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and Natural Resources Conference

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Plenary Session.
81st North American Wildlife and Natural Resources Conference

Welcome and Opening Remarks

Steve Williams
Wildlife Management Institute
Gardners, Pennsylvania

Welcome to the 81st North American Wildlife and Natural Resources Conference. WMI thanks you and all the conference partners, special session chairs and speakers, exhibitors, and federal and state agency sponsors who are critical to making this conference successful. I also offer special thanks to John Arway and Matt Hough for their "Welcome to Pennsylvania" address.

During the last few years, WMI has significantly expanded our conservation portfolio. We now assist in the administration of five Landscape Conservation Cooperatives and manage two Multistate Conservation Grants to enhance the industry/agency partnership and to help develop a National Hunting and Shooting Sports Strategic Plan. WMI has secured numerous competitive grants to enhance landscape scale conservation. We have developed contracts and cooperative agreements with state and federal agencies to assist them in conservation projects. WMI has also provided independent review and evaluations of agency programs for a number of state and federal agencies. These evaluations have identified program strengths and weaknesses and provided recommendations for agency consideration. Agency feedback has been positive and indicated that our efforts have enhanced agency performance. During the last eight years, WMI has transformed to become sustainable as an organization and to be more relevant to our profession and partners.

This morning's plenary session will focus on relevancy—the relevancy of conservation. I believe that one measure of relevancy is the political and financial support for conservation. In spite of listening to most of the presidential debates, I have not heard any discussion of conservation issues. Federal spending on fish and wildlife conservation is one-third of its level just 30 to 40 years ago. State agencies consistently identify sustainable funding as their top priority. Society has become reliant on technology and social media and has become increasingly detached from nature. By all these measures and more, I believe our profession faces a crisis of relevancy, one that threatens sustainable funding and social and political support for the future.

Recognizing the urgent need for sustainable funding, the Association of Fish and Wildlife Agencies designed the Blue Ribbon Panel on Sustaining America's Diverse Fish and Wildlife Resources. The Blue Ribbon Panel focused on identifying dedicated and sustained funding for the conservation of thousands of species identified in State Wildlife Action Plans. Former Wyoming Governor Dave Freudenthal and Bass Pro Shop's founder Johnny Morris cochaired the panel. Other members of the Blue Ribbon Panel included national leaders in fish and wildlife conservation, business, energy, manufacturing, and agriculture. This collection of diverse stakeholders was unprecedented and necessary to find a practical solution to the conservation funding challenges facing the nation.

The Blue Ribbon Panel's recommendations were to redirect existing revenue from the development of energy and mineral resources on federal lands and waters, providing a sustainable trust fund capable of investing $1.3 billion annually for conservation. The panel has developed legislative language and identified bill sponsors within the current congressional session. The conservation efforts, focused on species at risk, would increase species survival and habitat quality while reducing the regulatory risk and uncertainty for business and industry. In addition, Blue Ribbon Panel members will continue their work by evaluating conservation relevancy and the means to enhance that relevancy.

That brings me to my concluding remarks. For the last five years, I talked about the need for our profession to resonate with and be more relevant to the public. This year, I return to that message.

As I stated, it appears that conservation has lost some of its relevancy. Perhaps environmental legislation passed in the 1970s, such as the Clean Air Act and Clean Water Act, has led the nation to believe that important environmental issues have already been addressed—or perhaps the world has changed.

The world has changed dramatically since we started our careers. The human population has increased, demographics have changed, urbanization has increased, technology and social media have consumed our culture, and as a nation we have become largely detached from nature. As a profession, we have done an admirable job improving our biological science knowledge. However, the loss of relevancy is a function of our inability to understand the social impacts of a changing world. There are other disciplines to consider. The incorporation of economics, politics, sociology, demography, marketing, culture, and education will have more of an impact on the relevancy of conservation than do the articles in our scientific journals.

If we want to enhance the relevancy of conservation we need to communicate the benefits of conservation in a way that gets people's attention. First we need to recognize that people and their needs and desires are the keys to the door—we need to better understand what drives people to behave or act, and we need a stronger understanding and respect for economies, communities, and cultures. Our conservation programs should be culturally relevant, address issues of public concern, engage technology in outreach, base public opinion on scientifically sound surveys, employ marketing, and consider the economics of conservation. Natural resource conservation provides a large return on investment because of the multitude of public benefits that it provides.

I believe that our profession needs to transform its structure, programs, and messages to be relevant to the entire public. Our talk is wildlife-centric in a world that is human-centric. We need to explain habitat conservation by referring to ecosystem services rather than our ability to produce so many ducks per acre or bucks per square mile. We provide clean water, clean air, flood retention, ground water recharge, biodiversity, climate moderation, pollinators, and recreation. All of these services ultimately promote physical and mental well-being. That is what people really care about. That is what makes conservation relevant and that is what will sustain and support our work.

These benefits resonate with the American public, rural and urban alike. These benefits will drive public engagement, political support, and financial support for conservation. They will provide public health benefits, quality of life benefits, and ultimately enhance further conservation efforts. It is a matter of increasing conservation's relevancy to the public.

It is very simple: if we are not relevant to society, we will be irrelevant. I leave you with this quote from General Eric Shinseki, "If you don't like change, you're going to like irrelevance even less."

Thank you for participating in this conference and I thank you for your dedication to fish and wildlife conservation.

Remarks for the 81st North American Wildlife and Natural Resources Conference

Dan Ashe
U.S. Fish & Wildlife Service
Washington, D.C.

Thank you Steve. And thank you all for the warm welcome, for your friendship, and for your professionalism and dedication to conserving wild things and wild places.

More than ever, what we do requires creativity and innovation. Much has been written on these subjects, but everyone here should read *Steal Like An Artist* by Austin Kleon. It's an easy read because it's really more *Cat in the Hat* than *War and Peace*—really, the only kind of book I can read these days! It's basic premise is that there is no such thing as truly original work and that creativity originates through adaptation of the work of others. Here's an excerpt:

> ...a good artist understands that nothing comes from nowhere. All creative work builds on what came before. Nothing is completely original...

Relatedly, and important in thinking about what you will hear from this panel, Kleon says, "Everything that needs to be said has already been said. But since no one was listening, everything must be said again."

Today, I'm going to cover three topics:

- First, and briefly, the nature of the challenge we face today and will increasingly face tomorrow.
- Second, the growing dysfunction in the conservation community.
- Third, a specific part or symptom of that dysfunction—the growing irrelevancy of conservation.

So, first things first. Many—maybe most—of you have heard me say this: our challenge in conserving wild creatures is human ecology. Today, we share the planet with 7.3 billion others of our species. By midcentury, we will be approaching 10 billion—and it's not just our growing numbers, but our expanding affluence. More of the world's population will be more like us, with increasing access to things like electricity, education, transportation, and health care. We will demand more fuel, more fiber, more food, and we will consume more of the planet's ecological space. And though we would wish it were not so, that means less and less for the rest of what we collectively call biodiversity.

Continued success will require that we be smarter, faster, and stronger. Better focused. More unified. Collectively determined. And that's a good transition to my second point.

As a community, we have a significant and growing dysfunction. We seem to be increasingly viewing ourselves as an island in a rising sea of change. We are armoring ourselves against momentous tides of change. We are reflexive, defensive, and increasingly angry at the growing proportion of the population that just doesn't get it. Easy things are hard. Hard things are impossible.

Case in point is what we call a Sportsmen's Bill—and this is not a criticism of the congressional sponsors, because they are responding to us. We are the problem. This is our dysfunction. Rome burns; prairies are in crisis; Asian carp assault the Great Lakes; Burmese pythons strangle the Everglades; elephants, rhinos, and other wildlife are decimated by a global epidemic in trafficking; state and federal refuges in California (anchors of the Pacific Flyway) are starved of water; mule deer are disappearing from large expanses in the west; every native trout species is imperiled; grassland birds are declining precipitously—and in the name of sportsmen, we ask Congress to address the import of 41 polar bear trophies killed in 2008. The Land and Water Conservation Fund expires—but in the name of sportsmen, we ask Congress to exempt lead bullets from TSCA regulation, well knowing that lead bullets are not being regulated by TSCA. And then early this year, we witnessed the armed, illegal occupation of

Malheur National Wildlife Refuge by extremists who deny the legitimacy of federal and state government and the entire concept of public lands held in trust for the American people.

I'll pause here to recognize the organizations who stood up and spoke out publicly against the occupation at Malheur: the National Wildlife Federation, National Wildlife Refuge Association, Theodore Roosevelt Conservation Partnership, Trout Unlimited, Backcountry Hunters and Anglers, Defenders of Wildlife, and the Audubon Society.

We will need more strong voices as we see this cancer growing in Congress and state legislatures across the nation, where our ability to conserve and protect our public lands and native wildlife is being steadily undercut by politicians hostile to the very idea of public trust.

These ideologues are waging a relentless campaign to undermine the legitimacy of public lands, public resources, and wildlife held in trust for the public. They want the federal government to divest hundreds of millions of acres of public land—not for sportsmen or women, but for economic development, private use, and corporate profit. They're doing what we used to do so well. They're playing the long game and their larger aim is succeeding—to undercut public support and confuse the issue for voters.

The Malheur occupation didn't occur in a vacuum. It happened because there are people—many of whom occupy positions of power and influence across the west—who share their values and beliefs, even if they recoil at their methods—for now. Sadly, the public doesn't seem to realize the stakes, which brings me to my third point.

Conservation is increasingly irrelevant in today's changing American society. Relevance is the noun form of the adjective relevant*,* which means "important to the matter at hand." To us, and our predecessors—anglers, hunters, and outdoor enthusiasts, conservation has been relevant because it sustains the things we care about—the matters at hand. But fewer and fewer people are fishing, hunting, and spending time outdoors.

More than 8 in 10 Americans live in urban and suburban environments—and urbanization is accelerating. The nation will soon be made up of a majority of minorities. We—you, me, our organizations, our profession, our community—we do not look like America. We do not, therefore, think like America. How then can we even understand, let alone achieve, what is important to the matters at hand in a changing America?

I want you to look to your left or right or ahead of or behind you. Count 10 people. Raise your hand if at least four of those people are women. Raise your hand if at least four of those people are *not* white. This is a crisis for conservation, and we simply must address it. We must change and change rapidly.

Yes, change comes hard. But, as General Eric Shinsheki teaches us: "If you don't like change, you're going to like irrelevance even less." We are seeing the early stages of irrelevance. We need to embrace rapid and revolutionary change. We're facing big challenges—our conservation family has some key dysfunctions and we are facing a crisis of relevancy.

Here's what we need to do:

- We have to break out of the disciplinary silos that we built—and that served us so well—in the 20th century. We can't do 21st-century conservation if we see the world divided into fish, wildlife, range, and forestry. We have to unite these great disciplines and see conservation in a larger context and design conservation on a larger scale.
- We have to have zero tolerance for politicians, at all levels of government, who support divestiture of public lands. No candidate should be able to call himself or herself a sportsman or woman unless they defend, loudly and at every turn, the benefits and importance of public land ownership and professional stewardship.

It's an election year, and we need a true sportsmen's platform—not platitudes about rights to hunt and fish. We need politicians who will stand up for clean air and water and for protection of habitat and who will stand behind the professional public servants—local, tribal, state, and federal—who dedicate their lives to conserving wild places and wild creatures. We need a professional ethic that unites us as a community. Former President Ronald Reagan united his political party in the 1980s and coined what he called the Eleventh Amendment: “Thou shalt not speak ill of any fellow Republican.” We need an Eleventh Amendment: “Thou shalt not speak ill of any fellow conservationist.” Sure, we may disagree from time to time, but these are professional, courteous, and respectful differences. As Austin Kleon says, “Quit picking fights and go make something!”

Those in our community who sow seeds of anger and adversity must meet with what Aldo Leopold called social disapproval. If we let these people divide us and play us against each other, then we—and the resources we love—will lose. How can we expect the faith and confidence of the public if we do not reflect faith and confidence in one another?

We must diversify our organizations, our profession, and our community. This must be a collective priority. We need to set measureable goals and attain them. It is a myth that talented and diverse candidates are not available or that they do not represent the best and brightest. Who *is* the best and brightest at the age of 21 or 25? I wasn’t. We take people of good character and make them the best and brightest.

The reality is: we look in all the same places, we do what we have always done, and we settle for what we have always gotten. This has to change. It’s an issue of leadership, and it’s time for leaders to step up and lead.

There’s a new generation of conservationists out there. They’re in cities; they’re using iPhones and Androids; they don’t hunt or fish; they’ve never spent a night outdoors; their skin is red or brown; English may be their second language. We have to find them. We have to inspire and recruit them. They will become the best and brightest. They will make conservation relevant.

We need a Joint Venture for Professional Diversity.

We have to start today.

And finally, we all need to embrace the words of Eleanor Roosevelt: “Do one thing every day that scares you.” And I’d add: something that scares the living hell outta your boss!

Thank you for listening.

Special Session One.
2020 Vision: Federal Forest Management into the Next Decade

Federal Forest Management into the Next Decade: What Science Tells Us

John P. Hayes
Colorado State University
Fort Collins, Colorado

Understanding What Science Tells Us

Capturing "what science tells us" regarding the future of forest management is, at best, a daunting task. The breadth and depth of scientific information regarding forest management being generated by research institutions is increasing at an impressive rate, and our scientific understanding of forests is growing literally as you read these words. In addition, differences across regions and sites and among forests differing in management and disturbance history, vegetation, and a myriad of factors preclude the ability to provide a comprehensive overview of scientific understanding that applies to all forests across the country. Despite these limitations, general principles and patterns do emerge when viewed at a coarse scale. This coarse-scale, 30,000-foot view is the perspective taken in this paper.

Forest management options are fundamentally constrained by biophysical forces. Environmental conditions, weather, soil fertility, rainfall, fire regime, and a host of other factors determine what trees grow in a particular location, their productivity, and their response to management. Indeed, scientific understanding of the influences of biophysical factors on tree growth, forest stands, and the ecological communities and recognition of the way forests, biophysical forces, and management actions interact form the backbone of modern forestry.

Four Biophysical Driving Forces That Will Shape Future Management Decisions

In this paper, I argue that four biophysical factors will have overarching influence and constrain options for forest management and policy in the coming decade (and beyond): climate change; insects, disease, and forest health; altered disturbance regimes; and loss of native biodiversity. These forces are identified as paramount for two reasons. First, the very nature of these forces shapes the boundary conditions that limit forest management options. While highly intensive management actions conceivably can expand the suite of options imposed by these biophysical forces (such as through irrigation, fertilization, species translocations, or other efforts), actions to significantly overcome the constraints resulting from these forces will generally be economically prohibitive, often impractical given contemporary technology and resources, and typically unsustainable. Second, evidence indicates that these four factors are currently in strong flux. Changes in each of these will not only limit forest management options but will also, in some cases, impose fundamentally new conditions that necessitate a consideration of a novel suite of management alternatives. Recognition of the changing nature of biophysical forces and the ways that these changes influence forest management options will be critical to effectively provide the desired ecological and societal benefits of forests in the future.

