were at risk due to degrading habitat not likely to improve before impacts were realized. Fortunately, minimal Redband mortality was documented before fish rescues were implemented by CDFW. For McCloud River Redband Trout, rescue options included (in order of preference) instream movement, movement to another inner basin stream with genetically distinct McCloud River Redband Trout, and/or holding in a self-contained RAS at a hatchery.

Anticipating potential drought impacts on sensitive wild fish populations, CDFW customized, procured, installed, and employed self-contained RAS in expedited time at select CDFW hatcheries. In close proximity to the McCloud River, the CDFW's Mt. Shasta Hatchery was selected for providing drought-safe haven for rescued Redband Trout until conditions improved in natal streams. Before RAS were in operation, several logistical and infrastructural hurdles had to be addressed. These included accommodating RAS and electrical needs in a 100-year-old hatchery building, assembly of RAS components, and populating bioreactors with nitrifying bacterial species. By July 2014, RAS were ready to accommodate fish and by September biologists had provided drought safe haven to over 1,000 McCloud River Redband Trout.



Recirculating aquaculture systems used as drought safe haven by the California Department of Fish and Wildlife.

In addition to releasing fish back to the wild, CDFW is considering options for subsets of Redband Trout including a conservation program utilizing genetic analysis performed by the University of California at Davis. The CDFW staff rescued and provided drought safe haven for other coldwater fish species including the southern Oregon/northern California Coast Coho Salmon *Oncorhynchus kisutch* evolutionarily significant unit and the California Central Valley steelhead *O. mykiss* distinct population segment. Fish from those efforts were released to the wild as conditions did improve.

Extreme and changing climate and the related effects to aquatic habitats are anticipated products of global warming. As with the McCloud River Redband Trout example, modern fish husbandry offers an aide in the conservation of sensitive aquatic species in peril from climate change. The Fish Culture Section is poised to assist with this growing issue by disseminating information on successful projects, such as the McCloud River Redband Trout holding project; by helping to identify expertise for fisheries managers who need it; and by encouraging continued discussion of issues and solutions related to climate change. [AFS](#)

FISH HEALTH SECTION

Climate Change and Considerations for Fish Health and Fish Health Professionals

Luciano Chiamonte, Doug Munson, and Jesse Trushenski

Eagle Fish Health Laboratory, Idaho Department of Fish and Game, 1800 Trout Road, Eagle, ID 83616.

Corresponding author: Jesse Trushenski

E-mail: jesse.trushenski@idfg.idaho.gov

As the warmest years on record (Blunden and Arndt 2015; NOAA NCEI 2016), 2014 and 2015 brought greater attention to the issues of climate change. Though global precipitation has been average, severe drought conditions in the western United States (England 2014) have punctuated growing concern for the future of aquatic systems. A changing climate may affect the way we steward fisheries resources with intrinsic and extrinsic values, including our approach to fish health management.

Fish health professionals classically refer to a Venn diagram to characterize the factors that contribute to infectious disease; that is, environment, fish (i.e., the host) and pathogen (Figure 1; Sniezsko 1974). This diagram helps to conceptualize the difference between the mere presence of a pathogen and the conditions that make disease likely. For infection to occur, a pathogen must invade a fish, getting past natural barriers such as mucus, skin, and nonspecific immune defenses. Not all pathogen invasions result in disease—whether disease occurs depends on the strength of the fish's immune defenses, which are strongly

influenced by the environment. Favorable environmental conditions can maximize the ability of a fish's immune system to neutralize a pathogen. Hostile environmental conditions can result in a fish that is stressed, immunocompromised, and vulnerable to infection, but infectious disease will not occur unless a pathogen is also present. Thus, disease in fish requires a specific combination of fish, pathogen, and environmental conditions. Here, we consider how climate change might influence this triad, thereby affecting fish health and work of fish health professionals.

EFFECTS ON THE ENVIRONMENT

The effects of climate change on the terrestrial environment and inland waters are numerous and may include increases in temperatures, changes in precipitation patterns (e.g., changes in rainfall, reduced snowpack), alterations in flow regimes (e.g., lower summertime in-stream flows), more frequent extreme weather events (e.g., droughts and floods), and other abiotic

effects that impact the quantity and quality of surface water needed for aquatic life. Abiotic changes, in turn, cause biotic changes, affecting aquatic organisms whose geographic distributions, life histories, and biological requirements are directly tied to “master variables” like temperature and flow. Biotic shifts, such as advancing eutrophication or changes in species assemblages, may negatively affect the health of wild and hatchery-origin fish at an individual or population scale. Altered environments, defined by new abiotic and biotic norms, may present novel fish–pathogen interactions and the potential for emerging infectious diseases. For example, favorable thermal habitats that provide refuge from pathogens may be lost due to climate change, resulting in increased incidence of disease (Chiaromonte et al. 2016). Future conditions may further stress native fish and favor the introduction, establishment, and distribution of invasives (Hellmann et al. 2008; Quiñones and Moyle 2014), collectively compounding the likelihood of naïve populations (both indigenous and introduced) encountering new and more virulent pathogens.

EFFECTS ON FISH

Climate change may affect fish in myriad ways, but here we focus specifically on how temperature could influence interactions between fish and their pathogens. Every organism has a range of environmental temperatures it can tolerate, constrained by the lower and upper lethal limits. Within the tolerable thermal range is a narrower, preferred range of temperatures within which the species performs best—the thermal preferendum. Thermal preferenda vary among fish species and life stages, with larval and maturing or spawning fish typically being the most sensitive (Pörtner and Peck 2010). Thermal preferences and tolerances are somewhat plastic and are influenced by acclimation temperature, rate of thermal change, genetic differences among stocks, diel temperature cycles versus daily mean temperatures, etc. However, when fish are exposed to water temperatures outside the preferred thermal “windows,” their fitness may be reduced. In most climate change scenarios, the likelihood is that fish will encounter temperatures exceeding their upper tolerance. The stress associated with exposure to warmer temperatures may be acute or chronic and can interact with related stressors such as pathogenic infections.

Fish vulnerability to pathogens is a major determinant of disease and one likely to be affected both directly and indirectly by thermal stressors. Whether the result of increased fish susceptibility, greater pathogen virulence, or both, disease-related morbidity and mortality are influenced by water temperature. As long as temperatures do not exceed the pathogen’s thermal preferendum, bacterial and viral infections may progress more rapidly and be more severe when water temperatures are warmer or rising (Trust 1986; see Text Box). The effects of water temperature on parasitic infections are more variable, with warm temperatures associated with more severe infestations of some parasites (e.g., *Ceratonova shasta*; Udey et al. 1975), whereas cooler water temperatures can be more problematic for others (e.g., *Ichthyophthirius multifiliis*). It should be noted that linkages between higher water temperatures and more severe infections/infestations are largely derived from work with coldwater fishes; more rapid pathogenesis and greater disease-related mortality may be associated with colder

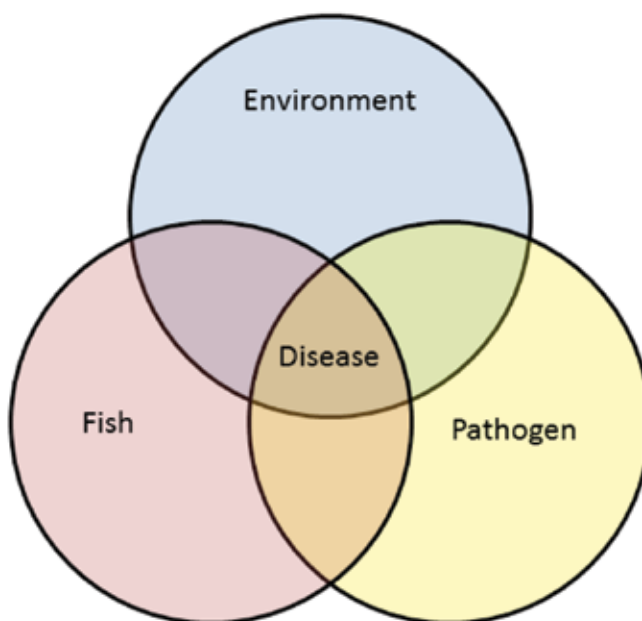


Figure 1. Venn diagram illustrating the relationship between fish, pathogen, and environment in the context of disease; disease is only possible when all three factors are present and favor infection or infestation.

or declining temperatures in warmwater fishes. Indeed, contrary to the generalizations above, cold water temperatures have been described elsewhere as generally immunosuppressive (Bly and Clem 1992), though these conclusions were based primarily on work with warmwater fish. It is also likely that variation in fish vulnerability is related to differential effects of warm and cold temperatures on different aspects of teleost immunity and the relative importance of these defenses in staving off one pathogen or another. Some mediators of immunity are suppressed by cooler temperatures, whereas others are less functional at warmer temperatures (Le Morvan et al. 1998; Sundh and Sundell 2015), meaning that defense against some, but not all, pathogens may be affected. Though less satisfying than a simple positive or negative relationship, disease in poikilothermic organisms is likely to be most frequent and severe when temperatures are variable and fall outside fish thermal preferenda.

EFFECTS ON PATHOGENS

Freshwater temperature increases can affect fish pathogens directly by altering their biological processes or indirectly by influencing the distribution and abundance of the fish they affect. On an organismal scale, temperature changes can affect the rate of pathogen replication inside the fish, the longevity of pathogen life stages outside the fish, the virulence of the pathogen, and the transmission of the pathogen among fish (Marcogliese 2001, 2008). On a population scale, temperature increases can alter the seasonal abundance, timing, and transmission efficiency of pathogens.

As noted above for fish, pathogens have thermal tolerances and preferences within which they perform optimally. Within a pathogen’s tolerable thermal range, increases in ambient temperature will typically accelerate replication of viruses, bacteria, fungi, and parasites in fish, worsening infections and disease (Fryer and Pilcher 1974). For pathogens that exist near the bounds of their thermal tolerances, effects of climate change will be the most evident (Lafferty 2009). In

The temperature of the water is of the utmost importance in the handling of fish diseases, whether these conditions are due to infections, parasites, or the results of nutritional and developmental disturbances which lower vitality. A temperature above the optimum range increases the onset of symptoms and the rapidity of death. It lessens the general resistance of the fish and, in many bacterial and protozoan diseases, favors the multiplication of the invading organism. A high temperature is favorable for epidemics of bacterial disease. ... The fish culturist who possesses an ample supply of cold water has one means of protection against bacterial disease since certain epidemics can be held in check by a low water temperature. (Belding 1928:105)

high latitudes where pathogen growth may be limited by cold temperatures, an increase in average water temperatures will permit pathogen development for a longer time period. For instance, increasing water temperatures are associated with higher prevalence of proliferative kidney disease in wild salmon in northern Europe, a response likely due to faster growth of the invertebrate host, accelerated parasite spore development in the host, and diminished immune responses in the fish (Sterud et al. 2007). Warmer waters can also reduce generation times of pathogens, allowing for faster replication within fish and other hosts and more life cycles to be completed within the year. For example, the salmonid ectoparasite *Argulus coregoni* can double the number of life cycles completed annually under warmer conditions (Hakalahti et al. 2006).

Many pathogens exhibit cycles of seasonal abundance, with highest levels occurring during warmer months. Warming temperatures could result in earlier peaks and longer “seasons” of maximum pathogen abundance. In addition to becoming more prevalent, some pathogens become more virulent at warmer temperatures, resulting in an expanded and more severe season of infectivity and disease. Temperature may also differentially affect different aspects of pathogen infectivity; in the case of some parasites, shedding rates and the abundance of infective stages may be increased at warmer temperatures, but the longevity of those same life stages may be reduced, giving them less time to find and successfully invade a fish or another host (Foott et al. 2007; Marcogliese 2008).

CONCLUSIONS

Despite the simplicity of the conceptual model illustrating the factors contributing to fish disease (Figure 1), the possible effects of climate change on this triad are complex. Abiotic and biotic attributes of the environment are likely to change in response to a changing climate. Increases in water temperature alone can directly affect fish and their pathogens; multifactorial environmental change may affect both in ways that are difficult to anticipate. The occurrence and severity of disease may increase, decrease, or merely shift in time or space, depending on the net effects on all three interrelated factors. Fish health professionals must consider each combination of fish–pathogen–environment as a unique scenario and use the tools available to them to minimize effects of altered thermal regimens on infectious disease in fish (e.g., temperature manipulations, invasive species control, timing of fish stocking to minimize pathogen overlap, improved fish culture practices, transitioning from flow-through to water reuse systems).

The American Fisheries Society Fish Health Section members, particularly the certified aquatic animal health inspectors and fish pathologists, will assist their fisheries colleagues and employers by helping to anticipate and address fish health challenges. Thorough inspections and biosecurity planning, rapid and accurate diagnoses, and—working with veterinarians as appropriate—effective disease treatment options are all essential services the fish health professional is called upon to provide. Increasingly, fish health professionals will also be asked to provide creative solutions to new challenges involving fish species not previously cultured; emerging pathogens or pathogens with altered virulence or emergence patterns; different, more intensive culture methods, such as recirculating aquaculture systems; and limited options for accessing vaccines and therapeutic drugs needed to provide effective and compassionate treatment when disease occurs. Like climate change itself, the implications of a changing environment for fish health are complex and will require the knowledge of fish health experts as well as expertise in fish culture, fisheries management and ecology, physiology, water quality, and other disciplines. Fish Health Section members will serve the discipline, our fellow fisheries professionals, and aquatic resources through continued engagement in the broader fisheries community and a commitment to innovation and adaptation.