Climate Change

Climate change is the proverbial 800-pound gorilla in the living room. The scientific community has a strong consensus that our climate has already begun to exhibit significant change and that further, increasingly dramatic changes are imminent (e.g., Melillo et al. 2014). Climate change will impose a new suite of stressors and disturbances to forest systems that are outside of the historic conditions to which they have been exposed, including both short-term, acute, high-intensity disturbances that cause sudden and rapid changes to forest ecosystems (pulse disturbances) and more gradual, longer-term, persistent changes (press disturbances; Holmes et al. 2014). Anticipated changes resulting from climate change that will impact forest ecosystems include shifts in distribution of exotic species, invasive plants and animals, and disease organisms; changes in the severity and frequency of droughts; altered hydrologic regimes and patterns of snowpack and rainfall; longer fire seasons and increased size, frequency, and severity of wildfires; milder winter conditions reducing mortality of insect pests; and decreased environmental suitability for some indigenous plants and animals. The magnitude of impacts imposed from the new disturbance framework resulting from climate change will vary geographically but is likely to be transformational in some areas (e.g., Harvey et al. 2016).

Despite overwhelming evidence documenting a changing climate and sophisticated scientific models indicating significant change rapidly approaching, denial of the reality of climate change is embraced in some quarters. Equally or perhaps more challenging is the fact that, even among managers that accept the reality of climate change, specific management actions that should be taken in response are often unclear. The lack of clear direction stems both from uncertainty in the specific ways that climate change will manifest in particular forests and from lack of well-developed, science-based management prescriptions for forests under climate change, impeding informed decision-making (Keenan 2015).

An underpinning of ecological approaches to forestry has been use of forest management to emulate or mimic historic disturbance regimes or to establish future desired conditions based on historic conditions; under a changing climate, the utility of historical conditions as a framework for forest management is significantly diminished (Safford et al. 2012). Primary approaches to address forest management in the face of a changing climate have focused on strategies to maintain or enhance resilience (the ability to return to a desired condition following disturbance) and resistance (the ability to maintain current state in the face of disturbance; Holmes et al. 2014). However, despite an extensive literature regarding forests and climate change, clear understanding of the most effective management strategies to address climate change remains elusive, highlighting the importance of well-designed, solutions-focused research with scientists working in close partnership with managers to craft management strategies.

Insects, Disease, and Forest Health

Impacts of insects and disease on forest health can significantly influence management options and the products and ecological goods and services provided by forests. In many parts of the United States, forest health is seriously impacted and the overall health of the nation's forest is in decline (Potter and Conkling 2015). In 2013, mortality caused by insects and disease was recorded on roughly 4.5 million acres in the United States, and significant defoliation occurred over a greater area (Jenkins 2015). Nearly one-third of this mortality was caused by a single species—the mountain pine beetle (*Dendroctonus ponderosae*), but more than 80 mortality-causing insect and disease agents and a similar number of defoliating agents have been recorded in U. S. forests (Potter and Conkling 2015). While both indigenous and exotic species are responsible for defoliation and tree mortality in our forests, the number of exotic invasives causing damage in our forests is high. Aukema et al. (2011) reported that 455 species of nonnative phytophagous insects established in forests of the United States. Although many of these species have minimal impact, nearly 15% of these species have been documented to result in significant tree mortality, with a handful of species (such as the emerald ash borer *Agrilus planipennis*, hemlock woolly adelgid *Adelges tsugae*, and gypsy moth *Lymantria dispar*) responsible for especially significant impacts. Impacts of exotic species almost inevitably will increase in the years to come with the volume of goods that flow into the nation's ports and across our borders and with the opportunity for exotic species to be transported in on vehicles, imported live plants, wooden shipping materials, and other substrates.

The overall decline in the nation's forest health is particularly acute in some geographic areas, forest types, and species. Left unchecked, these trends will result in shifts in forest species composition, diminished or lost productivity and commodity production, reduction in ecological goods and services, and reduced societal value of forests over significant areas. These forces will constrain management options and, in many cases, will demand intensive efforts focused on restoration to increase valuable forest functions and to enable a greater array of management options.

Altered Disturbance Regimes

The dominant large-scale disturbance force in many U.S. forests is fire. The number of large-scale fires and the acreage impacted by those fires has increased significantly in most regions of the western United States during the past three decades (Dennison et al. 2014). The causal factors responsible for this shift in disturbance regimes are multi-faceted and include the history of fire suppression in western forests, droughts and weather conditions, poor forest health, and other factors.

Although less dramatic and more difficult to perceive, changes in disturbance due to changes in intensity of herbivory pressure appear to have caused shifts in vegetative structure and species composition of some forests in the United States. The influence of increased herbivory on forest structure appears to be most profound in eastern and northern deciduous and mixed forests and primarily due to increased forage pressure because of high population densities of white-tailed deer (*Odocoileus virginianus*; Frerker et al. 2014).

Altered disturbance regimes pose at least three major challenges and concerns for forest systems. First and most obvious is the direct and immediate impacts of disturbance on the ecology, productivity, and characteristics of forest systems. While disturbance is a natural and critical element of forest ecology and the dynamics of forest systems, the types and magnitude of disturbance events currently seen in many federal forests in recent years is unprecedented with undesirable consequences. Second, altered disturbance regimes have dramatically influenced forest structure in many areas, and the resulting forest structure often narrows management options and, in some cases, reduces the societal and ecological benefits provided by forests. Finally, the economic costs incurred by management agencies from fire suppression activities severely impact the resources available for other management activities (USDA Forest Service 2015). Although not obvious to the public, the consequences of these increased costs to federal forest management are profound. Significant changes in the number, size, and severity of fires have ballooned economic costs of fighting fire and fire suppression activities. The proportion of the U.S. Forest Service's annual appropriated budget dedicated to fire has increased from 16% in 1995 to more than 50% in 2015, and under current funding mechanisms, it is projected to require two-thirds of the budget by 2025. These increased costs for fire management have gutted other critical management programs within the U.S. Forest Service, with huge budget reductions for road and facility management, planning, habitat management, and other programs.

Altered disturbance regimes in today's forests are the result of a long legacy of policy and management decisions. While the negative ramifications of this history have continued to increase over time and recognition of the problems that these changes invoke is not new, solutions to address the issue are becoming more and more difficult to achieve. Under a changing climate, extreme weather conditions and drought combined with reduced forest health establishes conditions that increase the probability of large-scale fire. Physical and ecological challenges in addressing issues related to altered disturbance regimes are compounded by social and human issues, including expansion of human populations into the wildland-urban interface; concerns for use of prescribed fire related to smoke, air quality, and human health; and in some cases, limited social license to reestablish disturbance regimes.

Loss of Native Biodiversity

In the 1970s, 1980s, and 1990s, concerns related to biodiversity became primary considerations in management of federal forestlands. The federal mandate to protect endangered species and provide habitat for the full array of species indigenous to the nation's forests—fueled by concerns of possible influences of forest management on high-profile species like the northern spotted owl (*Strix occidentalis caurina*), marbled murrelet (*Brachyramphus marmoratus*), red-cockaded woodpecker (*Leuconotopicus borealis*), Indiana bat (*Myotis sodalis*), and other species—resulted in dramatic shifts in federal forest policy and management of federal forests. While much of the public attention and concern regarding biodiversity on forests has diminished in recent years, threats to sustainability of forest species remain.

Conservation of species and habitats are defendable (and in my perspective, critically important) management goals for a number of ethical and societal reasons, but maintaining ecologically viable populations of many species is also fundamental to ecological functioning of forests and to maintenance of ecological goods and services important to society. Loss of species and species groups has potential for tremendous impacts on forests. For example, white-nose syndrome, a disease of bats caused by infection by the fungus *Geomyces destructans*, has resulted in rapid collapse of populations of common species of bats in the eastern United States (Frick et al. 2010). As the primary predator of nocturnal flying insects, bats play important roles in regulating populations of many species that are agricultural and forest pests. The economic benefit of insect predation by bats in agricultural systems in the United States has an estimated value of nearly $4 billion (Boyles et al. 2011). Although subject to some controversy, removal of large predators from forest systems and the resulting influences on populations of herbivores also appears to have had important influences on forest structure and composition (Beschta and Ripple 2009).

The Interplay Among Biophysical Drivers and Forest Management

Although I have largely presented each of the four biophysical forces as independent drivers of forest systems, clearly there are significant interactions and feedback loops among these biophysical drivers, influencing the impacts of each. In addition, the ways that these drivers influence forests can be strongly modified, mitigated, or exacerbated by forest management activities (Figure 1). This interplay among biophysical drivers is shaped by the current condition of forests as influenced through forest policy and forest management decisions. This interplay, in turn, profoundly effects and constrains options for the future.

The Social Dimension

As an ecologist who views the world through a biophysical lens, an ecological perspective strongly shapes the viewpoints presented in this paper. However, while effective management and policy options are constrained by biophysical reality, forest management options on federal lands are also significantly constrained by social and political dimensions. There are numerous examples across the country where management actions to achieve ecological goals, commodity production, restoration, or other aims have been thwarted by lack of social acceptance of the proposed activities. Strong understanding of the human dimensions of forest management and application of social science approaches will be critical to achieve effective forest management in the coming decades.

Linking Science, Policy, and Management in the Coming Decades

Forestry research has a rich tradition and science has long played a critical role in informing forest management and policy in the United States. Today, there is a dedicated cadre of forest scientists focused on many of the most important scientific questions to help address forest management and shape forest policy. At the same time, the complexity of questions regarding forest management and policy and the urgency of need for effective solutions to address many of the issues discussed in this paper is increasing dramatically.

While there are many examples of effective science-management partnerships that have resulted in solutions-based understanding and stronger forest management, there are also instances where increased effectiveness could be gained from enhanced and more effective partnerships. Here, I suggest three possible avenues to catalyze more effective science-management partnerships.

Funding Issues

While arguing that increased funding for research by researchers has become almost cliché, the reality is that federally funded forestry research is dwarfed by that of other program areas (especially health, and to a lesser degree, fundamental research, agriculture, and other fields). While differences in relative levels of funding do not inherently justify increases, the current status of our forests and the impending impacts of climate change, poor forest health, altered disturbance regimes, and loss of biodiversity on the critical benefits that forests play for society implores us to implement the best possible forest practices. Yet, the ability to implement those practices in the coming decades is severely limited because of information needs that could be met through research. Increased funding of programs directed toward forest management, such as the McIntire-Stennis program, and directed research funding to address forest health and other issues is fundamental to providing the foundation needed for strong forest management in the coming decades.

Building Relevance

While much of the research done by forest scientists is highly relevant to shape management and policy directions, despite the best intentions, this is not always the case. I argue that restricted relevance of forest research is a luxury we can ill afford given the importance of the issues facing the nation's forests. The responsibility for ensuring relevance in research is, in my opinion, a shared burden by scientists and managers. Building a strong scientific understanding regarding management of long-lived, spatially complex, dynamic systems undergoing change requires a strategic perspective. While there is considerable pressure to conduct research with immediate impacts to address issues with limited geographic and temporal scope, this approach will often be inadequate to significantly impact the most important issues facing management of our federal forests. Increased communication between forest managers, policy makers, and scientists to help craft solutions-oriented research relevant to the most critical elements of future management of our forests is key.

Boundary Institutions

Historic institutional structures in place within the scientific and research communities have spawned tremendous increases in understanding and knowledge of forest systems. These structures rely heavily on creative energies of researchers and increasingly on individual entrepreneurial strategies to generate resources needed for research. I anticipate that these same structures will continue to generate innovative solutions and essential understanding in the coming decades. However, given the speed of change in biophysical forces constraining forest management and the novel concerns that will emerge in the years to come, these structures may not be fully adequate to provide the essential and timely information needed for effective forest management in future decades.

As a consequence, stronger institutional structures to encourage and facilitate direct engagement of forest management and science may play an important role in linking science, policy, and management in the coming decades. I advocate consideration of development and more frequent and stronger use of boundary organizations at the interface of science, policy, and management as a potential mechanism to advance this goal (Guston 2001). Boundary organizations provide both the opportunity and the incentive for development and use of relevant information and directly engage individuals and programs from either side of institutional boundaries. In the absence of formal structures of this type, significant progress will still be made, but it may not be as directed, coordinated, and relevant as needed to address the compelling issues facing forests in the coming decades.

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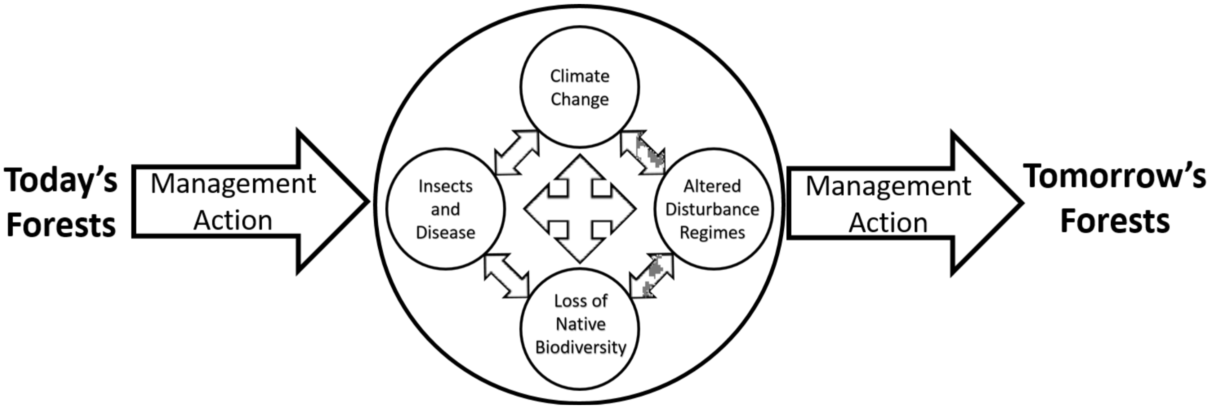
Figure 1. The interplay between forest management and biophysical drivers.



Special Session Two.
Effects of Climate Change on Inland Fish and Fisheries: Looking Back and Moving Forward

Physiological Basis of Climate Change Impacts on North American Inland Fishes

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Introduction

Climate change is altering the physical, chemical, and biological characteristics of freshwater habitats with concomitant effects on freshwater and diadromous fishes (Hartmann et al. 2013). Climate-induced physical habitat changes include increased mean water temperatures, frequency of extreme temperature events, and altered hydrologic regimes of lotic and lentic habitats resulting from changes in precipitation (Austin and Colman 2007; Kaushal et al. 2010; Magnuson et al. 2000; Leppi et al. 2012). Climate-induced changes in temperature and precipitation may directly affect freshwater habitats or effects may arise indirectly via changes in the terrestrial landscape (Isaak et al. 2010; Davis et al. 2013). Chemical characteristics of waterbodies, such as dissolved oxygen, salinity, and nutrient concentrations, are directly influenced by these climate-induced changes in thermal and hydrologic regimes (Ito and Momii 2015; Bonte and Zwolsmen 2010; Moss et al. 2011). 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) to directly or indirectly influence the physiological function of fishes (Staudt et al. 2013).

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 leaves fishes vulnerable to climate-induced changes in temperature and other environmental factors (Fry 1947). The consequences 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 (e.g., 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).

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 for higher-order population and community responses, such as altered phenology, range shifts, and biotic interactions (Pörtner and Farrell 2008; Cahill et al. 2013; Lynch et al. 2016). Physiological understanding can also be used to identify those species or populations most vulnerable to climate change that, in turn, can be used to generate management recommendations to mitigate the effects of climate change

(Williams et al. 2008; Huey et al. 2012; Paukert et al. 2016). 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 (Mommsen et al. 1999). The biochemical reaction rates responsible for the HPI response are regulated by temperature, whereby for every increase of 10ºC, 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 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), but chronic stressors are energetically costly to fishes and divert energy supplies away from growth and reproduction and may ultimately result in mortality (Schreck 2010). 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 (IGF-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) highlights 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; Figure 2; Box 1; Pörtner and Farrell 2008; Farrell et al. 2009). Ectothermic fish metabolic and oxygen uptake rates are profoundly influenced by temperature, 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; Fry 1947). Each individual, population, and species thus has a temperature where aerobic scope is optimal (T_{opt})—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; Jonsson and Jonsson 2009). The general warming trend in freshwater ecosystems, as well as the greater intensity and frequency of temperature extremes, represents the primary climate-induced changes that affect cardiorespiratory systems in fish. While 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 in British Columbia, Canada, temperatures during summer have increased by approximately 2ºC since the 1950s and are projected to continue to increase along the same trajectory (Patterson et al. 2007; 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, and at least some of this mortality has been attributed to insufficient aerobic scope to meet the energetic demands of upstream migration (Farrell et al. 2008; Hinch et al. 2012). 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; Eliason et al. 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 physiology. For example, hypoxia (Box 1) can interact with high temperatures to reduce aerobic scope and the functional thermal tolerance window (Figure 2C; Pörtner and Farrell 2008; McBryan et al. 2013). In addition, toxicants, metal pollution, and disease impair metabolic rates and swimming performance (Jain et al. 1998; Sokolova and Lannig 2008; Wagner et al. 2005). 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, although innate immunity functions independently of temperature (Dittmar et al. 2014; 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 as 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) suggests 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 during 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, growth, and reproduction (Wagner et al. 2005; Tierney et al. 1996; Rushbrook et al. 2007). These sublethal negative effects can also result in indirect mortality, as 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 and/or in the drier conditions associated with climate change, exposing potentially immunocompromised fishes to increased prevalence of infectious agents (Macnab and Barber 2012; Gagne and Blum 2015). Further, certain parasites (e.g., *Schistocephalus solidus*) can alter host behavior so that they seek out warmer environments, simultaneously compromising immune function while optimizing parasite performance within the fish (Macnab and Barber 2012). 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, while 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 and, as such, are at risk from increased drought frequency and duration resulting from global climate change (Peterson and Meador 1994; Seager et al. 2007 and 2013). Drought conditions result in elevated environmental salinity because of evapoconcentration, which oftentimes occurs in warm-water or intermittent streams but may be less frequent in cold-water or perennial systems (Mosley 2015; Datry et al. 2014). As 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, reproduction, and movement (Morgan and Iwama 1991; Hoover et al. 2013). 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 an 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—the 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 (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 (HPG) axis, and thus, temperature influences all aspects of fish reproduction (Pankhurst and Munday 2011; Miranda et al. 2013). 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* or threespine stickleback (Cingi et al. 2010; 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 to 8°C (normal range) but declined to 38% when temperatures were 10°C, and Whitney et al. (2013) found that sockeye salmon embryonic survival decreased with elevated temperatures (Brinkman et al. 2013). Given that fish eggs and larvae generally have the lowest thermal tolerance of any life stage in a species, elevated temperatures resulting from global climate change could result in a population bottleneck from lowered survival and recruitment (Rombaugh 1997; 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), nest building (i.e., changes in nest structure, building behavior, and gene expression for threespine stickleback in response to higher discharge), and larval survival (i.e., lower survival of fall-spawning salmonid larvae in New York in years with greater winter and spring discharge) (Munz and Higgins 2013; Rushbrook et al. 2010; Seear et al. 2014; 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. 2016). 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), whereas more specialized species may be unable to do so (La Sorte and Jetz 2012). Unfortunately, a species' or population's 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*) (e.g., 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 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 upward or poleward 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 and sex-dependent factors, but few studies have elucidated how species-specific age-classes or sexes are differentially sensitive to climate change (Box 2; Beer and Anderson 2011; Lawrence et al. 2015; Cooke 2004). 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 intraspecies 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. 2016). 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 and select suitable habitats for receiving translocated populations or species, although this management strategy remains controversial and could result in unintended negative consequences (Olden et al. 2011; Dunham et al. 2011; 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 or commercial fishing 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 (Arlinghaus and Cooke 2009; Raby et al. 2011). These measures may help ensure that anglers modify their behavior during climate extremes such that released fishes are likely to survive (Hunt et al. 2016). Physiological knowledge required to adapt management strategies is complex and requires several important pieces of information for each population or species, including (Somero 2010; Munday 2015):

- physiological tolerance to climate-altered environmental stressors,
- interactive effects of multiple climate and anthropogenic stressors on physiological tolerance,
- acclimatization capacity of physiological tolerance, and

- 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, while 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, as 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, they are the exception in studies examining fish physiological response to changing climate (Dudgeon et al. 2006). 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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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 clip art, web.)

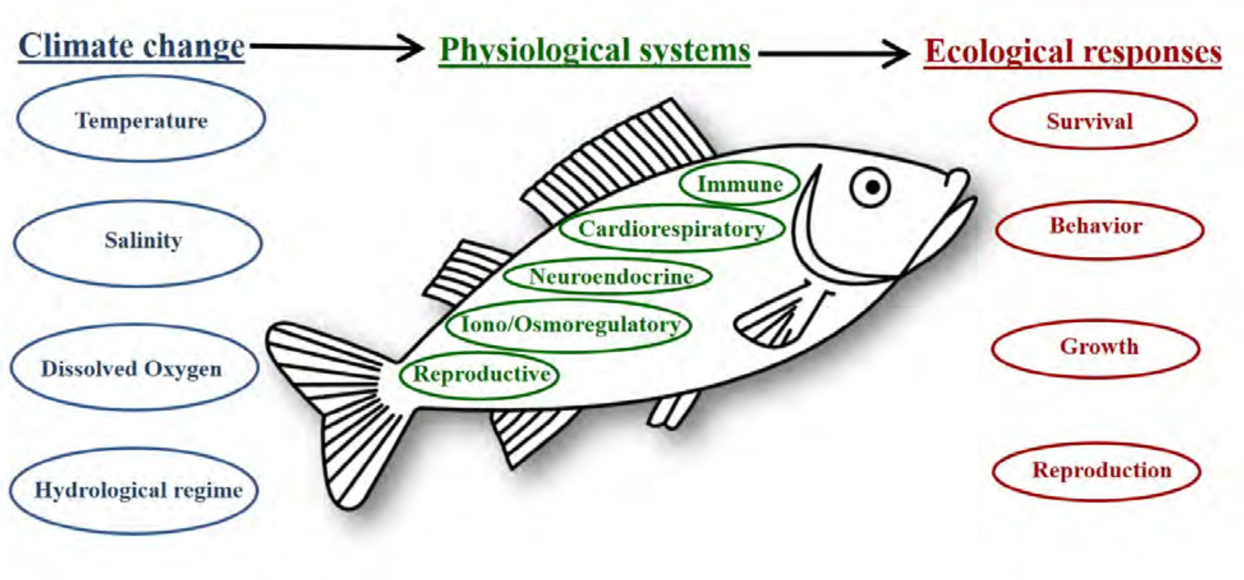


Figure 2. A) Changes in maximum metabolic rate (MMR; blue) and standard metabolic rate (SMR; purple) with temperature (aerobic scope = MMR – SMR). B) The aerobic scope curve is indicated in black, with the temperatures corresponding to maximal (T_{opt}) and zero aerobic scope (T_{crit}) indicated. Some activities (e.g., migration) require more aerobic scope than others (e.g., 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.

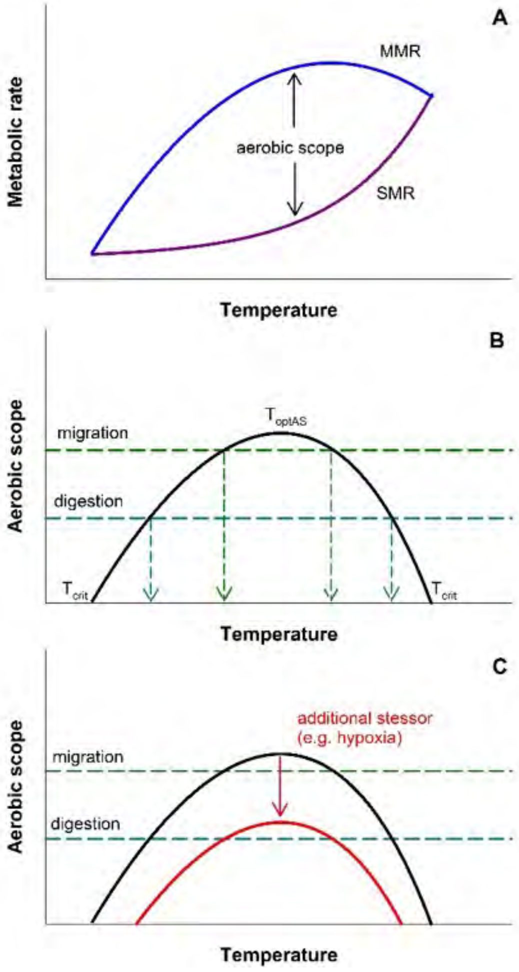
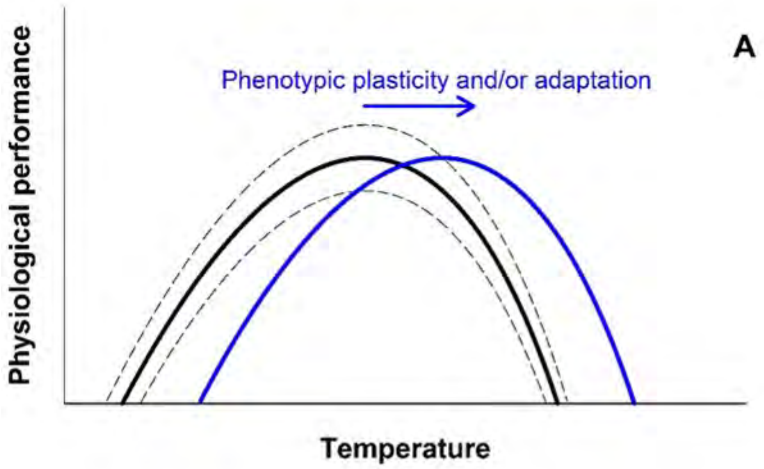
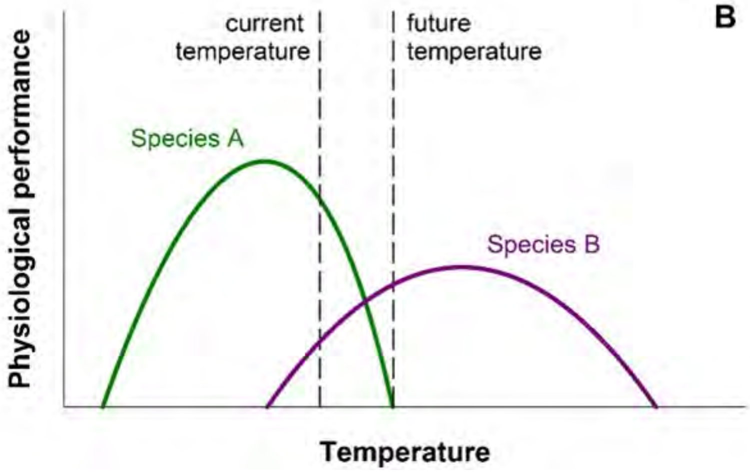


Figure 3. A) Mean physiological performance (black line) and associated estimate of individual variability (dashed lines) for a hypothetical fish population. The population may be able to respond to elevated temperatures through phenotypic plasticity and/or evolutionary adaptation to right-shift their reaction norm and increase their functional thermal tolerance. B) Under current climate conditions, Species A encounters near optimal temperatures while 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, while Species B may thrive under the new conditions.





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).
- *Critical thermal tolerance* (T_{crit}): 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 = hypo-osmotic).
- *Hypo-osmotic*: 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.
- *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 to 5.0 ppt (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 (e.g., 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?