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INTERNATIONAL FISHERIES SECTION

International Perspectives on the Effects of Climate Change on Inland Fisheries

Ian J. Winfield

Lake Ecosystems Group, Centre for Ecology & Hydrology, Lancaster Environment Centre, Library Avenue, Bailrigg, Lancaster, Lancashire LA1 4AP, U.K. E-mail: ijw@ceh.ac.uk

Claudio Baigún

Instituto de Investigación e Ingeniería Ambiental (3iA), Universidad Nacional de San Martín, Gral. San Martín, Buenos Aires, Argentina

Pavel A. Balykin

Southern Scientific Center of the Russian Academy of Sciences, Rostov-on-Don, Russia

Barbara Becker

Programa de Pós-Graduação em Biologia de Vertebrados, Pontifícia Universidade Católica de Minas Gerais, Belo Horizonte, Minas Gerais, Brazil

Yushun Chen

Institute of Hydrobiology, Chinese Academy of Sciences, Wuhan, Hubei, China

Ana F. Filipe

Centro de Investigação em Biodiversidade e Recursos Genéticos, Universidade do Porto. Campus Agrário de Vairão, Vairão, Portugal; Centro de Ecologia Aplicada, Instituto Superior de Agronomia, Universidade de Lisboa, Tapada da Ajuda, Lisboa, Portugal

Yuri V. Gerasimov

I. D. Papanin, Institute for Biology of Inland Waters, Russian Academy of Sciences, Yaroslavl Region, Russia

Alexandre L. Godinho

Fish Passage Center, Federal University of Minas Gerais, Minas Gerais, Brazil

Robert M. Hughes

Amnis Opes Institute and Department of Fisheries & Wildlife, Oregon State University, Corvallis, OR

John D. Koehn

Arthur Rylah Institute for Environmental Research, Department of Environment, Land, Water & Planning, Heidelberg, VIC, Australia

Dmitry N. Kutsyn

Southern Scientific Center of the Russian Academy of Sciences, Rostov-on-Don, Russia

Verónica Mendoza-Portillo

Colección Nacional de Peces, Instituto de Biología, Universidad Nacional Autónoma de México, México, Distrito Federal, México

Thierry Oberdorff

UMR 'BOREA' CNRS 7208/IRD 207/MNHN/UPMC, UAG, UNICAEN, Muséum National d'Histoire Naturelle, Paris, France

Alexei M. Orlov

Russian Federal Research Institute of Fisheries and Oceanography, Moscow, Russia; A. N. Severtsov Institute of Ecology and Evolution, Russian Academy of Science, Moscow, Russia; Department of Ichthyology, Faculty of Biology, Dagestan State University, Makhachkala, Russia

Andrey P. Pedchenko

Berg State Research Institute on Lake and River Fisheries, Saint-Petersburg, Russia

Florian Pletterbauer

Institute of Hydrobiology and Aquatic Ecosystem Management, University of Natural Resources and Life Sciences Vienna (BOKU), Vienna, Austria

Ivo G. Prado

Fish Passage Center, Federal University of Minas Gerais, Minas Gerais, Brazil; Piscos-Consultoria e Serviços Ambientais, Lavras MG, Brazil

Roland Rösch

LAZBW, Fisheries Research Station Baden-Wuerttemberg, Langenargen, Germany

Shane J. Vatland

Research Division, Department of Fisheries Resources Management, Nez Perce Tribe, Joseph, OR

INTRODUCTION

A range of perspectives is presented from the International Fisheries Section of the American Fisheries Society on climate change effects on inland fisheries from standing and flowing waters in Africa, Asia, Australia, Europe, and Latin America.

Many of the world's inland fisheries face common threats, such as eutrophication, overfishing, species introductions, and water development projects (Youn et al. 2014), which have essentially local solutions. However, most fisheries also face effects from the inherently global problem of climate change, which only can

be understood and ultimately managed from a truly international perspective. The potential extent and range of such effects were illustrated by Xenopoulos et al. (2005), who, assuming the A2 model for climate change, predicted a loss of 0% to 75% of the fish species in a variety of the world's river basins but with an uncertain time lag (Tedesco et al. 2013). Here, we provide a range of perspectives from the International Fisheries Section of the American Fisheries Society on climate change effects on inland fisheries from standing and flowing waters in Africa, Asia, Australia, Europe, and Latin America.

AFRICA

Most tropical fishes are eurythermal and able to tolerate high temperatures, and most climate change scenarios predict little temperature increase in tropical Africa. Consequently, relatively small effects might be expected. However, many tropical fishes live in waters with low dissolved oxygen levels, where temperature fluctuations approach upper lethal limits (Ficke et al. 2007). Thus, temperature increases of only 1°C to 2°C are likely to affect swimming ability, growth rates, and reproduction, which in turn are likely to affect wild fish and aquaculture production. Fish species extinctions due to reduced water availability arising from climate change in arid and semi-arid regions of northern Africa are very likely before the end of this century (Tedesco et al. 2013).

Even large African lakes with considerable buffering capacities are likely to be affected by climate change. For example, the fishery catch of Lake Naivasha in Kenya is strongly correlated with water level (Hickley et al. 2002), and water level is likely to be affected by anticipated reductions in precipitation. Similar impacts of climate change are also anticipated in Lake Victoria (East Africa), where changes in interannual and interseasonal variability in rainfall and temperature could affect the survival of aquatic life, increasing the variability of fish catches (Johnson 2009; Sewagudde 2009).

ASIA

Climate change may affect the hydrology and fisheries of inland waters through increased precipitation, air temperature, and glacier melting in the Qinghai–Tibet Plateau (QTP). The QTP has many lakes and contains the glacier-fed headwaters of the Yangtze, Yellow, and Mekong rivers. The QTP has warmed in recent decades (e.g., Wang et al. 2015; Yang et al. 2015), stimulating increased glacial melting (Krause et al. 2010; Wang et al. 2013). In some QTP regions, increased precipitation may have affected runoff more than increased air temperature (e.g., Qian et al. 2014). In lakes, fish may need to adapt to habitat changes associated with rising lake levels and altered thermal stratification and mixing. In rivers, particularly the headwaters, increased discharge may change local habitat and deliver more terrestrial inputs downstream, with eventual effects on riverine fisheries.

The Caspian Sea is the world's largest inland sea, and a century-long shift in the abundance and composition of its fishery is correlated with a change in the local climate and sea environment. Specifically, increased air temperatures coupled with decreased precipitation and winter ice covers are associated with increased salinity and decreased sea level. From 1900 to 1933, annual fish catches in the Caspian Sea were often over 600,000 tons. Semi-anadromous (Vobla *Rutilus caspicus*, Common Bream *Abramis brama*, Pikeperch *Sander lucioperca*, Common Carp *Cyprinus carpio*) and anadromous (sturgeons,

shads, Inconnu *Stenodus leucichthys*) fishes made up 79% and 16%, respectively, of the catch (Kuranova and Moiseev 1973). In the first years of the 21st century, catches of semi-anadromous and anadromous fishes declined dramatically and are significantly correlated with reduced Volga River discharges into the sea, lower sea levels, and higher salinities (Zhidovinov et al. 1985; Katunin and Strubalina 1986).

Inland fisheries occur across most areas of the Asian part of Russia and are particularly important, susceptible to climate change, and well-studied in Lake Baikal (Siberia). The most important fisheries species in this lake is Baikal Omul *Coregonus migratorius*, where catches increase 4 to 5 years after high water levels (Smirnov et al. 2015). There is a strong negative correlation between ice cover in the Arctic Ocean in the second half of August and Baikal Omul catches (Figure 1). During periods of low winter temperatures and long ice cover, conditions for Baikal Omul production improve because of increases in river flow, lake level, and subsequent juvenile survival (Smirnov et al. 2015).

AUSTRALIA

Australia is a large, dry continent that spans tropical to temperate zones. Its freshwater fishes and their habitats have suffered considerable degradation in many regions, leading to range reductions and reduced and fragmented populations. Consequently, a large proportion of Australia's endemic freshwater fishes are of conservation concern. Rainfall and river discharge patterns are highly variable with increasingly unpredictable intense droughts and floods forecasted (Hobday and Lough 2011). Such changes combined with other pressures pose serious threats to fishes and fisheries.

Though climate change may affect fishes directly (e.g., effects of increased temperatures on reproduction and early life stages), changes in water availability and reliability alter freshwater habitats and indirectly affect fishes and fisheries (Morrongiello et al. 2011). Changes in fish distributions are predicted (Bond et al. 2011), but there are limited opportunities for species to move upstream to cooler higher altitudes because Australia has few high mountains.

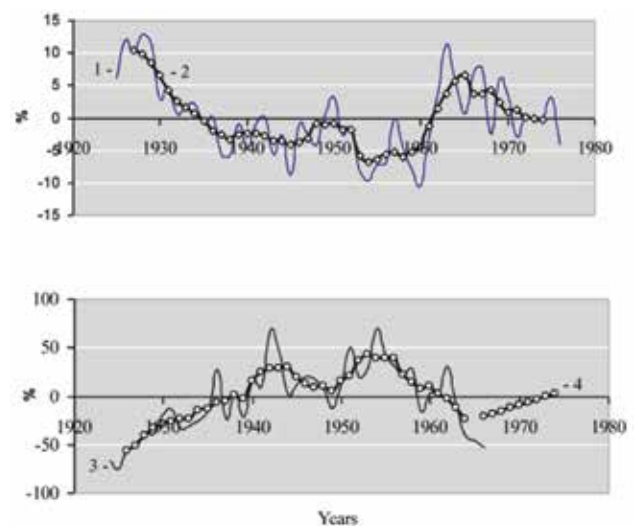


Figure 1. Square of Arctic Ocean ice cover in the second half of August as a percentage deviation from the mean for 1925 to 1976 (upper panel) and annual Baikal Omul commercial catches in feeding areas as a percentage deviation from the mean for 1925 to 1966 (lower panel). Lines 1 and 3 are 5-year means, and lines 2 and 4 are annual means (after Smirnov et al. 2015).

Climate-driven changes to popular recreational fisheries may have significant economic and social impacts, as well as indirect effects causing unexpected outcomes (Koehn et al. 2011). This complexity presents considerable challenges for water resource management (Kingsford 2011; Lester et al. 2011), within which prioritization must be given to the most vulnerable species, locations, and ecosystems (e.g., Barred Galaxias *Galaxias fuscus*; Crook et al. 2010). There is still considerable work to do in adapting management to the changed climate regime of Australia. The management of freshwater fishes under climate change must be undertaken in conjunction with existing stressors, including fisheries management and reforms to water extraction (Koehn 2015).

EUROPE

Europe contains great variability in climates and hydrological regimes, from northern alpine to southern Mediterranean; those regions are expected to be affected differently by climate change (Arnell 1999). A general reduction of annual discharge in the southern regions and an increase in the northern and higher altitude regions are anticipated. The duration, frequency, and intensity of floods and droughts will be exacerbated in the south (Figure 2), and runoff increases in winter and flow decreases in spring will be more frequent in northern and higher altitude areas (Arnell 1999; Christensen and Christensen 2003; Filipe et al. 2013a).

Fishes are expected to be affected strongly by climate change, tending toward local extirpations or displacements to higher elevations and more northern latitudes (Filipe et al. 2013a; Pletterbauer et al. 2016). This implies a decrease in local species richness and major changes in the structure of assemblages for some regions, with the most favored species being those that are alien or common and having low conservation or commercial importance (Buisson et al. 2008). For one of the most threatened species, Brown Trout *Salmo trutta* (Freyhof 2010), distribution forecasts for the Ebro, Elbe, and Danube river basins indicate that 64% of stream reaches will become unsuitable by the 2080s, with the highest risk of extirpation in the Elbe Basin (Filipe et al. 2013b). The greatest changes in fish assemblages are expected for the southern regions by the 2050s and 2080s, whereas boreal assemblages will change less over the same periods (Tedesco et al. 2013; Pletterbauer et al. 2015).

Fisheries provide important food sources and recreational opportunities throughout most of Europe and undoubtedly will

be affected by climate change. Such changes will be particularly intense in areas such as the southern regions, which host many endemic and threatened fishes that already are under great stress from a range of anthropogenic pressures (Smith and Darwall 2006). Those pressures must be successfully managed along with restoration of stream connectivity, establishment of conservation areas, and improved water infrastructure planning (Hermoso et al. 2015a, 2015b).

Climate change effects also are likely in the European part of Russia, including the Great Lakes of Ladoga, Onega, Ilmen, and Peipsi, where fisheries target whitefishes (Coregonidae), Burbot *Lota lota*, European Perch *Perca fluviatilis*, Northern Pike *Esox lucius*, Roach *Rutilus rutilus*, and other species (Kudersky and Ivanov 2011). Catch dynamics depend on climatic factors associated with increasing frequencies of W- and E-types of atmospheric circulation over the North Atlantic (Dubravin and Pedchenko 2010; Pedchenko 2011). In particular, more frequent E-type atmospheric circulation (low winter temperatures and long ice cover) is consistent with the dynamics of the total fish catch (Pedchenko, in press). Similar species are exploited in Rybinsk Reservoir, together with European Smelt *Osmerus eperlanus* and the invasive Black and Caspian Sea Sprat *Clupeonella cultriventris* (Gerasimov 2015). Since 1995, freezing-over has shifted from early November to late December (Litvinov and Roshchupko 2010), coinciding with a decline of coldwater species including Burbot and European smelt and an increase in Black and Caspian Sea Sprat. Growth rates of Burbot and other coldwater species have decreased, and warming-induced lowered oxygen availability has reduced benthic species such as Ruff *Gymnocephalus cernuus* (Wrona et al. 2006; Rijnsdorp et al. 2009). Like the Caspian Sea, the Azov Sea has been affected by increased air temperatures, decreased precipitation and winter ice covers, increased salinity, and decreased level, resulting in reduced commercial catches of Pikeperch and Common Bream (Goptarev et al. 1991).