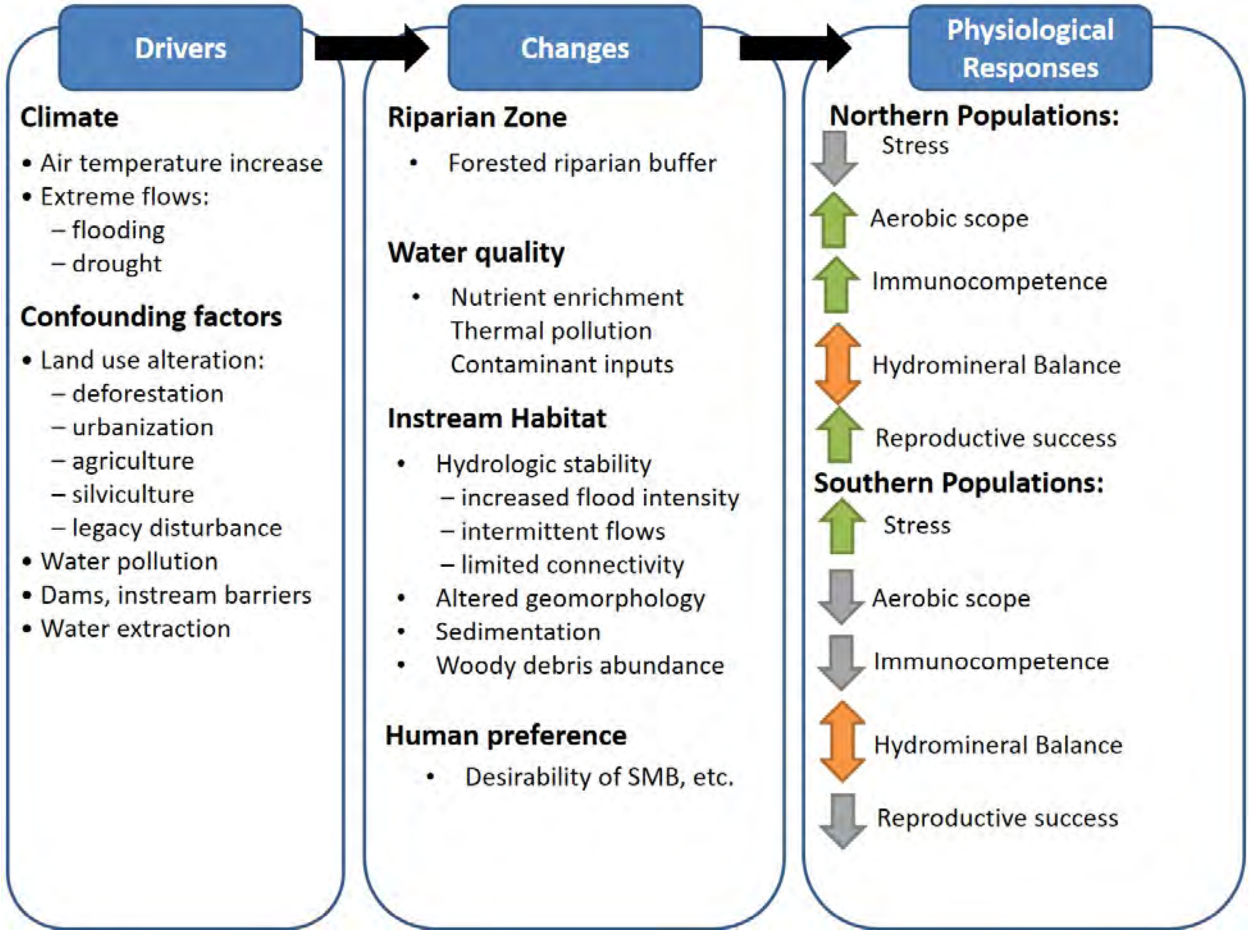
Iono- and Osmoregulatory

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

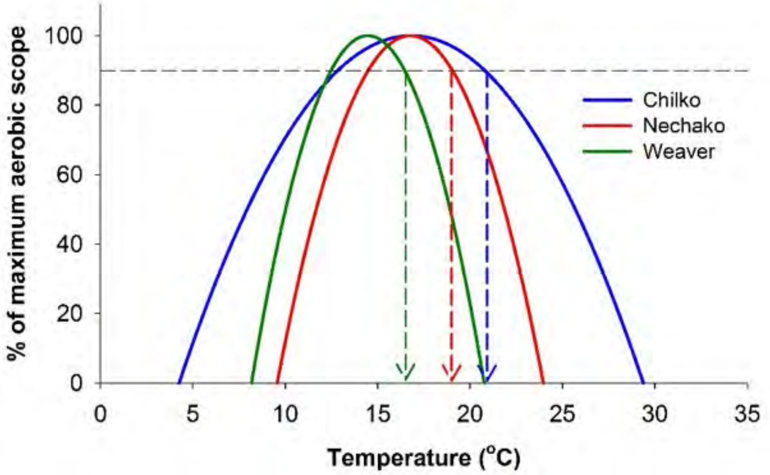
Reproduction

- 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?

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, while physiologically inhospitable conditions become more prevalent for southern populations. Green arrows indicate an increased response, gray arrows indicate a decreased response, and orange double-arrows indicate that responses varied. This variation may occur among or within populations and watersheds.



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 in the Fraser River watershed in British Columbia, Canada (Lee et al. 2003; Eliason et al. 2011; Eliason et al. 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.



Percent 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, 19.0, 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.

Climate Change Effects on North American Inland Fish Populations and Assemblages

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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, which are ecologically, culturally, and economically important (Burkhead 2012). 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. 2016). Fishes are also uniquely vulnerable to climate-mediated changes in temperature and precipitation because they are confined to aquatic habitats, and movement to alternative habitats is often more restricted than in terrestrial systems (e.g., fragmented stream networks).

We conducted a literature review of the empirically documented effects of climate change on North American inland fish populations (e.g., changes to distribution, phenology, abundance, growth, recruitment, genetics) and assemblages structure (i.e., species richness, evenness, and composition). We limited our geographic scope to North America to provide a continental-scale synthesis on climate change impacts to inland fishes. We included only peer-reviewed studies conducted in North America and published between 1985 and 2015. 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), we identified 31 publications that directly characterized climate change effects on North American inland fishes (Goodman 1961).

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 2). 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, while summer precipitation is expected to decrease in the southeastern United States, with variability in precipitation increasing throughout the continent (Dore 2005). 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, although response will also vary with local conditions (Adrian et al. 2009; Williamson et al. 2009; Schneider and Hook 2010; O'Reilly et al. 2015). On average, freeze and breakup dates of lake ice in the Northern Hemisphere have become later and earlier, respectively, and interannual variability in ice dynamics has increased over the past 150 years (Magnuson et al. 2000). Broadscale warming trends in lake 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) with concomitant impacts on lake ecosystem structure and function (Boehrer and Schultze 2008).

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). While altered thermal regimes in lotic systems have been observed, considerable variability is evident and observed patterns have been confounded by other anthropogenic factors, such as dams, diversions, and land use changes (Isaak et al. 2012; 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, significant changes are expected for coastal wetlands that exist at the transition between aquatic and terrestrial systems (Ingram et al. 2013; 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. 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 1). 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). During 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, and we are aware of only four studies from North America (Table 1; Comte and Grenouillet 2013; Pletterbauer et al. 2014). At midlatitudes (40°N to 50°N), warm- and cool-water species have exhibited increased presence, abundance, and distribution, while a cold-water species (bull trout *Salvelinus confluentus*) has experienced range contraction (Johnson and Evans 1990; Alofs et al. 2014; 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—our literature review produced 15 examples from North America (Table 1; Parmesan and Yohe 2003; Crozier and Hutchings 2014). 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 midlatitudes, alewife *Alosa pseudoharengus*, Atlantic salmon *Salmo salar*, American shad *A. sapidissima*, and sockeye salmon have begun spring migration events earlier in response to accelerated warming in the spring and to overall warmer spring and summer temperatures (Ellis and Vokoun 2009; Juanes et al. 2004; Russell et al. 2012; Otero et al. 2014; Quinn and Adams 1996; Cooke et al. 2004; Crozier et al. 2011). In Lake Erie, yellow perch *Perca flavescens* did not spawn earlier in the spring following shorter, warmer winters, but in Lake Michigan, yellow perch did, as did walleye *Sander vitreus* in some Minnesota lakes (Farmer et al. 2015; Lyons et al. 2015; 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; therefore, we suggest that additional research is needed to better understand the mechanisms and consequences of these changes (e.g., Cooke et al. 2004).

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). While 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).

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 cold-water fishes. Decreased growth and abundance of some cold-water species has been linked to increased temperature (e.g., Arctic charr *S. alpinus*, cisco *Coregonus artedi*) or to increased hydrologic variability (e.g., Chinook salmon *O. tshawytscha*) (Murdoch and Power 2013; Jacobson et al. 2012; Ward et al. 2015). Conversely, increased temperatures and altered aquatic conditions have facilitated increased recruitment and abundance for cold-water species (e.g., sockeye salmon) as well as for warm-water species (e.g., black basses *Micropterus* spp.) (Schindler et al. 2005; Kovach et al. 2014; Robillard and Fox 2006). Although compensatory dynamics can buffer some populations from climatic change, recent 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, with time, changes to this and other evolutionary processes, such as genetic drift and gene flow (e.g., range-contractions and decreases in the effective population size), are likely to be more frequent (Crozier and Hutchings 2014; 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 temperatures 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, suggesting that changes in genetic diversity may prove to be a common but currently understudied effect of climate change (Turner et al. 2014; 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 assemblages 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) has observed northward expansions of game fishes 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 case study below, "Complex Interactions of Stressors in Southeastern U.S. Stream Fish Assemblages"). 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 (Figure 3; Figure 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 and adult migration timing have occurred throughout the Pacific range (Kovach et al. 2013; Quinn and Adams 1996; Crozier et al. 2011; Kovach et al. 2015). These responses are variable across species and locations and in some instances may reflect natural selection (Crozier et al. 2011; Kovach et al. 2012). In general, salmon populations in Alaska demonstrate surprisingly diverse demographic responses to climate change (e.g., Rogers et al. 2013), and this diversity will ultimately contribute to long-term population stability, a phenomenon that has major implications for human harvest and ecosystem dynamics (Hilborn et al. 2003; Schindler et al. 2010). For example, salmon consumers, such as bears and gulls, actively exploit and benefit from spatial heterogeneity in salmon phenology and population dynamics (Schindler et al. 2013).

Salmon responses to climatic variation (and other stressors) have generally been more volatile at lower latitudes where environmental, population, life history, and genetic diversity have been reduced (Moore et al. 2010; Carlson et al. 2011). Unfortunately, the loss of abiotic and biotic diversity at the southern margins of their native ranges is likely to make salmon particularly susceptible to climate change, as 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) that are currently being impacted by climate change (OMNRF 2012). 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) estimates that a northward shift in the distribution of smallmouth bass within Ontario lakes has occurred at the rate of approximately 13 kilometers per decade during the past 30 years. This expansion is partially facilitated by human activities (e.g., intentional stocking) and opportunities to move through connected water bodies, but is primarily a result of climate-mediated increases in thermal habitat suitability (Table 1; Drake and Mandrak 2010; 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 (Figure 5; Figure 6). Smallmouth bass have already caused declines in littoral prey species abundances as well as contractions in cyprinid (prey) species ranges (Table 1; Vander Zanden et al. 2004; Alofs et al. 2014; Paukert et al. 2016). Smallmouth bass may also have negative impacts on native top predators, particularly cold-water 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) predicts 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, while 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 to 3°C during the past century with increased evaporation rates and decreased winter snowpack in the headwaters, which result in less surface water and greater aridity (Stewart et al. 2005; 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, exacerbating the direct effects of climate change (Hurd and Coonrod 2007). 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).

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 (Figure 7; Figure 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 during the past 70 years (Turner et al. 2015). While fishes of the Rio Grande have previously been exposed to strong climatic changes, 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 (Hurd and Coonrod 2007; Gutzler 2013). 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, but they are nevertheless an important and promising tool to complement other adaptive management and climate change mitigation strategies (Propst et al. 2008; Bunn and Arthington 2002; Gido et al. 2013).

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

The southeastern United States (the 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 (Figure 9; Figure 10). For example, human alteration of the landscape and riparian zone, like climate change, can result in aquatic habitat homogenization: heavily shaded, cool-water stream reaches with diverse in-stream physical habitat parameters (e.g., depth, velocity, substrate, and cover) become warmer, open-canopy reaches with lower habitat diversity and higher turbidity, sedimentation, and nutrient and contaminant loads.

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

Conclusions and Future Research Needs

Climate change impacts on inland fishes are complex and variable, and the current literature does not yet adequately represent the diversity of North American inland fishes that are being impacted (Figure 1). 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). While 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 datasets 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 1; see cisco case study in Paukert et al. 2016). 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 1). 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 nongame species as well as fishes from other regions of North America. Geographic underrepresentation is particularly acute in Mexico, much of Alaska, the North American Great Plains, the North American deserts, and the northern forests and territories of Canada. Taxonomic representation is poor in families beyond Salmonidae, Percidae, and Centrarchidae.

Document Sources of Resilience

As climate change continues to alter freshwater habitats and pressure inland fishes to move or adapt, research must 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—will 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 to 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, and will ultimately maximize opportunities for inland fishes to continue to thrive in the face of climate change (Peterson et al. 2003).

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

Map Data Point	Response	Driver (Climate/Habitat)	Geographic Area & 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 bass	Walleye abundance declined, Black Bass 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 Qamutissait, and Lake Tasiapik, Québec	Arctic charr	Growth decreased in one lakes	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. 2015
9	Distributional shift	Warmer air temperatures, less ice cover	Ontario lakes (n=1527)	13 games and nongame species	6 game fishes expanded their range northward, 5 of 7 nongame fishes 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 & 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	Earlier/warmer	Southeastern	Pacific	Sockeye salmon	Species	Kovach et al.

	shift	spring/summer	Alaska streams (n=21)	salmon	generally migrated later; coho, pink, and chum salmon migrated earlier		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 Cyprind, Catostomid, and Poeciliid species	Earlier spawning and egg hatching; lentic species increased	Assemblage	Krabbenhoft et al. 2014
20	Phenological shift	Earlier/warmer spring/summer	Connecticut ocean tributaries (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
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 1. 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).

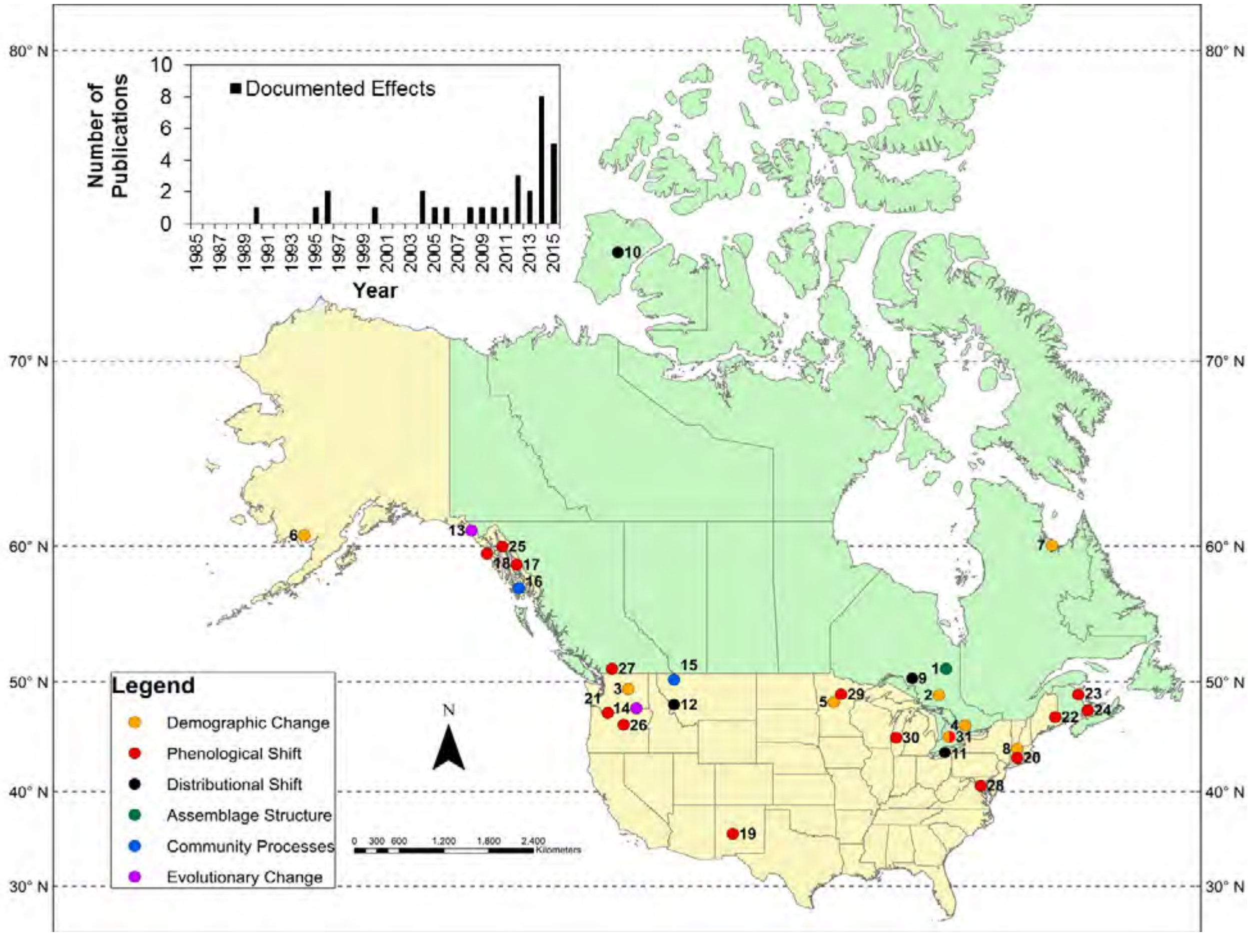


Figure 2. Conceptual model of the impacts of climate change and confounding anthropogenic factors on fish populations, assemblages, and aquatic communities. Climate and confounding factors may be, but are not necessarily, equally influential on fish populations, assemblages, and aquatic communities.

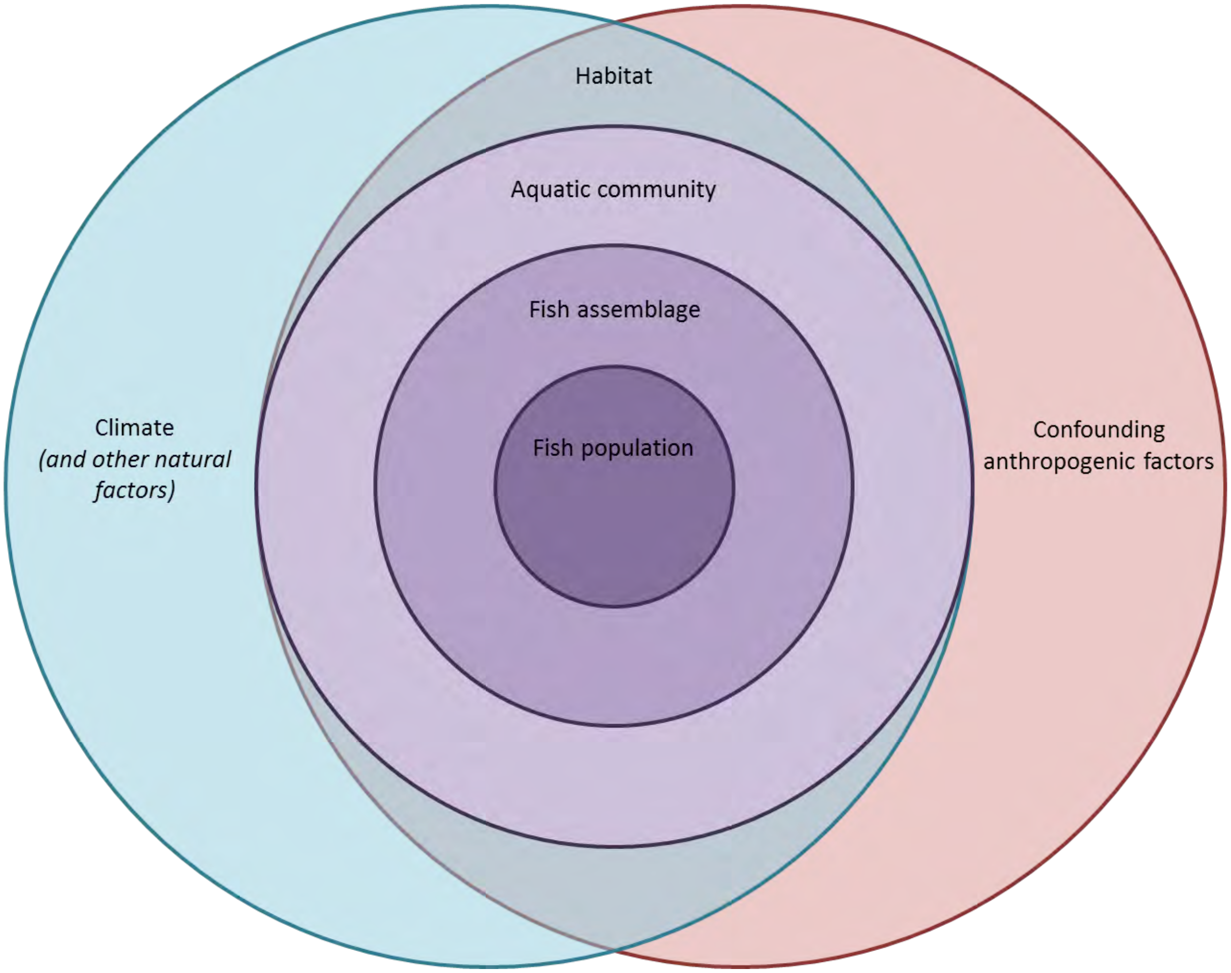


Figure 3. Sockeye salmon *Oncorhynchus nerka* migrations are shifting with climate change, though not always in ways that would be expected. Photo credit: Jonny Armstrong, University of Washington, web.

Figure 4. Documented responses of Pacific salmon to climate change. Green arrows indicate an increase or earlier seasonal response and gray arrows indicate a decrease or later seasonal response, while 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.

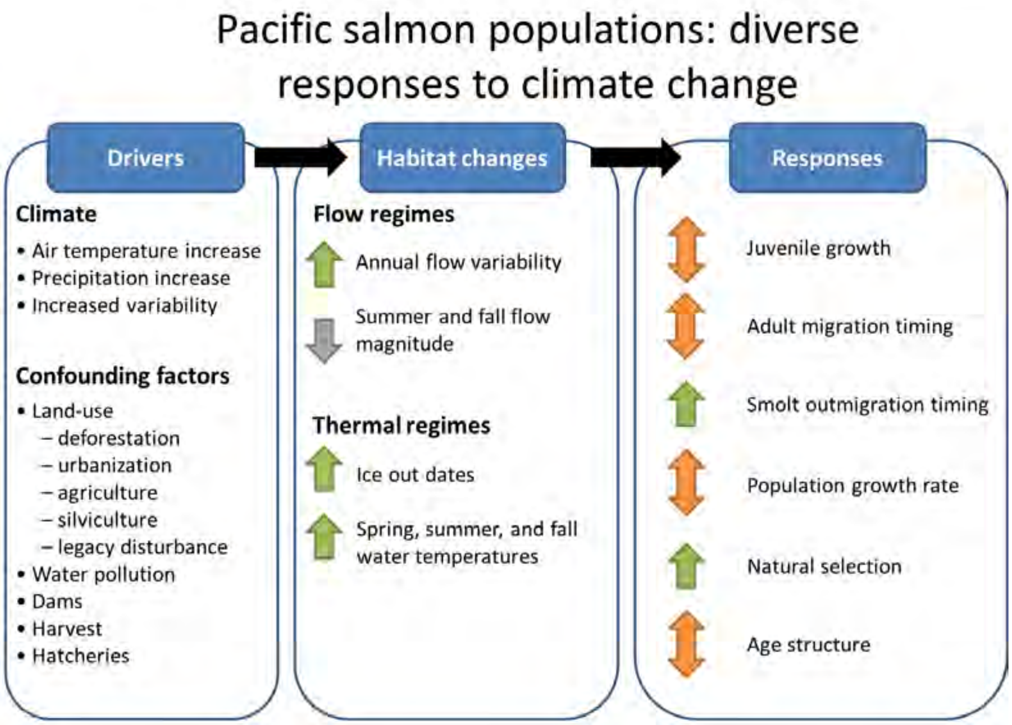


Figure 5. Smallmouth bass *Micropterus dolomieu* are finding Ontario's inland lakes more habitable with climate change. Photo credit: Gretchen Hansen, Wisconsin Department of Natural Resources.

Figure 6. Documented consequences of the northward expansion of nonnative smallmouth bass in Ontario's inland lakes facilitated by climate change. All symbols as shown in Figure 4.

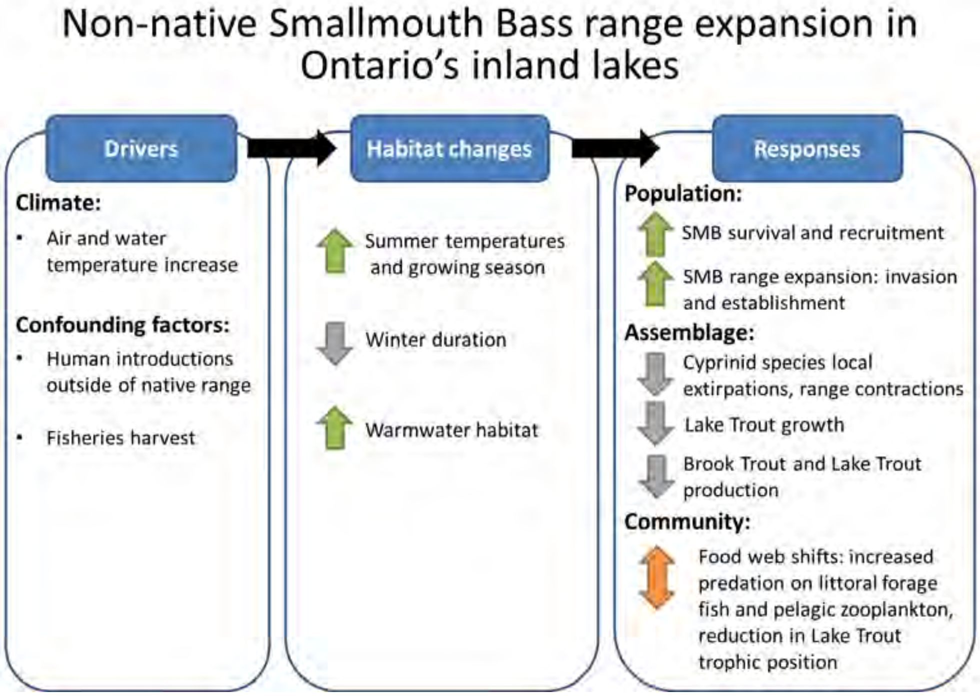


Figure 7. Climate change and flow regulation often leave species in the Rio Grande high and dry. Photo credit: Thomas Turner, University of New Mexico.