In central Europe, the transnational Lake Constance of Germany, Switzerland, and Austria has a long history of inland fisheries, particularly for European Whitefish *Coregonus lavaretus* and European Perch. Over the last 40 years, water temperature has increased by about 1.5°C (Jeppesen et al. 2012), and populations of several species including European Whitefish (Thomas et al. 2010) and European Perch (Eckmann et al. 2006) have changed. Recently, fisheries yields have decreased drastically (Rösch 2014), and in 2015 yield fell by approximately 50% from the already low yield of 2014.



Figure 2. The Ardila River in the Guadiana Basin, southern Portugal, in which the hydrological regime is highly seasonal and expected to become even more strongly affected by extreme floods and droughts. The two photographs were taken less than 1 day apart. Photo credit: Patrícia Tiago.

Since about 2014, pelagic expansion of the lake's unexploited Threespine Stickleback *Gasterosteus aculeatus* has occurred and comprised more than 80% of pelagic fish in 2015, increasing the possibility of competition with European Whitefish for zooplankton and predation on larval European Whitefish and European Perch. Although corresponding information is not available for European Whitefish, preliminary data indicate that the 2014 year class of European Perch is extremely weak. The reason for this expansion of Threespine Stickleback into the pelagic zone is uncertain, but its recent observation in Lake Constance suggests that it may result at least in part from climate change.

In the United Kingdom, investigations of climate change effects have centered on the glacial lake of Windermere for three main reasons: co-occurrence of coldwater salmonids and warmwater cyprinids (Winfield et al. 2006), 70 years of fish population studies (e.g., Craig et al. 2015), and diverse fisheries, including historical commercial fisheries, which are rare in U.K. inland waters (Winfield 2016). As Windermere has warmed since the late 1980s, Arctic Charr *Salvelinus alpinus* has declined to the detriment of a traditional recreational fishery for this native salmonid (Figure 3), whereas introduced Roach has expanded to the benefit of angling for this warmwater cyprinid (Winfield et al. 2008). Similar declines in Arctic Charr have occurred in other U.K. lakes and are thought to have resulted in part from climate change (Winfield et al. 2010). Warming also has changed Windermere's Northern Pike population by shifting the length structure of this top predator toward an increased proportion of medium-sized individuals (Vindenes et al. 2014). Climate change also has had wider impacts on the Windermere ecosystem. Expansion of a pathogen of European Perch into the lake has acted synergistically with warming to induce a regime shift within its European Perch–Northern Pike interaction, triggering a trophic cascade (Edeline et al. 2016). Trophic levels have responded differently to warming such that Windermere's phytoplankton, zooplankton, and timing of European Perch spawning have become desynchronized (Thackeray et al. 2013). Finally, age–size truncation of European Perch induced by the pathogen has altered the consequences of this phenological mismatch for fish survival (Ohlberger et al. 2014).

Further north, the Arctic region has experienced more and faster climatic changes (warming waters and shorter durations of ice cover) than other European regions. Unlike temperate regions, warming in the Arctic is projected to improve conditions for anadromous and diadromous fishes such as Atlantic Salmon *Salmo salar* and Arctic Charr, as long as there is sufficient water in spawning and rearing streams (Nordeng 1983; Nielsen et al. 2013).

LATIN AMERICA

Even more than Europe, Latin America contains great variability in climates and hydrological regimes, including alpine, desert, savannah, and tropical rainforest. Tropical parts of South America are likely to experience climate change effects similar to those already described above for tropical Africa, whereas alpine regions are expected to follow patterns similar to Europe. Reductions in annual precipitation are predicted for semi-arid regions, as well as in humid basins such as the Amazon Basin (Saatchi et al. 2012; Oberdorff et al. 2015). Semi-arid and humid regions are predicted to experience increased incidence of extreme precipitation periods (droughts, floods), meaning less predictable water bodies and artisanal fisheries



Figure 3. Recreational anglers fishing traditionally for the threatened coldwater Arctic Charr *Salvelinus alpinus* on Windermere, UK. Photograph: Ian J. Winfield.

(Marengo et al. 2013; Castello and Macedo 2016). Nonetheless, Xenopoulos et al. (2005) and Oberdorff et al. (2015) predicted very few losses of Amazon drainage fish species.

In Mexico, Mendoza-Portillo (2014) conducted a fish faunal inventory in the Sierra Madre Occidental and related current distributions of 16 endemic species to current environmental conditions. Based on those relationships and future climate scenarios, she projected species distributions in 2020, 2050, and 2080. Precipitation seasonality, elevation, and minimum temperature of the coldest period explained most of the variability in current species distributions. Future climate (temperature and precipitation) predictions indicated a reduction of viable ranges for 10 of the 16 endemic species, displacement of viable range to the north for one species, and increased viable ranges for two species by 2080. She proposed making the Yaqui, San Pedro, Nazas, Santiago, and Bravo catchments priority conservation areas or refuges because they support the greatest fish faunal diversity in the Sierra Madre Occidental and have the greatest probability of suitable sites and the greatest potential for species migrations.

Reduction in rainfall and increase in temperature due to climate change will affect recruitment of migratory fishes in the Rio São Francisco (RSF), Minas Gerais, Brazil, with significant implications for fisheries. Aggregation of young migratory fishes occurs annually in the tailrace of Três Marias Dam on the RSF (Godinho and Kynard 2006). The number of fish involved varies yearly (Prado et al., in press); usually there are low numbers (<3 fish per cast net, i.e., 162 fish in 80 casts), but in some years there are large numbers (up to 27 fish per cast net, i.e., 878 fish in 33 casts). Since 2005, large aggregations have occurred only twice, and Prado et al. (in press) determined that those occurred only after two consecutive years of major floods (>5,000 m³/s), which allowed for successful floodplain rearing and escape back to the river by young-of-the-year fish. Large aggregations did not occur in years of major flood preceded and/or followed by years of low or medium flood. Two consecutive years of major flood also increased the fish catch of RSF artisanal fishers from 3 kg/fisher/d to 25 kg/fisher/d only after two consecutive years of major flood (Godinho, unpublished data). Three kilograms of fish per day is insufficient for providing a livelihood for artisanal fishers. Marengo et al. (2012) predicted a 25% reduction in summer (fish spawning season) rainfall and annual mean temperature increase of 2.8°C for the RSF Basin by 2041–2070. Such reduction in summer rainfall will increase the recurrence

interval of two consecutive years of major flood from 2 years to 10 years. Higher temperatures may increase mortality of young-of-the-year migratory fishes because of reduced nursery habitat area due to evaporation. Both climate changes suggest a drastic reduction in migratory fish recruitment to a level that will not support the thousands of professional fishers along the middle RSF.

The Furnas Reservoir is the fourth in a series of 12 dams on the Rio Grande, Minas Gerais, Brazil. Becker (2010) sampled fish from 1996 to 2009, which encompassed a severe drought in 1998 and 1999 that reduced the reservoir volume by 75% from 1999 to 2002. Annual catch per unit effort was negatively correlated with reservoir volume, and total species richness declined after the drought. However, the species richness and abundance of alien species increased during and after the drought, and the fish assemblage composition was significantly different following it. If predicted reductions in rainfall for the Rio Grande Basin and other Brazilian basins occur (IPCC 2015), similar fish assemblage changes are likely in other reservoirs.

Climate change in Argentinean inland waters will affect fish assemblages and most relevant target species and related fisheries. In Patagonia, predicted air temperature increase and precipitation reduction will reduce salmonid recreational fisheries because of reduced abundance and distribution of salmonids (Aigo et al. 2008). In turn, in the shallow Pampean lakes located in the east-central region of the country, Pejerrey *Odontesthes bonariensis* populations support very important recreational fisheries that could be affected because that species displays a temperature-dependent sex determination. Finally, in the La Plata Basin, increased water temperatures will promote the movement of Brazilian species southward and colonization by alien species currently inhabiting the upper basin. Flow augmentation and controls in response to increased temperatures and droughts are likely to have impacts on important artisanal and recreational fisheries mainly based on migratory species (Baigún 2015).

CLOSING REMARKS

The preceding sections amply illustrate the diverse and pervasive effects of climate change anticipated and in many cases already experienced by inland fisheries around the world. The long-term studies of lake and river fisheries described above demonstrate the value of such studies for teasing out the mechanisms of fish and fisheries losses, whereas the spatially extensive studies demonstrate their importance for estimating the extent of predicted changes. Moreover, it is now known that our global climate temperatures and precipitation patterns will continue to change even if carbon emissions decline or cease altogether (IPCC 2015). Therefore, it is imperative that other anthropogenic pressures on inland fisheries (such as migration barriers, land use/abuse, fisheries overexploitation, excessive and poorly planned stocking of hatchery fish, alien species introductions, and physical and chemical habitat alteration), which are driven by continued human population and economic growth (Limburg et al. 2011), be limited to the maximum degree possible. In fact, Tedesco et al. (2013) reported that such pressures apparently explained more fish taxonomic biodiversity losses than did reduced habitat availability from climate change. Nonetheless, Xenopoulos et al. (2005) predicted greater taxonomic biodiversity losses from climate change than from water withdrawal in many rivers. However, in other rivers the reverse was predicted, for example in the Euphrates

(Iraq), Kura (Azerbaijan), Murgab (Afghanistan), Murray-Darling (Australia), and Rio Grande (United States). Examining functional versus taxonomic diversity, Buisson et al. (2013) reported that climate change is expected to yield substantial declines in the functional diversity of fish assemblages. Clearly, the combined effects of climate change and existing anthropogenic pressures are major challenges to freshwater fish biodiversity and fisheries in much of the world (Travis 2003; Dudgeon et al. 2006), and the scope of this challenge necessitates both local and international solutions.

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AFS

INTRODUCED FISH SECTION

What Can We Expect from Climate Change for Species Invasions?

J. S. Rehage

Earth and Environment Department, Florida International University, AHC 5 365, 11200 SW 8th Street, Miami, FL 33199.
E-mail: rehagej@fiu.edu

J. R. Blanchard

Earth and Environment Department, Florida International University, Miami, FL

The coming decades are expected to bring unprecedented climatological changes, with profound implications for inland fishes (Lynch et al., this issue), including for the many established nonnative (NN) species and new ones to invade (Diez et al. 2012; Sorte et al. 2013). Of interest are the effects of climate change on water resources: higher temperatures; changes to the timing, type, and intensity of precipitation; and alterations to extreme climates. For North American aquatic ecosystems, this translates to warmer waters, increased evapotranspiration, reduced ice cover, wetter conditions in the northern regions, drier conditions in the south, altered hydrological regimes, and changes to the frequency, timing and severity of extreme events, such as droughts and storms (Rahel and Olden 2008; Karl et al. 2009; Garcia et al. 2014). From the perspective of the Introduced Fish Section, major questions surrounding climate change center on (1) how will these changes tip the balance of fish invasions

(i.e., under what conditions will NN species be favored) and (2) how do NN invasions interact with other anthropogenic stressors to affect native fish diversity?

LOCAL VS. REGIONAL EFFECTS OF CLIMATE CHANGE ON FISHES

Changes to climate averages and extremes will present major challenges to native biodiversity, affecting habitat suitability at both local and regional scales (Garcia et al. 2014). Locally, these changing conditions will affect the physiology, morphology, and behavior of fishes and ultimately cascade to demographic parameters and the strength of interactions with other species (Garcia et al. 2014; Lynch et al., this issue). For instance, temperature is a “master” variable, with an overarching effect on physicochemical and biological processes in aquatic systems, particularly for ectothermic taxa such as

fishes (Ficke et al. 2007). Warming will increase physiological stress or, at minimum, physiological rates and reduce habitat suitability for many species (e.g., decreased thermal habitat for coldwater species), while simultaneously providing opportunities for invasion and range expansion for others (e.g., warm- and coolwater fishes; Ficke et al. 2007; Comte et al. 2013). These gradual effects will be punctuated by extreme floods and droughts that will constitute another major source of physiological stress and mortality for fish populations, and thus an important agent of selection under future scenarios.

At larger scales, the regional availability of climates will change, including the emergence of novel climatic conditions (Garcia et al. 2014). For example, southern latitudes will experience unprecedented high temperatures, beyond baseline variability (1960–1990s), which will affect the distribution of suitable habitats in both space and time. For fishes, their ability to respond to these regional changes and track suitable habitat conditions will depend on hydrological connectivity and the degree of habitat modification (e.g., dams, canals, water control structures). Thus, we expect fishes to experience higher vulnerability to habitat and hydrological modifications and to the synergistic effects emerging from the interaction of climate change and these human-induced modifications.

A third dimension of the response of fishes to changing local and regional climate is phenological effects, or effects to the timing of life history events such as migration and spawning. For fishes, these effects are better documented than distributional range shifts (Lynch et al., this issue), but data remain scant for NN species. Regardless, human-induced alterations to natural hydrological regimes and connectivity will interfere with the ability of both native and NN fishes to respond to climate change via latitudinal and/or altitudinal distributional changes in space, as well as via phenological shifts in time. In fact, a key concern is that stress on water resources will increase water development (e.g., construction of reservoirs, increased infrastructure for water withdraw), with further negative effects on both connectivity and habitat suitability (Rahel and Olden 2008) and, as a consequence, on the ability of fish to track regional climate suitability. For NN fishes, this could present an advantage over native taxa. The natural flow paradigm predicts that human-modified flows favor NN species (Propst et al. 2008; Gido et al. 2013). As an example, Kiernan et al. (2012) showed that restoration of natural flows and associated temperature regimes in California streams favored locally-adapted native species and suppressed NN fishes.

EFFECTS OF CLIMATE CHANGE ON INVASION OPPORTUNITIES

Climate change may translate into invasion opportunities for many species as habitat suitability and thus the invasibility of ecosystems increases (Rahel and Olden 2008; Sorte et al. 2013). One key outcome is that climate change may result in a new wave of “native invaders” or species that become invasive in their own native range (Carey et al. 2012) or as these native ranges respond to climate change. As species distributions expand, contract, or change placement, native fishes could become invasive and exhibit the types of harmful ecological and socioeconomic impacts typically associated with NN species. Without doubt, the existence of these native “climate” invaders will bring a suite of new challenges to NN mitigation and control practices, in light of potentially conflicting societal vs. resource management concerns.

Beyond redefining invasiveness, climate change can affect NN invasions in a variety of other ways. Climate change may alter the pathways of invasion, the climatic constraints or filters experienced by NN taxa, their distributional patterns and impacts on native taxa, and the effectiveness of management actions (Hellmann et al. 2008). For instance, climate change can create new or more effective vectors of invasion (e.g., ones with higher survivorship), whereby propagule pressure and thus the likelihood of successful invasion increases. Rahel and Olden (2008) pointed to the simple fact that more of North America will become suitable for aquaculture practices and thus more successful introductions may be anticipated. Van Zuijden et al. (2016) forecasted that warmwater nonnative fish will expand their range northward into new lakes faster than originally anticipated as thermal filters disappear, with major implications for co-occurrence and competition with native coolwater fishes, biotic homogenization, and the profitability of fisheries.

Similarly, a recent meta-analysis on gradual climate change (higher temperatures, higher CO₂ levels, and altered precipitation) showed that climate change can favor NN species, particularly in aquatic systems (Sorte et al. 2013). Although fish were underrepresented in the study, climate change inhibited the survival, growth, and fecundity of native taxa to a greater extent than those of NN taxa. The authors also showed that, interestingly, NN tended to respond more strongly, both positively and negatively, to the effects of climate change. Similarly, for extreme climate events, Diez et al. (2012) pointed to the fact that extreme events can result in abrupt stressful conditions for native species that can reduce biotic resistance (or the ability of a community to fend off invasion), create resource pulses, and thus provide “invasion windows” for opportunistic and broadly tolerant NN species.

Chief among climate change concerns for NN are the fact that (1) climate change can remove the filters or constraints that keep NN fishes in check (Rahel and Olden 2008) and (2) NN species may be better poised to take advantage of the loss of such filters (Sorte et al. 2013). Climate change may loosen the effect of climatic, environmental, and/or biotic factors that limit the geographic range and local abundances of NN fishes, preventing them from becoming dominant, and have large negative impacts on native biota. In south Florida, episodic cold spells can reduce the abundance and limit range expansion of tropical NN fishes, but predicted changes in the frequency and severity of cold events will lessen this “natural” control mechanism (Rehage et al. 2016). In colder areas, climate change will reduce or eliminate the occurrence of winter hypoxia associated with ice cover. Winter hypoxia can limit the establishment of NN piscivores and maintain assemblages of small-bodied fishes and amphibians that do not coexist well with NN predators (Rahel and Olden 2008).

Second, NN species have already succeeded at invading novel environments during an invasion and may be better equipped for dealing with the challenges of range expansion under climate change than native taxa (Sorte et al. 2013). Nonnative species are often characterized by their strong dispersal abilities, rapid population growth rates, broad environmental tolerances, and high phenotypic plasticity. These traits allow NN species to cope well with novel conditions and environmental variability, permitting them to commonly outperform natives. We would expect that these same traits would give NN a competitive advantage relative to natives when tracking changing climate conditions in both space and time

(Rahel and Olden 2008; Sorte et al. 2013).

We conclude by highlighting that aquatic systems may be particularly vulnerable to invasion as climate change proceeds (Rahel and Olden 2008; Sorte et al. 2013). Climate change may interact with other environmental stressors, particularly altered hydrologic regimes, to benefit NN fishes and negatively impact native fish diversity. Reducing or mitigating the impact of these other stressors and ensuring hydrological connectivity to allow for distributional shifts will be key components of climate adaptation to protect native fishes. Lastly, climate change and invasions may interact synergistically, exacerbating effects on native fish diversity and ecosystem structure and function. This will likely result in increased variability in inland fisheries, which may not be fully captured using extant management models. To ensure that fisheries resources can weather these stresses, it will be necessary for managers to adopt adaptive conservation strategies that allow stressed populations to respond to the interplay of climate change effects and NN species. Importantly, these effects, along with the trajectories of the ecosystems of the future, will be conditional on human responses to climate change, particularly those related to water resources.

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MARINE FISHERIES SECTION

Methodology for Assessing the Vulnerability of Marine and Anadromous Fish Stocks in a Changing Climate

Wendy E. Morrison

Earth Resources Technology, Inc. under contract to NOAA, National Marine Fisheries Service, Office of Sustainable Fisheries, 1315 East-West Highway, Silver Spring, MD 20910. E-mail: wendy.morrison@noaa.gov

Mark W. Nelson

Earth Resources Technology, Inc. under contract to NOAA, National Marine Fisheries Service, Office of Sustainable Fisheries, Silver Spring, MD

Roger B. Griffis

NOAA, National Marine Fisheries Service, Office of Science and Technology, Silver Spring, MD

Jonathan A. Hare

NOAA, National Marine Fisheries Service, Northeast Fisheries Science Center, Narragansett, RI

The National Oceanic and Atmospheric Administration's (NOAA) National Marine Fisheries Service (NOAA Fisheries) works with our partners to sustainably manage U.S. marine and anadromous fisheries and to conserve and protect marine mammals, sea turtles, and species listed under the Endangered

Species Act. NOAA Fisheries also recognizes that climate-related changes are affecting the nation's valuable living marine resources and the people, businesses, and communities that depend on them. NOAA Fisheries recently released a National Climate Science Strategy (Link et al. 2015) that outlines the

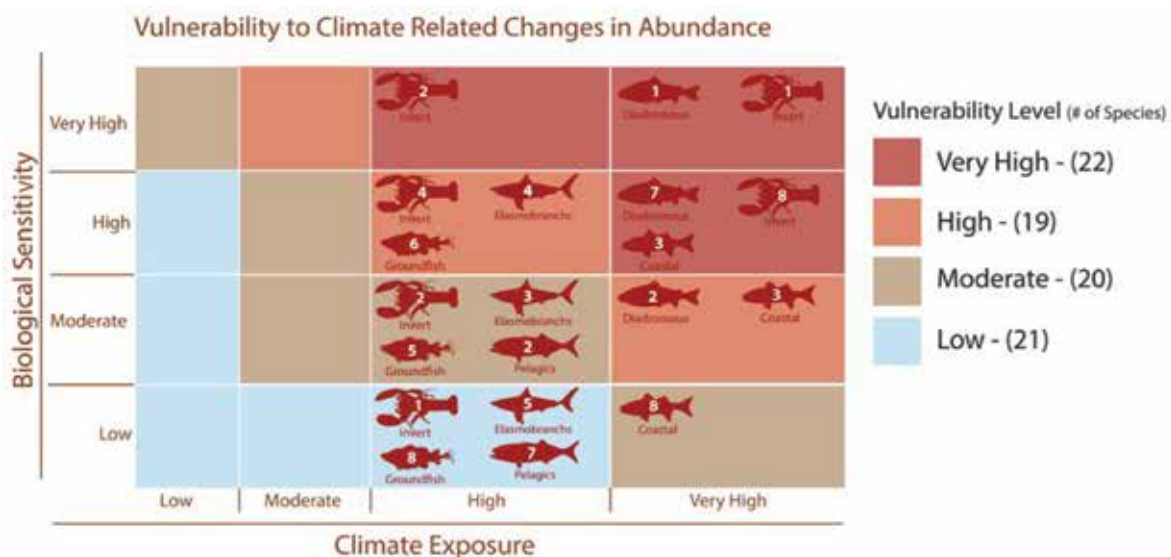
agency's approach to tackling the science needs for managing fisheries and protected species in a changing climate. A primary goal of the science strategy is to better understand which species are more or less vulnerable to environmental changes and the factors driving the vulnerability. NOAA Fisheries has developed a methodology (Morrison et al. 2015) for assessing the relative vulnerability of marine and anadromous fish and invertebrate species to climate change. Implementing the methodology will help identify areas for in-depth analysis and assist fisheries and protected species decision makers in considering how to prepare for and respond to climate-related changes. We have implemented the methodology for 82 fish and invertebrate species off the northeastern United States, including a mix of exploited, protected, and forage species (Hare et al. 2016). Similar assessments are currently underway for the Bering Sea and California Current ecosystems. The methodology is being modified in the California Current to better account for the vulnerability of Pacific salmon, an important anadromous protected species. NOAA Fisheries intends to replicate this process in other regions, depending on needs and available resources. In addition, NOAA Fisheries is in the process of creating a similar analysis for marine mammals and sea turtles.

The methodology is designed to generate three key results for each species: a relative vulnerability rank (based on exposure and sensitivity), an indication of a species' propensity for shifting distribution (based on a subset of the sensitivity attributes), and an overall directional effect (do experts expect the species to respond positively or negatively to expected climate changes). NOAA Fisheries designed the methodology to be applicable across tropical, temperate, and high-latitude marine systems and address a wide range of fish and invertebrate life history characteristics. The vulnerability rank is a combination of a species' expected exposure to environmental change and its biological sensitivity to that change. The methodology assumes that current biological parameters are an indicator of the relative sensitivity of a species. The exposure variables may vary between different regions (e.g., extent of sea ice will be important in some but not all regions). However, the 12 life history attributes used to determine a species'

sensitivity to climate change are consistent across regions and include habitat requirements, prey requirements, physiological tolerances, reproduction requirements, ability to change distributions, and other stressors. A subset of the life history attributes can be used to determine whether a species is likely to respond to changes in climate by shifting distributions, which could have a large impact on some fishing communities and on the overlap among fisheries and with protected species.

The methodology uses expert elicitation to rank multiple species at the same time. Experts assign scores based on four well-defined scoring bins (low, moderate, high, very high) to ensure that the scores are consistent across species. Each expert is asked to independently score the exposure and sensitivity of the species using species profiles, scientific literature, and general knowledge. Later the experts are asked to review their scores compared to the other experts and discuss the results and are allowed to adjust their scores based on those discussions. Using both individual and group expert elicitation practices helps minimize bias and increases precision of the results.

The results from a climate vulnerability assessment can be used to identify (1) species with high relative vulnerability that may need additional research or monitoring, (2) species that have a propensity to change distribution in response to a changing climate, (3) species that may be positively impacted by projected change, and (4) a list of major data gaps identified during the assessment. The assessment does not predict or quantify the scale or magnitude of expected change for a species in the future. We recommend that the results, along with other relevant information, be summarized for each species in a short species narrative that provides an easily accessible resource that can be used by scientists, fishery managers, or the public. Scientists can use these results to identify research priorities, such as identifying stock assessments that can benefit from explicit consideration of climate vulnerability and species that could benefit from increased monitoring. Managers can use the results to help identify specific attributes that make a particular species more or less resilient to climate change and to craft management measures that account for those differences among species.



Summary of the results from Hare et al. 2016. Approximately half the species assessed are estimated to have a high or very high vulnerability to climate change in the Northeast U.S. Continental Shelf Large Marine Ecosystem. In general, diadromous fish and benthic invertebrate species are predicted to be more vulnerable to climate effects in the ecosystem, and pelagic species are predicted to be the less vulnerable.

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PHYSIOLOGY SECTION

From the Equator to the Poles, a Physiology Section Perspective on Climate Change

Jay A. Nelson

Department of Biological Sciences, Towson University, 8000 York Rd., Towson, MD 21252-0001. E-mail: jnelson@towson.edu

Adalberto L. Val

National Institute of Amazonian Research (INPA)/ Brazil Ministry of Science, Technology and Innovation (MCTI), Manaus, AM Brasil

Anthropogenic climate disruption over the past century has driven significant physical, chemical, and biological changes in freshwater systems that directly affect fishes at all biological levels. Changes in temperature, precipitation, water flow, acidification, oxygen availability, and the food web are among climate-driven impacts on freshwaters. According to the Intergovernmental Panel on Climate Change (IPCC 2013), continued trends of greenhouse gas emissions and deforestation could produce global temperatures in excess of 3°C higher than pre-industrial values by the end of this century. Fifteen of the 16 hottest years recorded have all been this century, with 2015 being the hottest year ever. Furthermore, 2011–2015 was the hottest five-year period ever recorded. Under this rapidly changing climate, aquatic ecosystems are predicted to get warmer and become regionally more acidic and hypoxic. Patterns of precipitation and water flow are also predicted to change dramatically in many areas (Döll and Müller-Schmied 2012). Thus, aquatic organisms will have their homeostatic coping mechanisms pushed to their limits, and fish physiologists will be the ones to elucidate what those limits are.