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

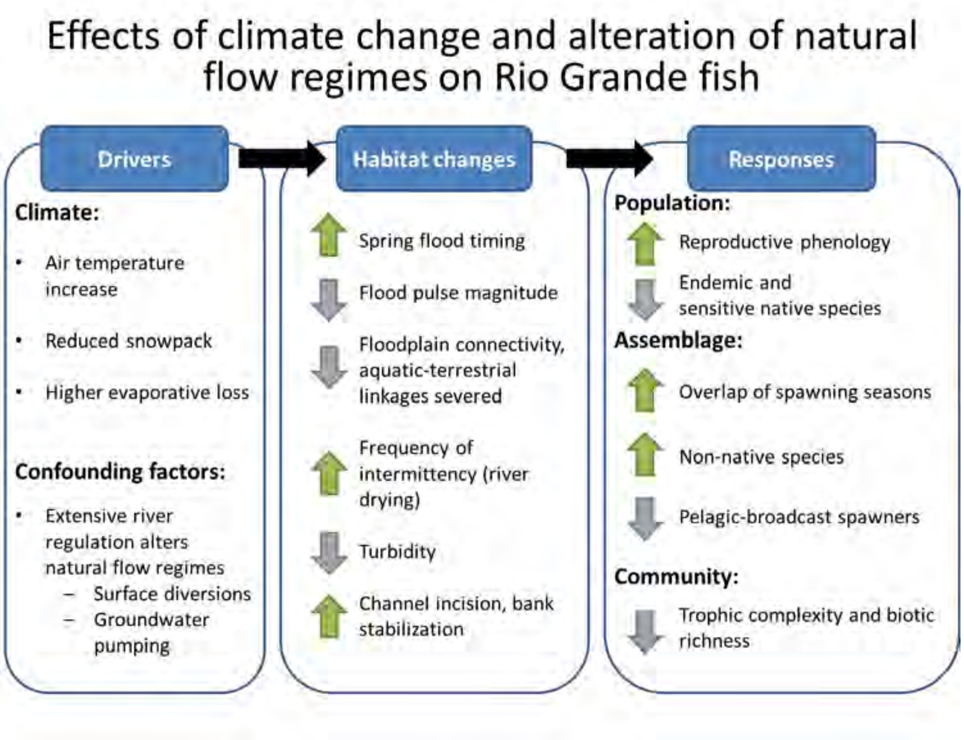
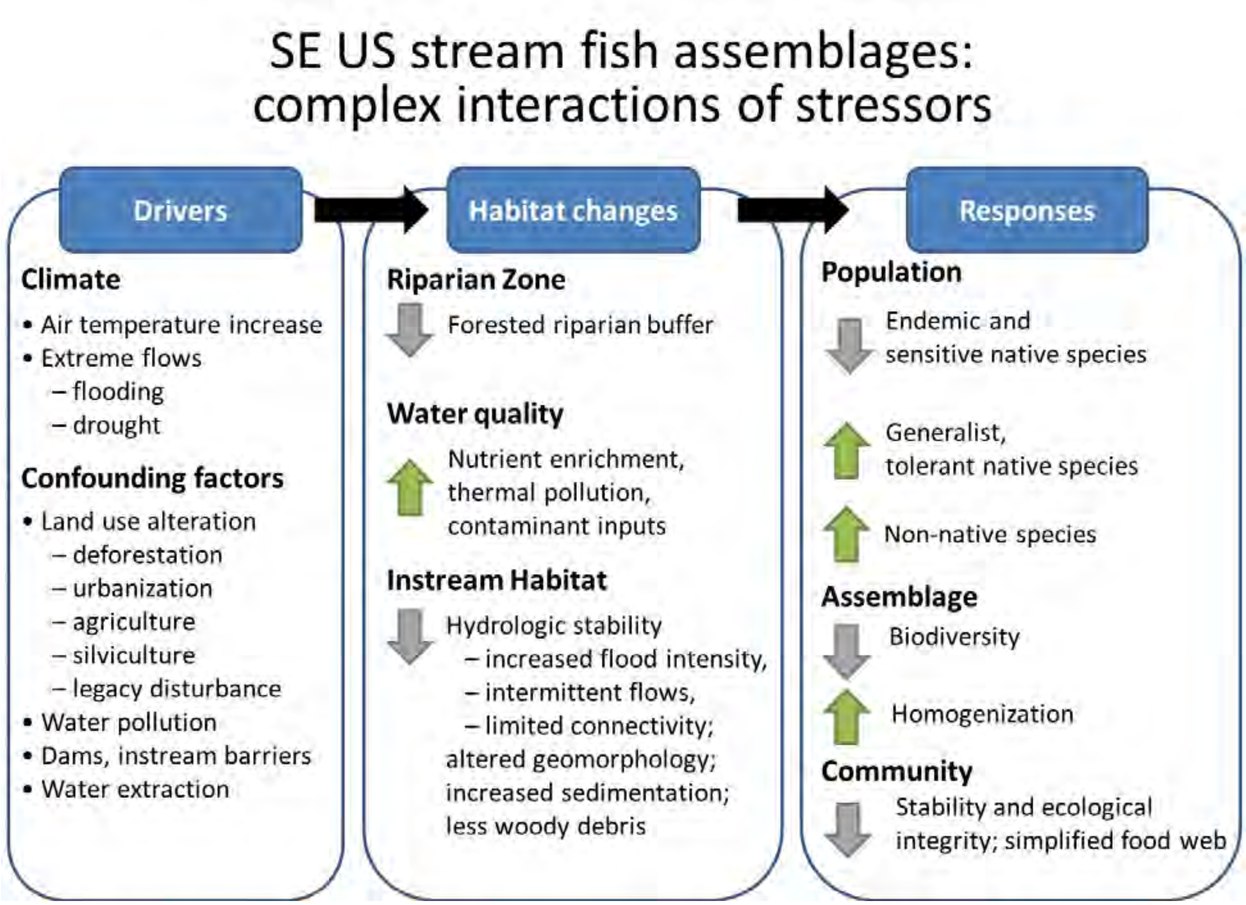


Figure 9. Streams and rivers of the southeastern United States support diverse fish assemblages and valuable recreational fisheries, but the environment and biota are changing with land use alterations, water pollution, dams and in-stream barriers, and water extraction, as well as climate change. Photo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

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.



Identifying Alternate Pathways for Climate Change to Impact Inland Recreational Fishers

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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.

While researchers understand some relationships among marine fish communities, fishers, and climate change, such insights about fishers are rare within inland fisheries (Pinsky and Fogarty 2012). 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. 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 (Intergovernmental Panel on Climate Change (IPCC) 2013). Annual precipitation is expected to increase, especially in far northern areas, with an exception in the southwestern U.S. 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, and 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. 2016; Whitney et al. 2016). 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 while a companion paper provides managerial advice including climate change adaptation strategies for inland fisheries (Paukert et al. 2016).

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—greatly complicate assessments of climate change impacts on fishers (Hunt et al. 2013).

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 and economic welfare, which collectively measure how much people prefer fishing compared to other options (Arlinghaus 2006; Train 1998; Fenichel et al. 2013b). The value of these net benefits can be thought of as ecosystem services such as food provisioning and cultural services and are connected to wealth-based and sustainability metrics (MEA 2005; World Bank 2011; Fenichel et al. 2016). However, measuring well-being also provides a model of human behavioral adaptation to environmental and policy change that is critical for planning for climate change (Abbott and Fenichel 2013).

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

(2009). 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 system includes fishers and managers although our attention is centered on fishers (see Paukert et al. 2016 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, while 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) through environmental conditions that affect fish and, thus, fishers;
2) through environmental conditions that directly affect fishers; and
3) through 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 independently 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; Figure 2) are implicitly believed to dominate fishers' behaviors, especially for commercial marine fisheries (Fenichel et al. 2016). While there is little doubt that fish affect fishers' well-being and behaviors, the strength of these effects are debatable and likely variable (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. (2016) and Whitney et al. (2016) 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). While 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 $8.4 million to a net benefit of $37.3 million (based on fiscal year 2015 dollars) for a doubling of CO_2 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 while 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 $95 to $911 million per year (in fiscal year 2015 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 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 $101 million and $7.1 billion (in fiscal year 2015 dollars) during the period 2009 to 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 (USDOI et al. 1993, 2011; DFO 1990, 2010). We used these data sources to summarize the target species of resident inland fishers by State, province, and territories 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), coolwater (walleye *Sander vitreus*), or 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 to 18°C), coolwater, (19 to 25°C), and warmwater (≥26°C) guilds (Coker et al. 2001). In the early 1990s, fishers in western, mountainous, and northeastern States and all Atlantic Canadian provinces mostly targeted a 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. 2016). 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 highly 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: Nonfish (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) suggests 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. While researchers have developed indices from these conditions to identify potential climate change impacts to tourists, such indices have not been applied to recreational fishers (Scott et al. 2015).

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 (USDOI et al. 2011). However, climate change is likely to reduce participation 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 and are projected, by 2100, to reduce the ice fishing season in northeastern Ontario by between 6% and 15% (Scott et al. 2015; Hunt and Kolman 2012). Even if fishers concentrate their existing ice fishing efforts 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 $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. While consistent with other beliefs, the conclusions are limited by only considering thermal conditions from this one pathway and assuming homogeneous effects from temperature on all fishers (Morris and Walls 2009). 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), 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, 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 (Fusco 2013).

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 meters 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 while more than one-half had conducted dredging activities to combat low water levels at some point since owning a marina (Bergmann-Baker et al. 1995). While 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 also 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; 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 (Kossoy 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 (CAD) 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 efforts 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 (CCSP 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, could become more common (Jaeger 2004). 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, while warm waters could make fishing itself less desirable through impacts on fish).

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. While 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 (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 (Box 1). Additional research is also needed to better understand the complex network of direct and indirect feedbacks between fish and fishers (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. While 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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Figure 1. Recreational fishing activity and revenues in the United States, 196502915. Revenue from license sales in 2015 US$.

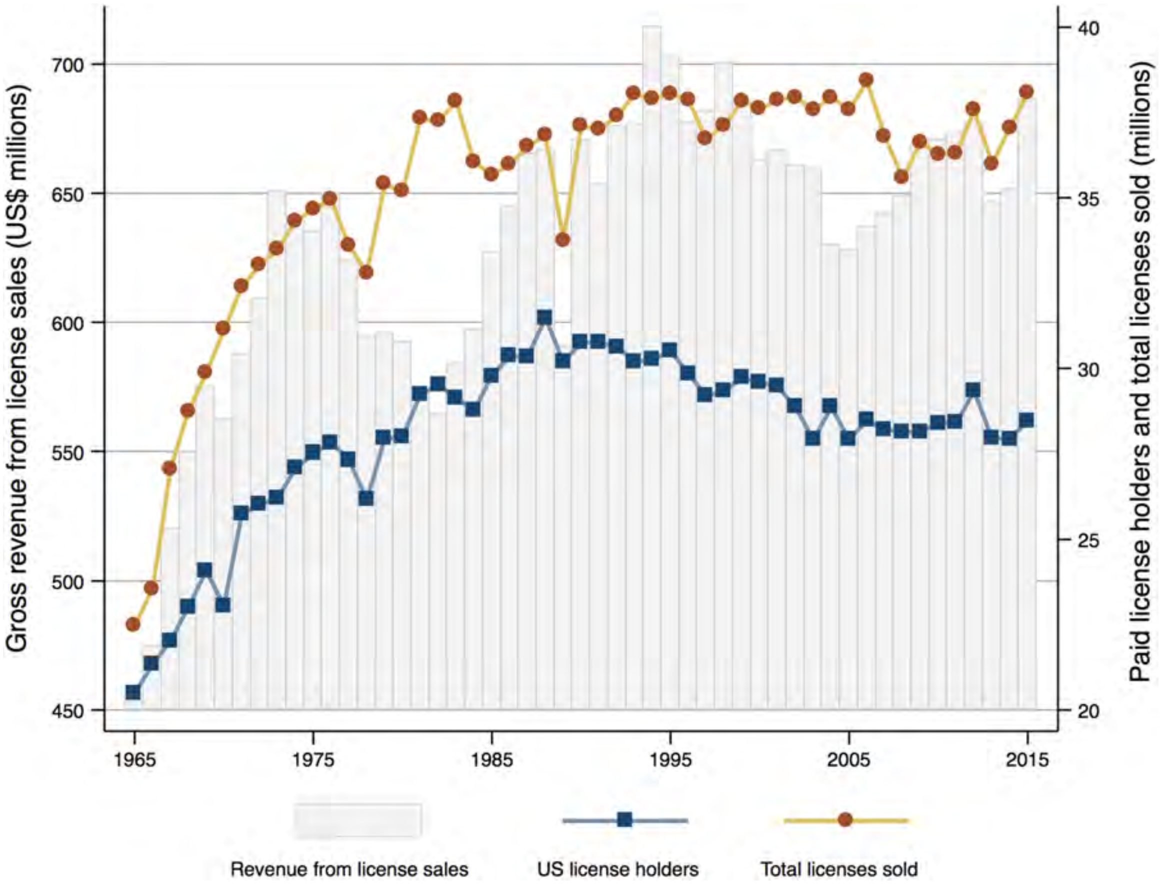


Figure 2. Pathways for climate change impacts on fishers within a social-ecological system of inland recreational fisheries. The numbers correspond to climate pathways that impact fishers.

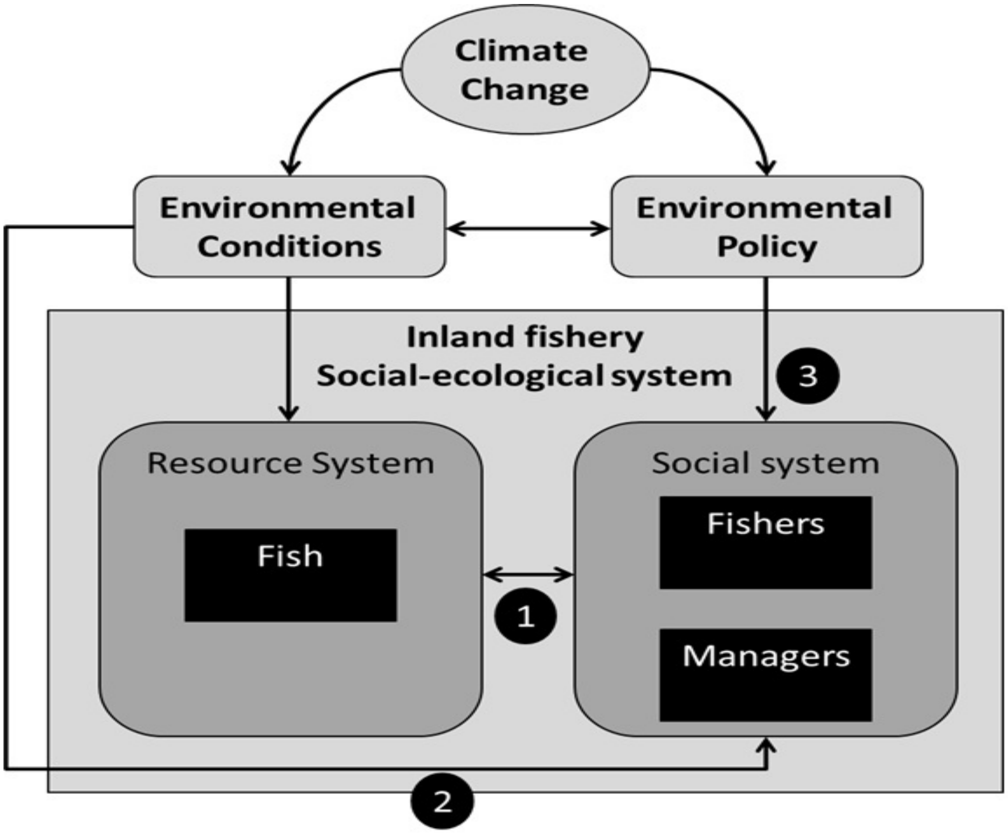


Figure 3. Thermal guild of most targeted species by inland recreational fishers in Canada and the United States. Dark blue, light blue, and pink shading refer to cold (10-18ºC), cool (19-25ºC), and warm (≥26ºC) water species guilds; 2011 North Dakota data were unavailable; for Canadian data, primary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