Normally, natural selection would favor a close match between local environmental conditions and animal physiological performance capacity, through either maintenance of sufficient phenotypic plasticity or evolutionary adaptation. How effective these processes are at compensating for rapid environmental change will depend heavily on each species' physiology in addition to ecological factors such as generation

times and population size. Presently, a species' response to climate change is predicted from correlative distribution models. These models correlate environmental factors (e.g., temperature and precipitation) with current distributions of species to predict future species' distributions by assuming a species will follow this same "climate niche" as climate changes. These models are inherently flawed because they do not incorporate any knowledge of the species' physiological capacity to compensate or to adapt through natural selection. A clear view of the future of fish will require substantial input from fish physiologists and their collaborations with geneticists to provide this vision.

Temperature is a well-known controller of physiological and ecological processes in fishes and can also influence potential fitness determinants as diverse as morphology, life history, and behavior. The past 70 years of fish physiology research has produced a wealth of data to help predict temperature change effects on fishes. But a changing thermal regime is not the only factor that fishes will have to successfully respond to as climate changes. Water availability, quality of that water, and magnitude of flow are all factors that can change a fish's biology and distribution. Accurately predicting how a species will respond to climate change will require knowing its capacity for physiological response not only to temperature but to this suite of coincidentally changing environmental variables as well as its ability to evolve and/or migrate to more amenable environments. Again, predicting this will require not only physiologists but collaborations with ecologists and evolutionary biologists.

An unparalleled diversity of fish species inhabit tropical freshwaters, where they are often endemic to narrow geographical ranges and where they have very specific ecological niches. These niches will not be solely determined by environmental variables but will have involved coevolution with biological resources, the microbial community, competitors, predators, and parasites. All of these are subject to change as species with different thermal, oxygen, water, ion, and pH requirements drop in and out of changing ecosystems. In the Amazon, for example, it is foreseen that part of the region will experience a “savanization” (Cândido et al. 2007), with profound effects on existing water bodies and the niches of the local fish species they encompass. It has been demonstrated that organisms, including freshwater fishes, from thermally stable environments such as the tropics tend to be thermal specialists (Campos et al. 2016). The Amazon is already experiencing extreme floods and droughts predicted by climate change models, particularly during El Niño–influenced years. The physicochemical characteristics of the waters of the Amazon define the distribution of many fish species across the biome. Recent unpublished analyses indicate, for example, that only a small portion of the fish species existing in the region occur simultaneously in all three types of water of the region (white, black, and clear water), and only a few migratory fish species swim back and forth between types of water (E. J. G. Ferreira, Brazilian National Institute for Research of the Amazon, unpublished data). This suggests that a species highly adapted to a specific type of water would face a size reduction of their habitat due to persistent drought that will likely occur in some parts of the region. The effects of these altered flows and water availability on fish biology and reproduction need to be understood. Without this information, nothing can be done regarding mitigation—more fodder for fish physiologists.

Moving to a part of the planet where climate is changing most rapidly, Arctic freshwaters, the problem is somewhat different. Fish diversity is far less, but large populations of predatory fishes that have sustained important fisheries for millennia and ecosystems for far longer are imperiled. Many of these coldwater fishes are also stenothermal and are threatened directly by warming planetary waters. Current climate projections predict not only temperature increases for most polar waters but also flow regimes that are more stochastic (Döll and Müller-Schmied 2012). Lotic and anadromous fish populations may have to deal with both unprecedented flows as well as the risk of their stream drying up. Lentic fishes may face longer and more stable stratification as well as contraction of their water body. Functional relationships between morphology and the magnitude of water flow have been reported frequently in freshwater fishes, yet physiological and performance traits driven by occupying different flow environments have only been studied rarely (Nelson et al. 2015). Understanding how these fish will cope with the altered flow regimes and water supply will be essential to predicting their futures. Thus, fish physiologists need to start addressing our lack of knowledge concerning how fish are able to respond to changes in flow and lacustrine dynamics.

Temperature influences on fish metabolism have been studied for over 100 years now (Ege and Krogh 1914), and we have long had temperature/swimming performance curves for a variety of fishes (Brett 1964) and similar temperature/function curves for many subordinate physiological processes (Taylor et al. 1996). Presently, the ability of animals to shift those performance curves as climate changes, through either plasticity or natural selection, is a subject of much interest

and a place where fish physiologists are already contributing mightily to the climate change conversation (e.g., Pörtner 2010; Clark et al. 2013). Additionally, because all fish require oxygen to complete their life cycle, the predicted climate change reduction of dissolved oxygen in many waters may be more critical to future fish success than temperature changes alone. Many tropical fish species are obligatory air breathers; others facultatively breathe air, but the great majority are gill breathers and depend on dissolved oxygen. The gill breathers include species that are hypoxia resistant and those that are not. In many cases, closely related species use different strategies to maintain oxygen transfer to tissues. Therefore, though air breathers, both obligatory and facultative, would face climate change–driven challenges from increased time at the water–air interface (e.g., increased ultraviolet exposure, predation, etc.), gill breathers may be directly excluded from habitats as the water oxygen level falls below their ability to compensate. In addition, we are also learning that even if hypoxia is not outright lethal to a given fish species, there are many sublethal effects of hypoxia exposure that can compromise Darwinian fitness (Domenici et al. 2012). As dissolved oxygen decreases, the difference between an animal’s maximum metabolic rate and resting routine metabolic rate often decreases, limiting an animal’s capacity to engage in metabolically expensive activities such as swimming and digestion (Claireaux and Chabot 2016). Even a short (<1 h) exposure to hypoxic water can produce a metabolic disturbance that lasts for many hours in some fish (Plambech et al. 2013). Reduced swimming ability, reduced growth, compromised immune system function, disorientation, and reduced ability to respond to stimuli have all been reported as outcomes of mild hypoxia exposure (reviewed by Chapman and McKenzie 2009; Diaz and Breitburg 2009). These sublethal effects of hypoxia exposure can influence survival and the ability to carry out routine biological functions and therefore Darwinian fitness, but even more alarming is that hypoxia can also act as an endocrine disruptor, including sex reversal, that could lead to a rapid demise of populations (Wu et al. 2003; Cheung et al. 2014). Many Physiology Section members are currently studying how fish deal with these lower oxygen levels; their experiments, especially their collaborations with geneticists, will help predict the future for the many fish species that will see their environmental oxygen levels diminish over the coming years.

In summary, physiologists can contribute to our understanding of climate change impacts by directly gauging the capacity of fish to respond to future environments. Physiologists can also use historic records and species distribution patterns to find populations from extreme environments that will help infer the capacity of a species to respond to climate change through natural selection. Furthermore, collaborations with geneticists and ecologists will greatly improve our power to predict climate disruption’s effects on fishes. Many fisheries scientists are already reporting declines in fish populations that they attribute to climate change. By analyzing the functional and mechanistic responses of fish to climate-driven stressors, this “conservation physiology” practiced by members of the Physiology Section will help illuminate the future of freshwater fishes.

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STUDENT SUBSECTION

Climate Change and Fisheries Education

Andrew K. Carlson

Michigan State University, Center for Systems Integration and Sustainability and Program in Ecology, Evolutionary Biology, and Behavior; Department of Fisheries and Wildlife, 115 Manly Miles Building, 1405 S. Harrison Rd., East Lansing, MI 48823. E-mail: carls422@msu.edu

Nathan J. Lederman

Minnesota State University, Mankato, Department of Biological Sciences, 168 Trafton South, Minnesota State University, Mankato, MN 56001. E-mail: nathaniel.lederman@mnsu.edu

Climate change is predicted to affect aquatic ecosystems in diverse ways with implications for management of inland fishes and fisheries. For example, the frequency of weather events that alter the availability and movement of water (e.g., droughts, heavy precipitation, heat waves) is predicted to increase with climate change (Saha et al. 2006). Rising sea levels are predicted to cause saltwater intrusion (i.e., replacement of freshwater by saltwater) in coastal aquifers (Iyalomhe et al. 2015), which may alter habitat suitability for freshwater and marine fishes.

Warmer air temperatures resulting from climate change are expected to increase water temperatures, with effects on growth, reproduction, and survival of fishes and their prey (Woodward et al. 2010; Hershkovitz et al. 2015; Kanno et al. 2015). Moreover, climate change is predicted to alter species interactions, the timing of important life history events (e.g., migration, spawning), and the spatial distribution of fish populations (Lynch et al., this issue). On a physiological level, effects of climate change on individual fish include reduced immune function, decreased cardiovascular performance, and changes in reproductive investment (Whitney et al., this issue).

As leaders of the Student Subsection of the Education Section (Student Subsection), we recognize the importance of

understanding how climate change will affect inland fisheries and making this knowledge meaningful for fisheries students and young professionals. The Student Subsection serves to facilitate interactions between fisheries professionals and students by providing member services consistent with the mission of the American Fisheries Society (AFS), for which professional development is a primary goal. To prepare students and young professionals for rewarding careers in fisheries conservation, it is our duty as Student Subsection leaders to anticipate issues and trends that are relevant for future fisheries professionals. As climate change intensifies, we believe that it is imperative that students and young professionals acquire basic and applied knowledge of climate change as it relates inland fisheries. Not only must students and young professionals understand the process of climate change, they must develop skills to apply this knowledge for fisheries conservation. How can fisheries professionals ensure that students have climate change know-how as they prepare for their careers? We describe five action items that we believe will enable fisheries students and young professionals to tackle the challenges imposed by climate change.

1. Incorporate climate change into university fisheries programs, particularly undergraduate courses. All graduates should have a working knowledge of climate change and its ecological and sociological effects on fisheries management. Design education programs so that students are prepared to think critically about the implications of climate change, identify knowledge gaps, and develop research projects to address unanswered questions.

2. Foster undergraduate and graduate research opportunities on how climate change is affecting (and will affect) inland fishes and fisheries management. Provide resources (e.g., fish sampling equipment, water temperature loggers, geographic information systems) that students need to conduct research and thereby fill knowledge gaps. Research will enable students to increase their understanding of climate change complexities and advance the state of fisheries science relative to climate change. In addition, ecological studies, research on fisheries stakeholders (e.g., anglers, boaters, commercial fishers) should be conducted, allowing students to understand the social effects of climate change and ultimately apply this knowledge as fisheries professionals.

3. Enable students to share climate research findings through existing and yet-to-be established forums. Traditional avenues such as *Fisheries* “Student Angles” and research articles enable students and young professionals to convey their results to other fisheries professionals. In addition, creating and enhancing nontraditional communication mechanisms such as blogs, discussion boards, Facebook pages, podcasts, and webinars will allow students to describe their research findings in less formal settings and develop skills for communicating with non-scientists.

4. Solidify the nexus between climate change and fisheries stakeholders by equipping future fisheries professionals with public engagement skills for conveying the projected effects of climate change to resource users and the general public. Fisheries professionals need skills to effectively communicate realistic expectations for future fisheries to stakeholders. Students and young professionals can develop these skills by preparing written documents for stakeholders that describe fisheries in a changing climate; coordinating meetings with angling groups, watershed associations, and other organizations; and enrolling in courses and directed training programs focused on communicating science to the public.

5. Encourage established professionals in fisheries and other fields to share their perspectives regarding present and future effects of climate change on fisheries and the fisheries profession. This can be achieved by inviting researchers, managers, biologists, and human dimensions specialists to speak at universities, research conferences, AFS Student Subunit meetings, and other events. By sharing their professional wisdom on climate change, established professionals will provide students and young professionals with valuable information for applying climate change knowledge in their careers. For example, a human dimensions specialist could describe the strategies used to convey climate change science to general audiences and thereby help future fisheries professionals bridge the gap between climate change and fisheries stakeholders.

As climate change continues to affect inland fisheries, it is our responsibility as Student Subsection leaders to work with the broader fisheries community to ensure that the fisheries professionals of tomorrow have basic and applied knowledge of climate change. By enhancing climate change education, research opportunities, communication mechanisms, public engagement training, and intergenerational information flow, we believe that the professional fisheries community will be better equipped to face the current and future challenges imposed by climate change. Adding climate change know-how to the toolboxes of students and young professionals will benefit the fisheries profession now and in the future.

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Anticipated Water Quality Changes in Response to Climate Change and Potential Consequences for Inland Fishes

Yushun Chen

Institute of Hydrobiology, Chinese Academy of Sciences, 7 South Donghu Road, Wuhan, Hubei 430072, China. E-mail: yushunchen@ihb.ac.cn

Andrew S. Todd

U.S. Geological Survey, Crustal Geophysics and Geochemistry Science Center, Lakewood, CO

Margaret H. Murphy

Integrated Aquatic Sciences, LLC, Lake Placid, NY

Gregg Lomnicky

CSS-Dynamac, Corvallis, OR

INTRODUCTION

Healthy freshwater ecosystems are a critical component of the world's economy, with a critical role in maintaining public health, inland biological diversity, and overall quality of life. Globally, our climate is changing, with air temperature and precipitation regimes deviating significantly from historical patterns. Healthy freshwater ecosystems are a critical component of the world's economy, with a critical role in maintaining public health, inland biological diversity, and overall quality of life. Globally, our climate is changing, with air temperature and precipitation regimes deviating significantly from historical patterns. Changes anticipated with climate change in the future are likely to have a profound effect on inland aquatic ecosystems through diverse pathways, including changes in water quality. In this brief article, we present an initial discussion of several of the water quality responses that can be anticipated to occur within inland water bodies with climate change and how those changes are likely to impact fishes.

WATER TEMPERATURE INCREASE IN SURFACE WATERS

As global surface temperatures increase with climate change, associated increases in water temperature have the potential to significantly shift the variety of aquatic thermal environments that assemblages of fish occupy (Buisson et al. 2008). The distribution, reproduction, fitness, and survival of fishes are all inextricably linked to the thermal regime of their environment. Diverse laboratory studies highlight the direct effects that increasing water temperatures can have on fish, including increased lethality as thermal limits are exceeded (Selong et al. 2001; Zeigler et al. 2013); changes in feeding behavior, metabolism, and growth rates; and altered reproductive success (Pankhurst and Munday 2011). Indirect effects may result from uncoupled trophic interactions (Winder and Schindler 2004), shifting prey availability, interspecies competition (Buisson et al. 2008), and increased susceptibility to disease and parasitism (Marcogliese 2001; Hari et al. 2006).

Many recent studies have predicted significant shifts in thermally suitable fish habitat under climate change scenarios.

These scientific predictions have been particularly bleak for stenothermal fish species (e.g., trout and salmon), with anticipated widespread contraction of suitable salmonid habitat remaining largely within higher elevations and northern latitudes (Eaton and Scheller 1996; Isaak et al. 2012). Moving forward, studies that systematically document realized fisheries impacts would enable us to ground truth laboratory- and model-based climate change predictions (Kovach et al. 2016).

Importantly, one significant ecological consequence resulting from the loss of lower elevation mainstem habitats to warming is the increased fragmentation and resultant isolation of remaining thermally suitable habitats in colder headwater streams. Fishes in these isolated, fragmented streams typically have a much higher risk of extirpation due to an insufficient quantity and diversity of habitat to complete life cycles (Hilderbrand and Kershner 2000), increased vulnerability to genetic diversity issues resulting from inbreeding within functionally smaller populations, and increased risk of loss through stochastic events (Brown et al. 2001).

In small, shallow, and low-gradient streams, water temperature increase may have severe impacts on aquatic biota (Chen et al. 2015). For instance, many small streams in the Mississippi River Basin (Figure 1) have very poor habitat conditions (e.g., no clear riffle-run pattern, no in-stream or riparian vegetation, single sediment particles dominant such as silt), which may exacerbate the water temperature stress, and fish and other aquatic organisms that do not have natural shelters to escape the heat stress.

Compared with lotic waters, water temperature increases in lentic waters (e.g., lakes, ponds) may persist longer and have larger potential impacts on aquatic biota because of longer periods of stratification (Wetzel 2001). Increased water temperature in these seasons would have strong impacts on aquatic biota, especially on those surface dwelling organisms. Moreover, organisms in small (e.g., less than 0.1 ha) and shallow (e.g., less than 0.5 m deep) ponds (Figure 2) may be impacted more by the increased water temperature than those in larger and deeper lakes, because the former do not have space to escape the added heat stress.



Figure 1. A typical small low-gradient stream in the Lower Mississippi River Basin. Photo credit: Yushun Chen.

DISSOLVED OXYGEN PROBLEMS IN STATIC WATERS AS WATER TEMPERATURE INCREASES

As surface water temperatures increase with predicted climate change, the solubility of dissolved oxygen (DO) in those waters will decrease (Ficke et al. 2007; Solheim et al. 2010). Examples of potential widespread outcomes may include (1) a general 10% decrease in DO availability, dropping concentrations below survival thresholds for resident aquatic organisms (e.g., native indicator species in the California Sierra Nevada) by 2100 (Ficklin et al. 2013); (2) native fish biodiversity may also change with habitat loss for coldwater fish as increased water temperatures and lower DO concentrations occur, leading to a northern range expansion of nonindigenous species (Sharma et al. 2011); (3) elevated air temperatures would create deeper and longer lasting thermoclines in lentic water bodies, leading to greater metabolic activity in the hypolimnion, further reducing DO (Schindler et al. 1996); (4) decreased surface water mixing may decrease direct DO inputs and increase sediment metabolic activity in the isolated hypolimnion, further reducing DO to harmful or lethal levels for freshwater fish (Ficke et al. 2007); (5) decreased DO may lead to increased sediment solubility and availability of nutrients (Blumberg and Di Toro 1990) and other compounds, potentially increasing toxicity to fisheries from pollutants (Ficke et al. 2007); and (6) increased algae growth during daytime but more DO consumption during the night, especially in shallow, small static water bodies, such as a fish pond where low DO problems usually occur during nights and early morning hours (Farrelly et al. 2015).

HYDROLOGY-RELATED WATER QUALITY CHANGES

Increased air temperature and changes in precipitation patterns are likely to alter stream and river discharge regimes

(Clow 2010; Leppi et al. 2012). In ice- or snow-covered regions, increasing air temperatures will hasten snowmelt, altering hydrological regimes by increasing adjacent stream flow earlier and creating deficits later in the season (Stewart et al. 2005). Importantly, these late season deficits leave less water in the channel to be warmed during the warmest months of the year.

Though chemical concentrations are likely to be diluted during high flows, the total contaminant load may increase (Novotny 2003; Grigas et al. 2015). During low flows, chemical concentrations (and water temperatures) will increase, but the total load may decrease as well. For instance, in the Mississippi River Basin, runoff of agricultural nutrients (e.g., nitrogen and phosphorus) and sediment would have relatively higher concentrations but low total loads. In some extreme conditions, high flow can cause high concentrations of these agricultural pollutants as well (Reba et al. 2013). This similar flow–chemical concentration/load pattern has been observed in urbanized watersheds as well (e.g., Grigas et al. 2015).

Similarly, many components of rock weathering and solute transport are influenced either directly or indirectly by the local climate. Local hydrology, which is directly linked to climate, governs the subsurface flow of oxygen and water, as well as the surface and subsurface transport of weathering products (Nordstrom 2011). Further, both temperature and hydrology have a strong influence on watershed geochemical reaction rates and, as such, define resultant water chemistry in waterbodies draining those watersheds. As such, significant change in climate conditions (e.g., thermal and hydrological regimes) within mineralized areas has the potential to change watershed chemistry (Rogora et al. 2003).

Several studies have documented increases in rock weathering solutes (e.g., dissolved sulfate) over the last several decades and have attributed these increases to climate warming (Lami et al. 2010; Mast et al. 2011). One recent study has documented a concomitant increase in concentrations of



Figure 2. A typical small, shallow fish pond in the Lower Mississippi River Basin. Photo credit: Yushun Chen.

dissolved metals known to be both products of pyrite weathering and toxic to freshwater fishes (e.g., Zn, Cu, Cd; Todd et al. 2012). In this study, it was concluded that observed increases of instream toxic metal concentrations were likely attributable to a number of climate-influenced factors, including increased rock weathering, new subsurface flow and weathering pathways resulting from loss of frozen surface ground, and a decreasing groundwater table (Todd et al. 2012). Importantly, if such water chemistry changes cause downstream water quality to worsen, it may result in exceedances of toxicity thresholds, extending fisheries impacts downstream.

DISSOLVED ORGANIC CARBON AND METAL PROBLEMS AS AIR EMISSIONS CHANGE

Air emission of CO_2 , SO_2 , and NO_x can affect water quality through the change in precipitation chemistry. For instance, when the emission of SO_2 is increased, more SO_4^{2-} will be available in receiving water bodies, reducing pH in the water. One chemical within water bodies that appears to be increasing as a result of a combination of declines in acidification, as well as increasing temperatures, is dissolved organic carbon (DOC; Evans et al. 2005). Increasing pH and decreasing aluminum in water bodies recovering from acidification also have been accompanied by increasing DOC (Lawrence et al. 2013), which partially offsets pH increases and complicates assessment of recovery from acidification. DOC change affects drinking water quality, metal and organic contaminant transport and toxicity, nutrient availability, and attenuation of solar radiation (Erlandsson et al. 2011).

In addition, there is concern with the link between DOC and mercury concentration in biota. For instance, Driscoll et al. (1995, 2007) have reported increasing concentrations of mercury in lakes and biota of the Adirondacks with increasing concentration of DOC. Other related studies have also shown

that lake water chemistry, particularly pH and DOC, influence the bioavailability of mercury at the base of the aquatic food chain (Adams et al. 2009; Dittman and Driscoll 2009). Where atmospheric mercury deposition is a problem, the increased DOC can lead to increased tissue concentrations of mercury in aquatic organisms. In areas without a mercury point source, tissue concentrations may continue to climb resulting in new or sustained advisories for fish consumption.

CONCLUSIONS

In summary, global climate change is predicted to change air temperature; precipitation; emissions of CO_2 , SO_2 , and NO_x ; and other aspects. These changes are expected to lead to increased water temperatures (in most cases), decreasing dissolved oxygen concentration, altered water chemistry and chemical loads, and, in certain regions, create new water quality challenges including increased dissolved organic carbon and toxic metal loads. As fishery professionals, we suggest the need to be proactive and anticipate these changes to allow for adaptation in fisheries management and conservation.

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was used by Schlesinger et al. (2011) to assess vulnerability of species at risk. Access to big data could better inform national initiatives such as the National Fish Habitat Partnership, better enabling resource managers, policy makers, and stakeholders to address questions that might otherwise not be answered working with data limited by source and scale. Practical examples such as these illustrate why having these datasets organized and available allows natural resource managers to act quickly without the need to commit substantial monetary and time investments in order to address important questions.

Throughout its existence, the AFS Fisheries Information and Technology Section (FITS) has advocated for the development of big data for purposes including analysis of climate change. The idea of using big datasets may sound intimidating to some, however tools could be developed that provide automation of data importation and analysis. Two examples are the Multistate Aquatic Resources Information System (MARIS) and the NorWeST project.

MARIS

For nearly two decades FITS served as the coordinating body for the MARIS. MARIS began in the 1990s as an exploratory endeavor between state natural resources management agencies and federal resource agencies as a mechanism for distributing select information collected by state agencies to apply to the analysis of status and trends of fish populations over watersheds, ecoregions, and across jurisdictional boundaries (A. J. Loftus, MARIS coordinator, personal communication). Among the earliest discussions during the formation of MARIS was its application for tracking (at the macro level) the impact of climate change on the distribution of fish species (particularly those close to the edge of their ranges) and correlations with changes in water temperatures and watershed factors (Beard et al. 1998). MARIS has flourished, and now contains over 1 million fish sampling and water quality records for more than 1,000 fish species in 24 states with some data extending back 100 years. MARIS is being applied for many purposes directly or indirectly related to climate change studies, including:

- Compiling stream and river temperature time series records to relate to the fish community data.
- Fish passage studies to identify opportunities for barrier removal, thus opening additional habitat for species being pushed out of changing habitats.
- Investigating fish assemblages and distribution in southwestern and southeastern rivers related to human water uses and climate change.
- Historical occurrence of fish species in the specific drainages and changes in range over time.

- Invasive species tracking and distribution.
- Species occurrence in the past 10 years for populating third-party web query results for identifying species locations (A.J. Loftus, MARIS coordinator, personal communication).

NorWeST

Another example of the application of big data is the NorWeST project, a collaboration across the American West by fisheries biologists and hydrologists from >100 agencies which has resulted in synthesis products that are directly applicable to the assessment of climate change to inland fishes (Isaac et al. 2011). In brief, the project began in the Pacific Northwest due to concerns about the effects of climate change on cold water fish species and grew organically to encompass all streams and rivers in the West by cleaning and organizing datasets into digital formats that make it easy for data contributors to access and use stream temperature information for many purposes. One important application has been the development of a stream temperature model that uses all the data with sophisticated spatial-stream network data mining tools (Ver Hoef et al. 2014) to create consistent sets of high-resolution climate scenarios, which are also available for download from the website. Many organizations now use the NorWeST scenarios for climate vulnerability assessments, and Isaac et al. (2016) provide a recent example for the Pacific Northwest. Similar big data applications for many types of stream data (e.g., habitat surveys, water quality parameters, biological samples) have also been made easier with toolsets provided through the National Stream Internet project so that biologists throughout the conterminous United States can use new stream network models in their local watersheds. As more data are compiled, organized, and shared, a proliferation of new information about stream resources will follow, and these efforts will be greatly accelerated by the collaboration of biologists and hydrologists working for dozens of agencies.

FITS Fosters Data Sharing

For the past two decades, AFS and FITS have advocated for the sharing of datasets for the purpose of harnessing the wealth of information being collected by fisheries biologists every year. Since 1998, FITS has played an active role in hosting three national fisheries data summits with an underlying theme of facilitating access to existing datasets (see www.fishdata.org for summaries). These summits have incrementally provided a pathway toward the development of a National Fisheries Data Exchange Standard. More recently, FITS has hosted and co-hosted symposia focused on developing a National Fisheries Data Exchange Standard. The objective of this initiative is to provide common codes and metadata and data elements that can be used by freshwater fisheries biologists. This will facilitate

Table 1. Impediments to sharing agency fisheries data (N=62; Loftus 2006).

	Very Important	Important	Somewhat important	Not important
Legal	23%	24%	27%	26%
Policy	16%	24%	35%	24%
Technical	27%	42%	24%	6%
Financial	32%	27%	29%	11%
Personnel	48%	39%	10%	3%
Time	61%	27%	10%	2%
Fear of misuse	30%	25%	34%	11%

sharing and collating of datasets into the big data described above in a timely fashion to allow the use of current and relevant data in science and advance the goals of regional and national initiatives. Currently, the creation of large geographical and temporal datasets through the compilation of smaller datasets is hindered because the translations are excessively time consuming. A National Fisheries Data Exchange Standard will provide the benefits seen through programs like NorWeST and MARIS at a larger scale.

Through our newsletter and website we highlight tools which aid in the development of big data, opportunities for data sharing, and research which has leveraged big data and technology to address important questions in inland fisheries. The use of big data will be critical to addressing many of the questions pertinent to the impacts of climate change on inland fisheries, and we at FITS want to encourage the development and use of these data sources.