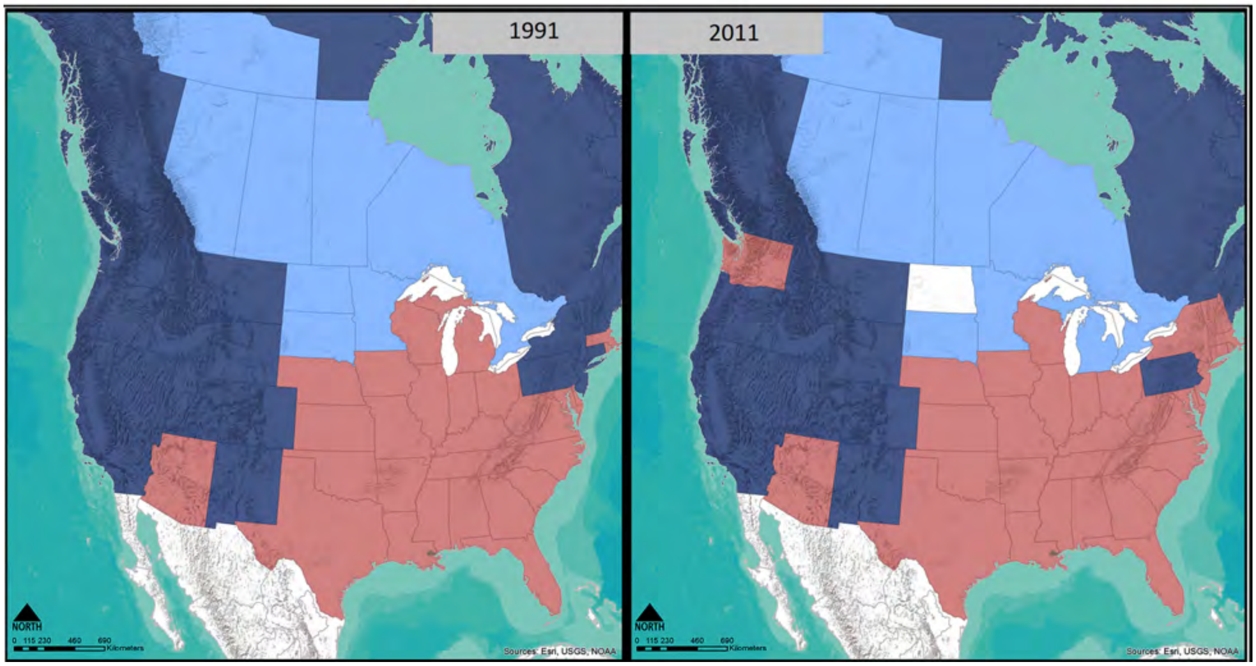
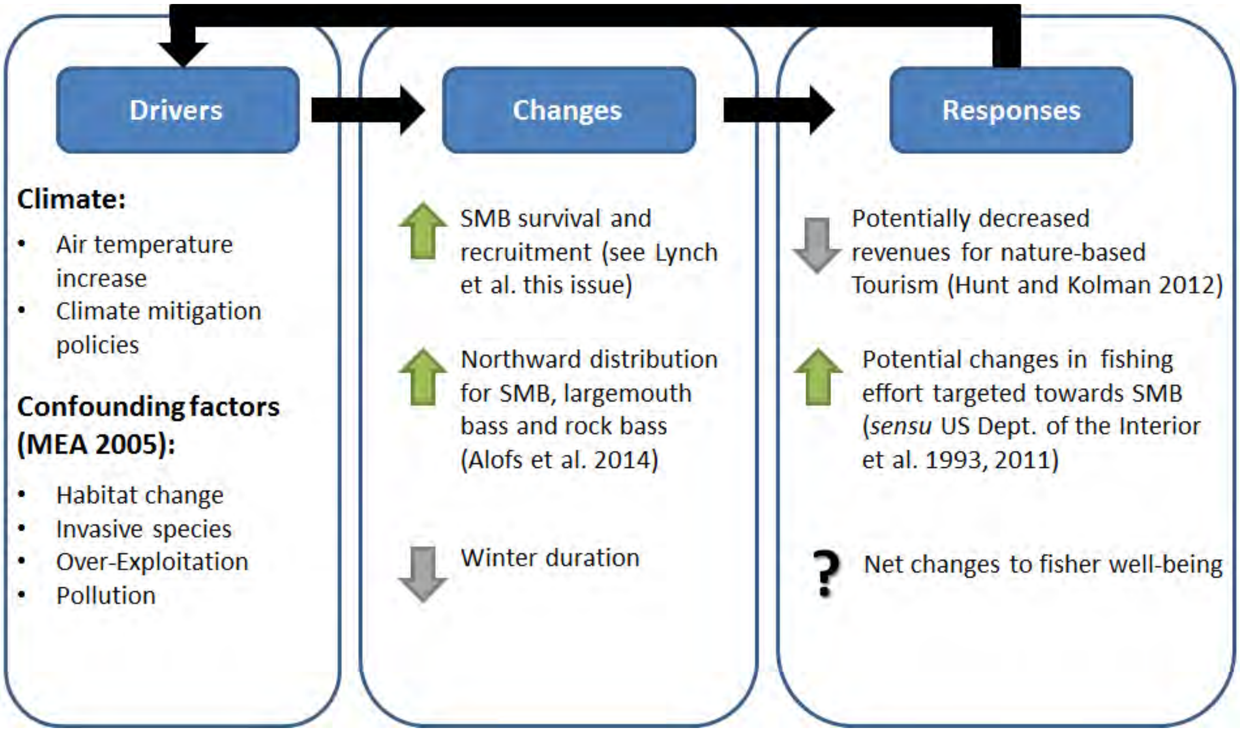


Figure 4. Possible climate change impacts to fishers from northward range expansion of nonnative smallmouth bass (SMB) in Ontario lakes facilitated by climate change (changes to SMB from Lynch et al (2016); green arrows indicated an increased or earlier seasonal response, gray arrows indicated a decrease or later seasonal response, while the question mark represents an unsure response.



Box 1. Potential for climate change to impact fishers from 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. While 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) demonstrate 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 (e.g., 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.

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 floatplane to access lodges and camps on remote lakes. For northern Ontario, the 770 lodges and camps that were accessible only by floatplane 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 along with the presence of smallmouth bass. Combined with projections of changes to walleye abundance from climate change scenarios, a potential modest decrease of revenues (approximately 8.5%) was estimated for establishments situated on lakes with smallmouth bass (Chu and Fischer 2012; Hunt and Kolman 2012). While this decrease was driven by 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 and management agencies respond by removing seasonal restrictions on harvest of nonnative species, climate change can exacerbate this negative impact on nature-based tourism operators in Ontario (Alofs et al. 2014; Paukert et al. 2016). 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 (Figure 4).

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 United States 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 understanding 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 fish. 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.

Adapting Inland Fisheries Management to a Changing Climate

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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 in Peterson et al. 2003; structured decision-making in 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, they 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. 2016). Adaptation can be facilitated by forecasting future climate conditions but such predictions are fraught with uncertainty, which is compounded by uncertainty in how natural resources respond to these changes (Lourenco et al. 2015; 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 importantly it depends on our ability to manage ecosystems in a way that buffers against some of these predicted changes by using a management structure 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), 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 (Leopold 1949). Ecosystems that have already been degraded by anthropogenic activities will make climate adaptation even more challenging. Ensuring that managed systems operate within acceptable boundaries to maintain certain characteristics or a diverse portfolio of fish populations in the face of climate change and other interacting stressors is challenging because interactions may be unforeseen, complex, and dynamic (Scheffer et al. 2015; MEA 2005; Haak and Williams 2012; Staudt et al. 2013). Managers need to apply the best available science on how fish and habitats are responding to climate change—coupled with a strong focus on how resource users may respond to these actions (Lynch et al. 2016; Whitney et al. 2016; Hunt et al. 2016). 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 agencies, nongovernmental organizations [NGOs], and 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 paper 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 the 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 anything from protecting watersheds (e.g., forest conservation easements) to minimize nutrients entering lakes, which reduces dissolved oxygen levels, to ensuring a diversity of population age classes through harvest regulations to buffer against year-class failure due to extreme events (Jacobson et al. 2013; 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, and we call attention to managing for the resilience of both ecological and social systems for fisheries management (Figure 1; Berkes and Folke 1998; Biggs et al. 2012; Walker and Salt 2012).

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). Nonharvest 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; if one approach fails due to incomplete understanding or unanticipated events, other approaches may be more effective (Elmqvist et al. 2003). 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 artedi* example (Box 2), the persistence of cisco and other native cold-water 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% to 400% higher than forested lands). In other cases, trade-offs exist between managing for specified versus general resilience, 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 (Folke et al. 2010; 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 (Box 3; Pierce et al. 2013). 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 as well as 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 following section below) 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; an absence of action is itself a management decision, which can potentially come at a high cost (Berkes and Folke 1998; Walker and Salt 2012). Therefore, management entities should be structured to allow responses to unforeseen events to minimize and contain potential impacts (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 cold-water 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. 2016). Such a shift in focus from extraction of a single species to a 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. 2016). 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 (i) 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 (ii) 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 (Box 5).

Monitoring programs may produce information relevant to decisions, thereby allowing for evidence-based management (Wagner et al. 2013). These programs should not just monitor biophysical changes but also the attitudes and actions of the human users of inland aquatic systems (Hunt et al. 2016). 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 if 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 multiagency 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 (e.g., 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 (Box 2). In Ontario, monitoring has identified shifts in both the spawning dates and distributions of centrarchids and, thus, has led to changes in recreational fishing regulations (Figure 2).

Challenges to Adaptation Strategies

The spatial and temporal scale 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 broadscale conservation objectives necessary for managing resilience in aquatic systems. For example, protecting cold-water 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 (Box 3). While 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 broadscale 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 (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. While cool/cold-water 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. 2016). 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 (Whitney et al. 2016; Lynch et al. 2016). 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. 2016). System monitoring can help increase the quality and quantity of information available to policy makers (e.g., question-driven monitoring) and also help assess if outcomes match expectations (e.g., metric-driven monitoring). Furthermore, we believe 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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Figure 1. Conceptual models of how climate change may overlay upon development of management strategies, including how individual fish, populations and communities, and human behavior influence or respond to management decisions (Whitney et al. 2016; Lynch et al. 2016; Hunt et al. 2016). 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.

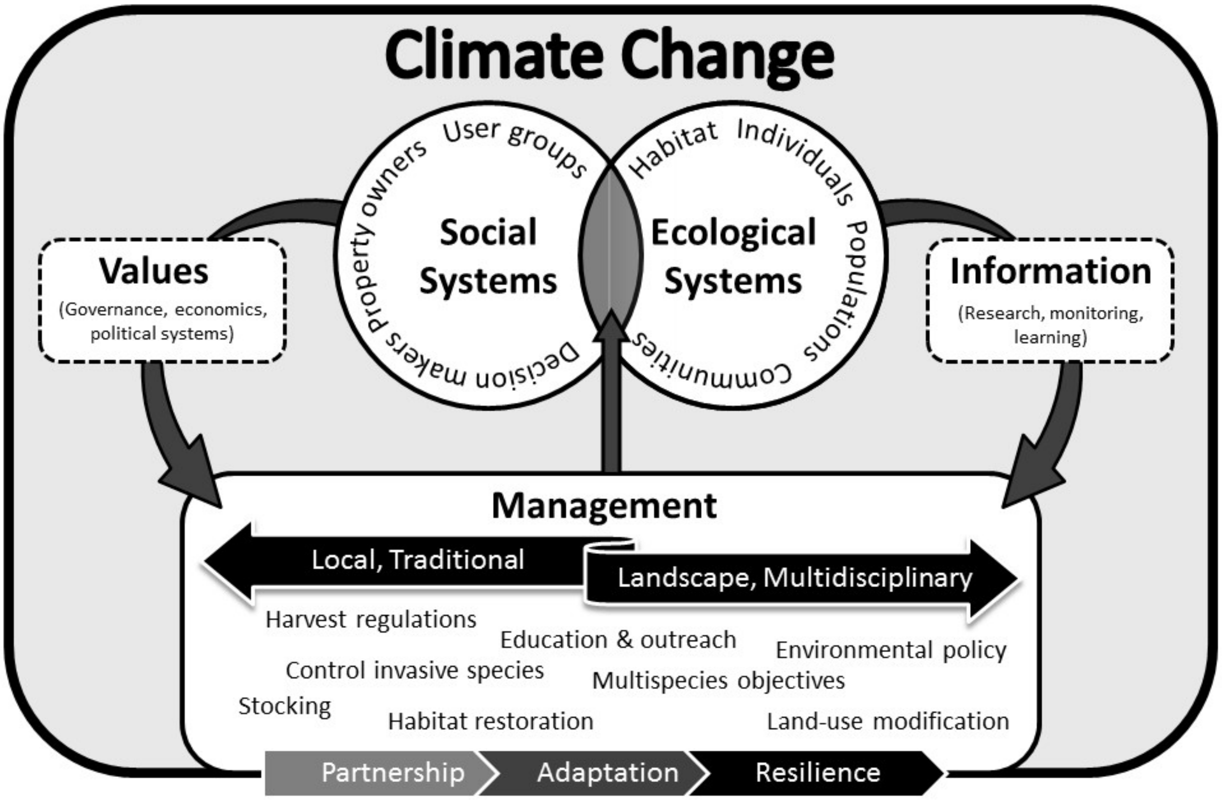
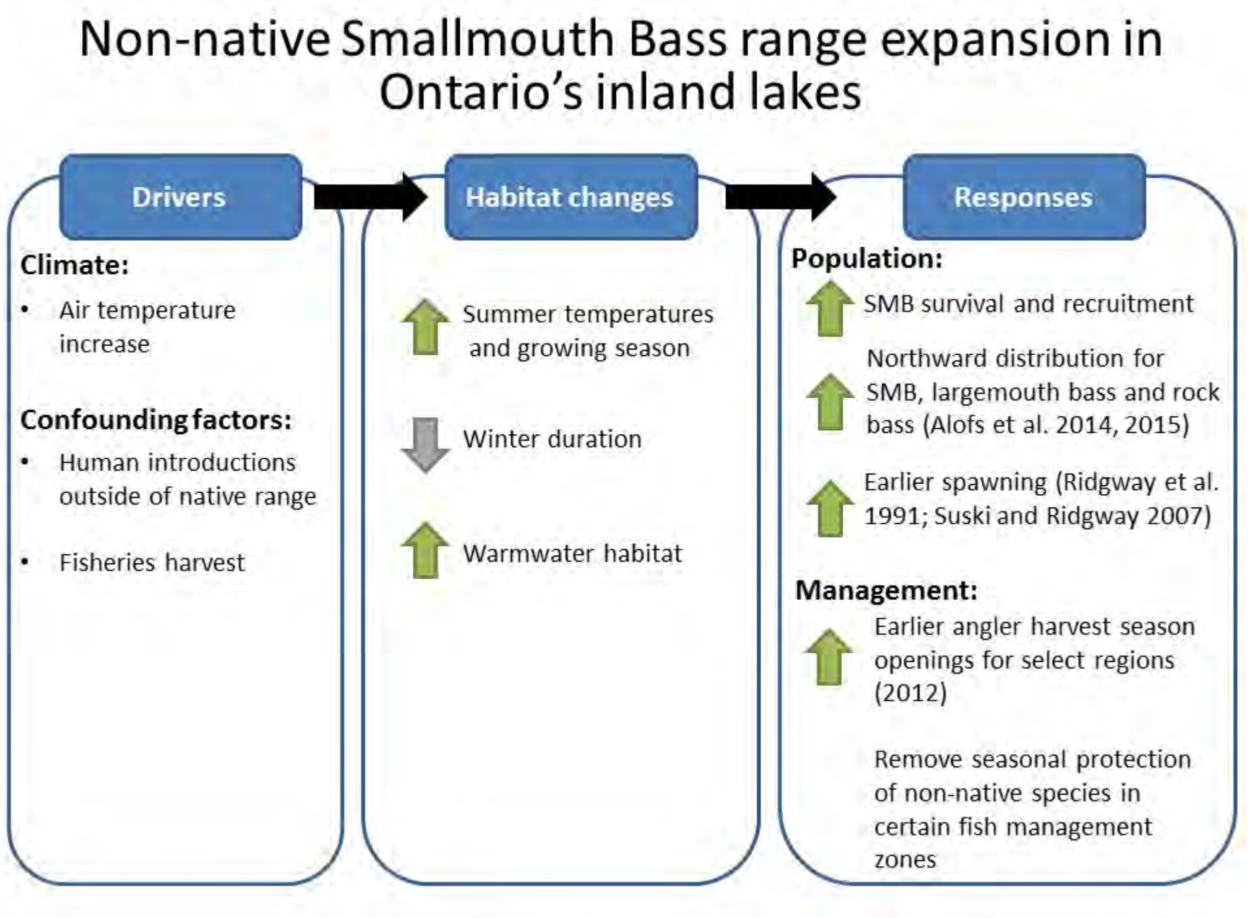


Figure 2. Documented consequences of the northward expansion and changes in spawning phenology of nonnative smallmouth bass (SMB) in Ontario's inland lakes facilitated by climate change and the adjustment in harvest regulations by agencies to adapt to these changes. Green arrows indicate an increase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



Box 1. Terms.