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FISHERIES MANAGEMENT SECTION

Effective Stewardship Incorporates Expertise and Innovative Approaches to Aquatic Resource Management

Mark T. Porath

President, Fisheries Management Section, Nebraska Game and Parks Commission, 2200 North 33rd Street, Lincoln, NE 68503. E-mail: mark.porath@nebraska.gov

A professional position as a “fish biologist” or a “fisheries manager” suggests a singular focus on fish, which is a bit misleading. Modern fisheries management encompasses more than a fascination with these underwater evolutionary marvels. The long-held visualization of a three-legged stool consisting of habitat, fish and people symbolizes the entwining of these components and the wisdom in managing them collectively rather than exclusively. Similarly, aquatic ecosystems include both the components and the forces (natural and anthropogenic effects) that have been at work through time to arrive at the current set of abiotic conditions (Ponomarenko 1996) and biotic communities (Infante et al. 2009; Wootton 1992) encountered today. Climate change is yet another force that further complicates our understanding as well as the long-term beneficial management of these aquatic ecosystems. Fortunately, training, continuing education, professional involvement and experience are available for biologists and managers to continually incorporate new information to aid in their stewardship responsibilities.

MANAGEMENT COMBINES AN UNDERSTANDING OF SYSTEMS WITH ACTIONS TO REACH A DESIRED GOAL

The discipline of fisheries management strives to attain a specific state or condition for the resource under stewardship (e.g., goals and strategies). Whether a recreational fishery, nature preserve or commercial fishing operation, to be an effective steward you need to not only have a solid grasp on how the current forces (natural and anthropogenic) are acting on communities within the system, but then must also be able to anticipate how changes (natural, induced, or prescribed) will influence existing system dynamics to predict future conditions. A new impoundment on a river can dramatically alter system connectivity, while changes to land use practices (e.g., no-till farming, phosphorus fertilizer bans, pet waste ordinances) can be much more subtle. Challenges faced by fisheries managers today, range from preserving genetic diversity of at-risk populations (Vrijenhoek 1998), to managing for sustainable yields of commercial harvest (Botsford et al. 1997), or providing

unique recreational fishing opportunities (Neely et al. 2015; Pikitch et al. 2005). Changes to the underlying habitat condition complicate these challenges.

Beneficial management actions (or lack thereof) require an understanding of the forces already acting upon the resource, as well as knowledge of how a system will respond, ideally prior to prescribing an appropriate strategy. For example, a fisheries manager responsible for a healthy, intact and pristine system often takes a protectionist viewpoint and usually prescribes a very conservative suite of management tactics to minimize impacts to what is perceived as a system in good working condition. In contrast, the manager of a system that is highly altered and degraded, and comprised of numerous introduced or habitat-detrimental species, is likely to take a much more aggressive approach to purposefully nudge the existing system towards a more desirable state. Even if both the pristine and altered systems have identical goals, each approach requires substantially different levels of active management and system strategies, often referred to as resilience management (Pope et al. 2014). The recognition and application of appropriate tactics to meet a desired goal across a diverse range of systems and conditions, is the basic tenet of fisheries management (McMullin and Pert 2010).

AQUATIC SYSTEMS, LIKE TIME, NEVER STAND STILL

While many of the techniques used in fisheries management have been vetted, improved, and refined over time by the application of fisheries science, hard work, and experience, they have been developed for conditions encountered over the last century, but the real challenge will be developing the approaches and tools needed for future conditions (Paukert et al., this issue). Climate science is focusing on predicting rates of change while fisheries and resource professionals are applying this information to predict future system conditions and subsequent influence to dependent communities.

Fortunately, the management process is well suited to meet the challenges imposed by climate change. As more of the earth's natural resources are exposed to anthropogenic (e.g., land use and pollution emissions) and climate change impacts (e.g., temperatures rise, precipitation patterns change), system forces will continue to alter making the prediction of future conditions even more uncertain. As our aquatic ecosystems serve as poor experimental units because of their scale and complexity and rates of general condition decline, this will necessitate an ever-increasing need for more active and enhanced management applications. But it will also further complicate our ability to evaluate and determine which actions were successful. Design and implementation of habitat rehabilitation and enhancements projects, forecasting future water conditions, stock assessment modeling and even recreational fishing (e.g., stocking and

regulations) will need to consider these uncertainties and incorporate them into an adaptive management decision-making process that adequately considers multiple causal factors simultaneously (Hillborn 2016) to truly understand the system mechanics and adjust strategies accordingly to be successful.

To meet this challenge, communication of the science behind system influences and responses will be critical in determining the impact to our resources and more importantly how we respond to manage effectively in the wake of climate change (Essig, this issue). AFS will need to continue being the leading source for communicating fisheries science information and research, but that will not be enough. As fisheries professionals and resource stewards, it will be up to us to perform the due diligence needed to research and adapt techniques, the science and ultimately our management strategies to meet the challenges presented by climate change. AFS and the Fisheries Management Section must collaborate to provide continuing education and training opportunities, sponsor symposia and publish information on advanced management techniques and topics to train the next generation of "fish biologists" or "fisheries managers" for the challenges facing our next generation of aquatic ecosystems.

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Plenary Speakers' Abstracts for the 146th Annual Meeting

We Only Manage What Has Value: Establishing Value for Fisheries Resources

Hal Schramm, Jr., Mississippi State University and Mississippi Cooperative Fish and Wildlife Research Unit

The Mississippi River provides diverse and abundant fisheries resources. Fisheries and aquatic scientists have learned much about this highly altered system, and priority conservation needs have been identified. Efforts to conserve and rehabilitate this system have been initiated, but more action is needed. Like other complex, multi-use fisheries resources, conserving the Mississippi River will require changes in social value. Understanding social value can best be achieved by recognizing the diverse cultures and drivers of value. Assessing values and accomplishing change will require partnerships with other disciplines, organizations, and sectors.

Using Social Media and Technology to Inspire and Educate

Danielle Brigida, U.S. Fish and Wildlife Service

Social media allows us to share experiences, connect with others, and discuss the very important topics (or cat videos). It's up to us to find a way to engage respectfully and distribute meaning through our interactions. In this session I'll talk about techniques for meaningfully engaging in social media so that we educate and inspire those interested in our topic. I'll also discuss how we can use social media, content strategy and connectivity to build meaningful relationships.

Using Science and Storytelling to Create a Global Voice for Freshwater Fish Conservation

Zeb Hogan, College of Science, University of Nevada, Reno

My travels have crisscrossed six continents—North America, South America, Africa, Europe, Asia, and Australia. I have come face-to-face with some of the biggest freshwater fish in existence, such as Thailand's 14-foot-long freshwater stingray or Mongolia's six-foot trout. The purpose of these travels? One is a singular focus for finding, studying, and protecting the world's largest freshwater fish. These megafish are defined as being six feet long and 200 pounds—or larger. However, by focusing attention on these charismatic megafauna allows me to bring attention to the growingly fragile freshwater ecosystems that these endangered inhabitants live in, and also provides an opportunity to define their migratory patterns and better understand their population status. My vision is to help preserve the delicate balance and thoughtful coexistence between humans and their environments, especially as it relates to endangered freshwater fish. Most importantly, I am driven to use education to incite world-wide recognition of the plight of these fish and the need to conserve and manage their habitats by making connections and building partnerships through various media outlets such as TV, the Internet, and print. I will discuss my travels, the interesting fish I have seen, and the habitats that they live in. However, most importantly, I will discuss how you can make connections and build partnerships to conserve and manage species that are important to you.

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Journal Highlights

TRANSACTIONS OF THE AMERICAN FISHERIES SOCIETY

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[Note] Generation of Quantitative Polymerase Chain Reaction Detectability Half-Lives and Comparison of Sampling Protocols for Genetic Diet Studies of San Francisco Estuary Fishes. *Scott C. Brandl, Brian M. Schreier, J. Louise Conrad, Bernie May, and Melinda R. Baerwald.* 145: 441–449.

Using Hierarchical Bayesian Multispecies Mixture Models to Estimate Tandem Hoop-net-Based Habitat Associations and Detection Probabilities of Fishes in Reservoirs. *David R. Stewart and James M. Long.* 145:450–461.

Quantifying Recruitment Compensation in Florida Large-mouth Bass, with Implications for Fisheries. *Stephanie L. Shaw and Micheal S. Allen.* 145:462–475.

Feeding Ecology of Native and Nonnative Salmonids during the Expansion of a Nonnative Apex Predator in Yellowstone Lake, Yellowstone National Park. *John M. Syslo, Christopher S. Guy, and Todd M. Koel.* 145:476–492.

Evaluation of Back-Calculated Size and Timing Estimates for Juvenile Chinook Salmon Using Otolith Structure and Chemistry. *Andrew M. Claiborne and Lance A. Campbell.* 145:493–501.

Ontogenetic and Long-Term Diet Shifts of a Generalist Juvenile Predatory Fish in an Urban Estuary Undergoing Dramatic Changes in Habitat Availability. *Brittany J. Hall-Scharf, Theodore S. Switzer, and Christopher D. Stallings.* 145:502–520.

Predation by Northern Pikeminnow and Tiger Muskellunge on Juvenile Salmonids in a High-Head Reservoir: Implications for Anadromous Fish Reintroductions. *Mark H. Sorel, Adam G. Hansen, Kristin A. Connelly, Andrew C. Wilson, Erin D. Lowery, and David A. Beauchamp.* 145:521–536.

Ontogenetic Development of Otoliths in Alligator Gar. *James M. Long and Richard A. Snow.* 145:537–544.

Factors Influencing Stream Fish Species Composition and Functional Properties at Multiple Spatial Scales in the Sand Hills of the Southeastern United States. *Michael H. Paller, Blair A. Prusha, Dean E. Fletcher, Ely Kosnicki, Stephen A. Sefick, Miller S. Jarrell, Sean C. Sterrett, Andrew M. Grosse, Tracey D. Tuberville, and Jack W. Feminella.* 145:545–562.

Density and Survival of Walleye Eggs and Larvae in a Great Lakes Tributary. *E. S. Rutherford, J. Allison, C. R. Ruetz III, J. R. Elliott, J. K. Nohner, M. R. DuFour, R. P. O'Neal, D. J. Jude, and S. R. Hensler.* 145:563–577.

Components of Mortality within a Black Bass High-Release Recreational Fishery. *Janice A. Kerns, Micheal S. Allen, and Joseph E. Hightower.* 145:578–588.

Can Weighted Useable Area Predict Flow Requirements of Drift-Feeding Salmonids? Comparison with a Net Rate of Energy Intake Model Incorporating Drift-Flow Processes. *John W. Hayes, Eric Goodwin, Karen A. Shearer, Joe Hay, and Lon Kelly.* 145:589–609.

Monitoring Demographic and Genetic Responses of a Threatened Inland Trout to Habitat Reconnection. *Helen Neville, Dan Dauwalter, and Mary Peacock.* 145:610–626.

Coast-Wide Nursery Contribution of New Recruits to the Population of Atlantic Menhaden. *Kristen A. Anstead, Jason J. Schaffler, and Cynthia M. Jones.* 145:627–636.

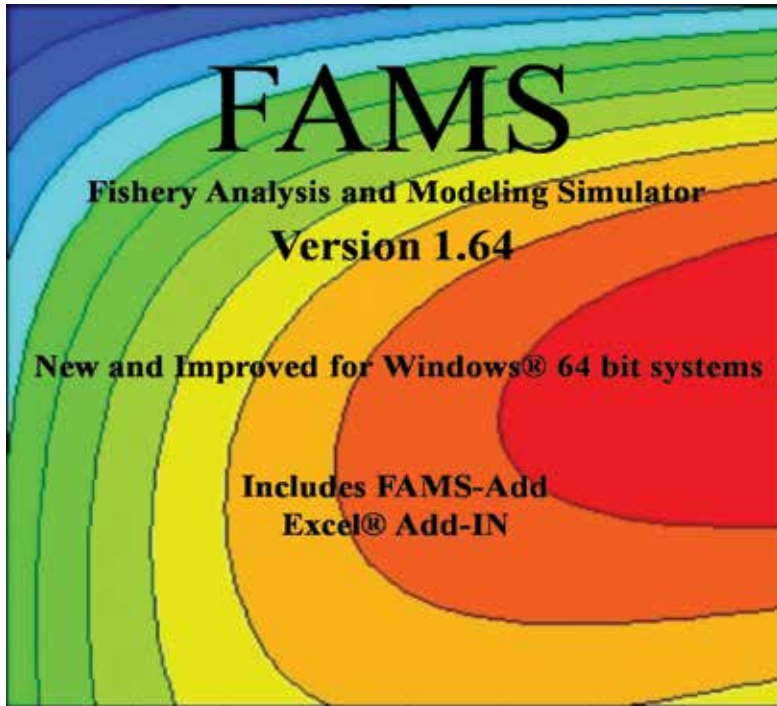
Harvest-Induced Size Structure Shifts Alter Nutrient Release by a Population of Omnivorous Fish. *Matthew J. Catalano and Maynard H. Schaus.* 145:637–648.

Interactions between Hatch Dates, Growth Rates, and Mortality of Age-0 Native Rainbow Smelt and Nonnative Alewife in Lake Champlain. *Paul W. Simonin, Donna L. Parrish, Lars G. Rudstam, Bernard Pientka, and Patrick J. Sullivan.* 145:649–656.

Carbon Dioxide as a Tool to Deter the Movement of Invasive Bigheaded Carps. *Michael R. Donaldson, Jon Amberg, Shivani Adhikari, Aaron Cupp, Nathan Jensen, Jason Romine, Adam Wright, Mark Gaikowski, and Cory D. Suski.* 145:657–670.

Maximum Likelihood Estimation of the Proportion of Hatchery-Origin Fish on Spawning Grounds Using Coded Wire Tagging and Parentage-Based Tagging. *Richard A. Hinrichsen, Craig A. Steele, Michael W. Ackerman, Matthew R. Campbell, Shawn R. Narum, Maureen A. Hess, William P. Young, Barbara A. Shields, and Brian L. Maschhoff.* 145: 671–686.

Fishery Analysis and Modeling Simulator (FAMS), version 1.64 (for 64-bit operating systems)



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FAMS is designed to simulate and evaluate the dynamics of exploited fish populations. It allows for the evaluation of minimum, slot, and inverted length limits and bag limits on exploited fisheries. Input parameters require age-structure data and use the Jones modification of the Beverton–Holt equilibrium yield equation to compute both a yield-per-recruit and a dynamic pool model. For the dynamic pool model, the entire population is simulated over time. In addition, it helps to analyze several predicted population parameters, including the number of fish harvested and dying naturally, mean weight and length of harvested fish, number in the population above and below some lengths of interest, total number of fish and biomass in the population, stock density indices, number of age-1 fish, and the spawning potential ratio.

The FAMS-Add portion of the software package is a Microsoft Excel add-in that contains a number of handy data analysis tools: age–length key, frequency distributions, weight–length regression, catch-curve regression, back-calculation and more. These functions are accessed via a menu item placed on the Excel menu bar. Collectively, these functions are useful for summarizing fish sampling data, identifying outliers, and simple statistics.

Compatible with Windows Vista, Windows 7, and Windows 8 64-bit environments (for Windows XP and earlier versions, purchase FAMS version 1.0).

CALENDAR

To submit upcoming events for inclusion on the AFS website calendar, send event name, dates, city, state/province, web address, and contact information to sharrison@fisheries.org. (If space is available, events will also be printed in *Fisheries* magazine.) More events listed at www.fisheries.org


July 6–10, 2016

Joint Meeting Ichthyologists and Herpetologists | New Orleans, Louisiana | conferences.k-state.edu/joint-meeting


July 11–14, 2016

Freshwater Invasives – Networking for Strategy (FINS-II) | Zagreb, Croatia | finsconference.eu

July 25–28, 2016

 Joint Summer Meeting of the Centrarchid, Esocid, and Walleye Technical Committees - North Central Division of AFS
| Gretna, Nebraska | ncd.fisheries.org/Walleye

August 21–25, 2016

 146th Annual Meeting of the American Fisheries Society | Kansas City, Missouri | 2016.fisheries.org

August 24–25, 2016

3rd Annual International Conference on Fisheries and Aquaculture | Sri Lanka | aquaconference.com/2016

September 5–8, 2016

Australian Society for Fish Biology Conference | Hobart, Tasmania

October 2–6, 2016

The World of Trout: 1st International Congress | Bozeman, Montana | troutcongress.org

November 10–12, 2016

2nd International Congress on Applied Ichthyology and Aquatic Environment | Mesolonghi, Greece | hydromedit2014.apae.uth.gr

December 6–7, 2016

Flatfish Biology Conference | Westbrook, Connecticut | nefsc.noaa.gov/nefsc/Milford/flatfishbiologyworkshop.html

December 10–15, 2016

Restore America's Estuaries and The Coastal Society: 2016 Summit: Our Coasts, Our Future, Our Choice | New Orleans, Louisiana
| estuaries.org/Summit

habitat management, fish dispersal, education, monitoring, research, funding, and management to reduce ecosystem stressors. AFS sent letters to President Obama in January 2013 and the U.S. Environmental Protection Agency administrator in June 2014 promoting the policy statement.

Climate change has been the subject of many symposia at Society and AFS Unit meetings in recent years. The 2015 Annual Meeting had sessions on ocean acidification and impacts of climate change on populations, distributions, and habitats. The 2016 Midwest Fish and Wildlife Conference, where the North Central Division meets, featured a session on climate science for state-level resource management. There will be symposia on drought and impacts of climate change on inland fish at the AFS 2016 Annual Meeting in Kansas City. Symposia like these provide an opportunity for researchers and managers to share the latest climate change science that is tailored to aquatic species and habitats.

AFS organized two Congressional Hill briefings in recent years where climate change was a major focus. The Society and its Potomac Chapter presented a briefing entitled “Climate Change and Fisheries” on May 9, 2013, with speakers from federal and state agencies, academia, and a Native American tribe. A March 19, 2015, briefing on marine fisheries management included a presentation entitled “Addressing Climate Change as a New Challenge to Fisheries Managers.”

AFS staff is currently working through Cornell University on a three-year project to review the work of the eight Department of Interior Climate Science Centers (CSCs) in the United States. The scientific goal of these reviews is to assess the contribution of each CSC in climate modeling, climate change impact assessments, vulnerability and adaptation analyses, and developing adaptation strategies. Review objectives also include evaluating partner engagement and graduate student training of the CSCs.

There are other ways that AFS is likely to engage in the climate change issue in the future. Sections like Fish Habitat and Water Quality are well positioned to work on the issue, and there has been discussion of forming a new AFS Climate Change Section. Through its Future of the Nation’s Aquatic Resources initiative, AFS is currently gathering information on important issues for the incoming U.S. Presidential administration that are very likely to include climate change.

Finally, this thematic issue of *Fisheries* is the most recent example of AFS involvement in climate change. It includes a cross section of articles organized by active members Craig Paukert and Abby Lynch that are sure to pique your interest. Please take some time to explore and enjoy the issue. Perhaps you can apply some of the science contained within to your current or future fisheries work. **AFS**

To tackle these issues, and in conjunction with the United Nations World Water Day, the White House Water Summit was convened on March 22, 2016, to

- raise public awareness of water issues and potential solutions,
- catalyze ideas and actions to help build a sustainable and secure water future through innovative science and technology, and
- frame ideas for the next administration.

The summit focused domestically on the full range of topics relevant to aquatic systems, small communities, and metropolitan utilities. This event was livestreamed by the White House and is likely to be archived on that site.

The Association of Fish and Wildlife Agencies convened its own “Drought Forum” on February 29, 2016, to prepare for discussions at the National Fish Habitat Partnership’s board meeting mentioned above. And the discussion will continue at the American Fisheries Society Annual Meeting in Kansas City, where the Estuaries Section and Fish Habitat Section have joined forces on a special symposium on drought.

The momentum of these events, coupled with a snowy first day of spring covering my earliest-ever cherry tree blossoms, has me hoping for great success on all three goals for the Water Summit. Perhaps this discussion will expand from drought to the broader issues of flow because the water that doesn’t fall in parched watersheds will fall elsewhere. Our challenges just doubled!

Note: This column represents my personal opinions, as based on the comments of Ellen Gilinsky at the National Fish Habitat Partnership March 2016 Board Meeting. They do not necessarily represent those of the American Fisheries Society. Comments are invited at tbigford@fisheries.org.

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Back Page Photo Series:

Dichotomy

An Interview with Sarah Lehnert

Interview by Natalie Sopinka | AFS Contributing Writer

Photographer: Sarah Lehnert, Ph.D. Candidate, Great Lakes Institute for Environmental Research (GLIER), University of Windsor. E-mail: lehnert@uwindsor.ca

Location: University of Northern British Columbia's Dr. Max Blouw Quesnel River Research Center, Likely, British Columbia, Canada



What species of fish do these eggs belong to and why is the coloration so distinct?

These are unfertilized eggs from Chinook Salmon *Oncorhynchus tshawytscha* from the Quesnel River, British Columbia. The distinct difference in color is due to genetic polymorphisms that affect deposition of carotenoids, naturally occurring red pigments. Variation in deposition results in two distinct color “morphs”: red and white Chinook Salmon. Although both morphs incorporate red carotenoid pigments into their diet by eating animals like krill and squid, they differ in their ability to deposit the pigments into their tissues. Their eggs are different colors as the photograph shows, but they also differ in flesh color and external spawning coloration. Carotenoids are thought to be very important to salmon, because they are

powerful antioxidants; therefore, it is interesting that the white phenotype continues to exist in nature.

How did you end up studying this phenomena?

I started studying Chinook Salmon for my M.Sc. with Daniel Heath (GLIER). My M.Sc. focused on understanding the potential impacts of farmed salmon escapes on wild salmon populations. Through this research, I spent a lot of time at Yellow Island Aquaculture Ltd. (YIAL), which is an organic Chinook Salmon farm in British Columbia. YIAL was a great place to do research because we could design large-scale experiments and monitor Chinook Salmon over their entire life. During this time, I connected and collaborated with academic, government, and industry researchers, which led

to the opportunity for my Ph.D. project. For my Ph.D., I was interested in continuing to study Chinook Salmon, but I wanted to get experience working with a wild population and answer big-picture, evolutionary questions. The opportunity to study the importance of carotenoids to salmon really excited me, and it is something that my supervisors (Daniel Heath and Trevor Pitcher, GLIER) and our collaborator (Robert Devlin, Fisheries and Oceans Canada) have been determined to understand for a long time.

What was your reaction to seeing your first white-morph Chinook Salmon?

Before I started my first field season, I was quite nervous that it might be difficult to tell red and white Chinook Salmon apart. I wasn't sure if Chinook Salmon truly existed as these two color morphs that I had read about. But luckily, they did! Most of the Chinook Salmon that I've caught in the Quesnel River are either very pigmented (red) or gray (white) in external spawning color. I was very excited the first time that I saw a white Chinook Salmon in the wild. It was surreal to see this different salmon morph in person! Although white Chinook Salmon don't have the characteristic red coloration that we know and love in Pacific salmon, they are still impressive in a different way. Some of the white Chinook Salmon seem to have a hint of blue coloration during spawning. Also, of all the Chinook Salmon that I've caught in the Quesnel River, the biggest ones tend to be white.

What is the proportion of white-morph individuals in a given population?

It's thought that around 10% of all Chinook Salmon in the world are the white morph. The proportion of white-morph individuals within a river system varies across populations and ranges from 0% to 100%. In British Columbia, the Harrison River in the Lower Fraser watershed represents a population that is 100% white, whereas a lot of populations on Vancouver Island are composed of only red individuals. Chinook Salmon in the Quesnel River are 50% red and 50% white, which is why I study this population. By having equal proportions of red and white Chinook Salmon, I am able to design and carry out experiments that examine the genetic and fitness differences between the morphs.

Who are the stakeholders interested in flesh color?

Enhancing flesh color is a major goal of the aquaculture industry as consumers associate the color of a salmon fillet with its quality. Flesh color is not only an economically important trait, it is also an evolutionarily important trait. The degree of pigmentation can vary between individuals within a species (e.g., the red- and white-morph Chinook Salmon that I study), as well as among species (e.g., Sockeye Salmon *O. nerka* have the highest carotenoid content relative to other Pacific salmon, whereas Chum *O. keta* and Pink *O. gorbuscha* salmon have the lowest carotenoid content). This variation may reflect evolutionary adaptations related to different environmental conditions and/or life history strategies. My research is contributing to our understanding of salmon evolution, as well as benefitting the aquaculture industry.

Is flesh color heritable?

Yes! Previous work done by Ruth Withler (Fisheries and Oceans Canada) on Chinook Salmon in the Quesnel River

showed that there were likely two major genes that controlled flesh color in this species. Withler's research suggested that each flesh color gene has two alleles, an allele coding for the red morph (R allele, dominant) and an allele coding for the white morph (W allele, recessive; Withler 1986). Withler found that a Chinook Salmon needs to have at least one red allele at both of the color genes to be red (e.g., $R_1W_1; R_2W_2$ = red salmon). If a Chinook Salmon only has one red allele at one of the two genes, it will be white (e.g., $R_1W_1; W_2W_2$ = white salmon). Determining the exact genotype of each color morph can be complex as different combinations of the alleles can produce either the red or white morph. A mating between a red and a white Chinook Salmon can produce different proportions of red and white offspring depending on the genotype of the parents.

What remains a mystery regarding pigmentation in salmon?

Why salmon evolved to use and deposit carotenoid pigments is still a mystery. My Ph.D. dissertation is providing answers to a number of questions to help solve this mystery. In populations where red and white Chinook Salmon coexist: Does pigmentation (carotenoids) provide salmon with benefits in terms of mating success? Does the maternal provisioning of carotenoids increase egg survival and offspring immune function? Are red eggs more noticeable to predators compared to white eggs? Where are the color genes located in the salmon genome (i.e., on which chromosomes)? What evolutionary mechanisms are responsible for the maintenance of the red/white color polymorphism in nature?

What parts of the red/white mystery have you unraveled so far?

So far, we have found that in the Quesnel River, red and white Chinook Salmon do not mate assortatively based on color (Lehnert et al. 2016). This finding tells us that color assortative mate choice is not the evolutionary mechanism that maintains the color polymorphism in nature. Some form of natural selection must be responsible. Therefore, we also examined differences between red and white adult salmon at two immune genes (major histocompatibility complex [MHC] I-A1 and MHC II-B1). We chose to study immune genes because carotenoids are often correlated with immune function in birds and fishes. We found significant differences between morphs at both genes. For example, at MHC I-A1, we found that white Chinook Salmon were more heterozygous (i.e., more diverse). So, if white Chinook Salmon are in fact at a disadvantage in terms of immune function (because they lack carotenoids), they may be able to compensate by having more diverse MHC genes than red individuals, which could allow white salmon to deal with a wider range of pathogens. This hypothesis could explain how white Chinook Salmon can overcome the expected carotenoid-immunity handicap and be able to coexist with red salmon in nature.

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