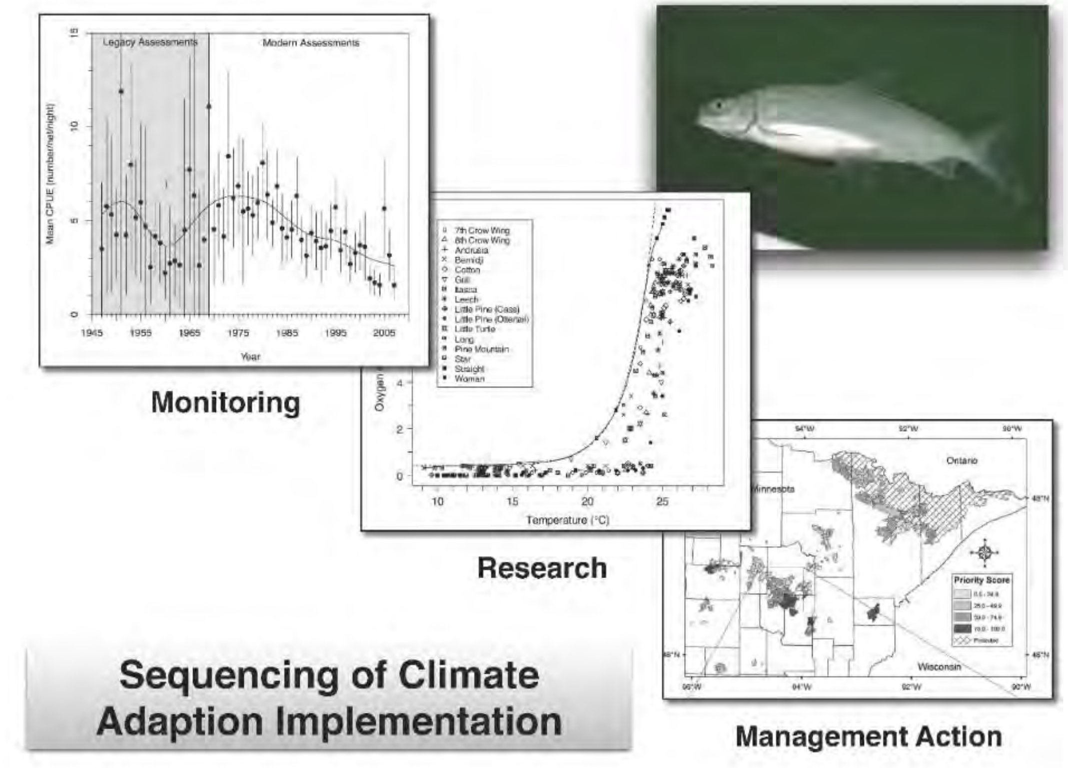
- Ecological resilience: The capacity of a system to absorb or recover from disturbance while retaining its essential structure and function (Holling 1973).
- Resilient management: Management designed to adapt to rapidly changing ecological and social conditions.
- Social resilience: The ability of human 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.

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 artedi*) and identified a declining trend in abundance (Box 2). These trends led to a research program to identify causes of the declines and potential management solutions. Although cisco are a cold-water 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 (Box 2; Jacobson et al. 2008). Other deep, clear lakes in the region maintained excellent cold-water 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 (i.e., sufficiently deep and clear to provide suitable habitat for cold-water 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 cold-water 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 NGOs (Jacobson et al. 2012). Extensive forests are being protected in the watersheds of these resilient systems that offer multiple benefits beyond cold-water 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). Approximately $4 million have 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., Leech Lake Area Watershed Foundation).



Schematic diagram of sequence of steps used to develop and implement a climate adaptation strategy to protect cisco in Minnesota lakes. The sequence included 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*. 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 brout (*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.

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).

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 kilometers of coastline. Of the 4,368 species of plants and animals (invertebrate and vertebrate species) analyzed 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." Given this mission, the FWC is responding to threats related to a changing climate by developing resources, processes, and projects that can (i) anticipate changes to landscapes and seascapes, (ii) identify species and systems that are most vulnerable, and (iii) devise adaptation strategies that increase the adaptive capacity of the resources the FWC is mandated to conserve.

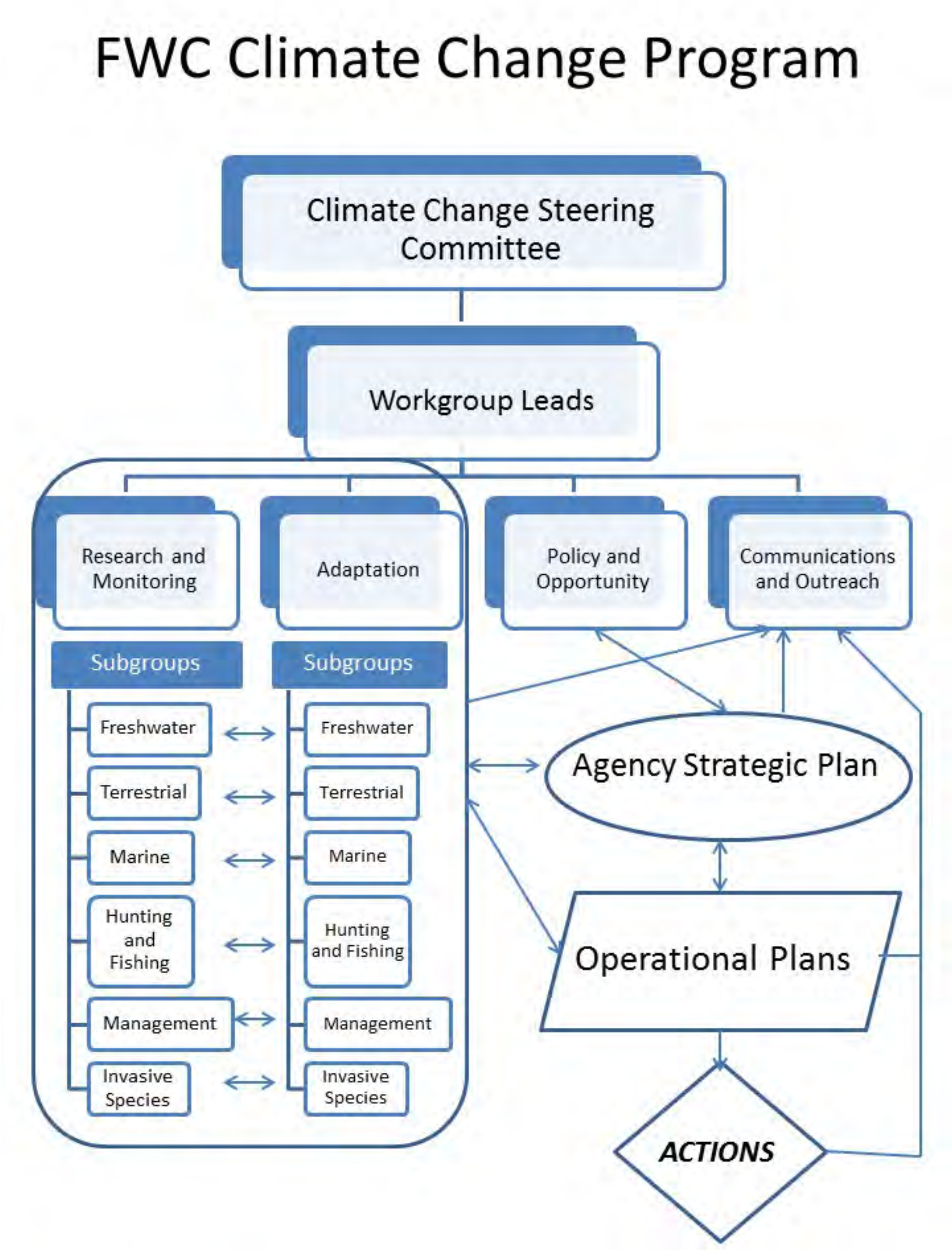
In 2008, the FWC developed a program designed to add internal capacity within the agency, thereby facilitating the development and incorporation of adaptation options within the agency's planning and operations. The structure of that program addresses priorities of a natural resources management agency 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 workgroups are overseen by a steering committee of senior managers and administrators (Box 4).

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 workgroups 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.

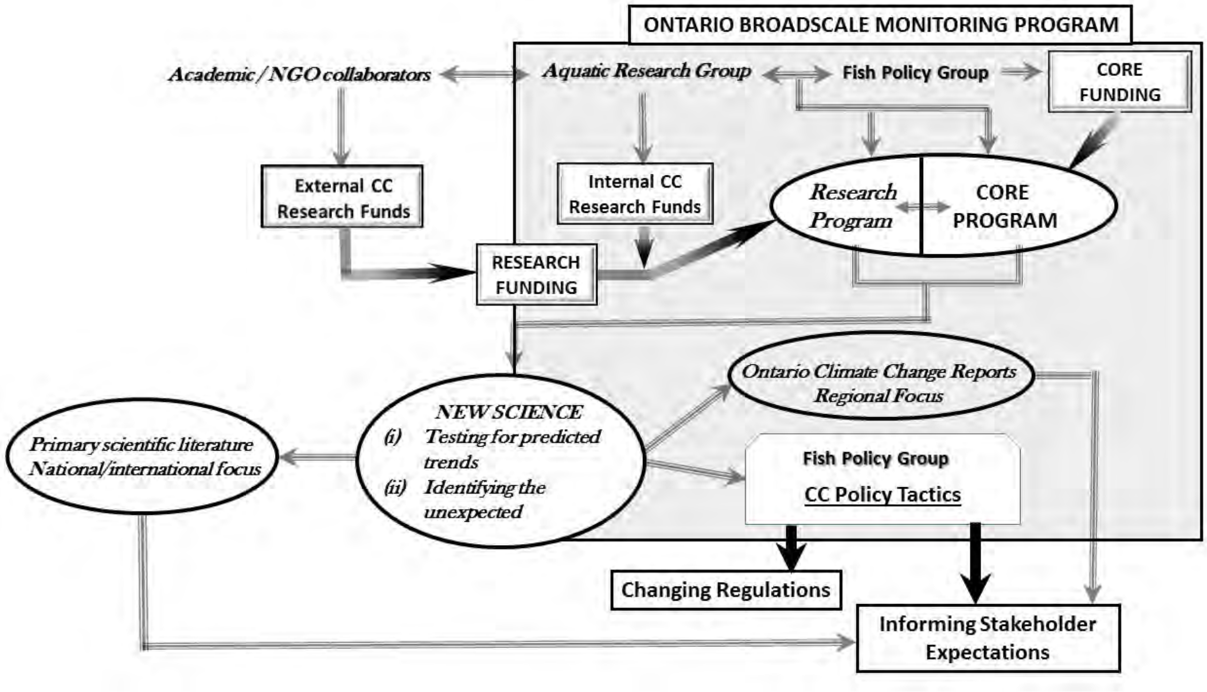
To date, several FWC planning processes have integrated climate impacts, including a dedicated chapter in the 2015 revised version of the State Wildlife Action Plan, Imperiled Species Management plans and associated Integrated Conservation Strategy, and Wildlife Management Area plans as they cycle through 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 FWS 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 to instill a culture of considering a changing climate in the agency’s plans.



The Florida Fish and Wildlife Conservation Commission's (FWC) climate program structure, including the linkages to operational plans and actions. The Adaptation and Research and Monitoring workgroups are comprised 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 (OMNRF) Broadscale Monitoring Program (2008 to 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. Its dual structure of research and core components (Box 4) ensures that (i) the research program develops new knowledge about the likely impacts of climate change on Ontario's freshwater resources and (ii) 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 during 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 hectares in Ontario. These lakes are surveyed within a two-month window using identical survey protocols. Data from the core survey program characterize: (i) lake water chemistry and temperature, (ii) zooplankton abundance, (iii) fish community composition, (iv) relative abundance and life history characteristics of sport fish (e.g., lake trout *Salvelinus namaycush* and walleye *Sander vitreus*), and (v) fishing intensity and other indices of human use. Data from the core program—and related OMNRF 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, 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., Vander Zanden 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.

Special Session Three.
Science-Based Management Strategies for Fish and Wildlife Diseases

Widespread Detection of Highly Pathogenic H5 Influenza Viruses in Wild Birds from the Pacific Flyway of the United States

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Avian influenza viruses (AIV) have been identified in more than 100 wild bird species and *Anseriformes* (ducks, geese, and swans) and *Charadriiformes* (gulls, terns, and waders) are considered to be the primary wild reservoirs for these viruses (Webster et al. 1992). Wild birds infected with AIVs often display no signs of clinical disease, although this can vary widely based on the bird species and virus subtype involved. The classification of AIVs as high pathogenic or low pathogenic is based on the lethality of the virus in chickens (World Organisation for Animal Health 2012). Highly pathogenic avian influenza viruses (HPAIV) often cause substantial mortality in chickens, other domestic birds, and in some cases, wild avian species, although HPAIVs are not thought to persist or circulate widely in wild birds (Lebarbenchon et al. 2010). Low pathogenic H5 and H7 influenza subtypes have the ability to evolve into HPAIVs that are lethal in domestic poultry and so these subtypes are of particular concern because of their potential to cause large-scale avian mortality and economic losses (Webster et al. 1992; Verhagen, Herfst, and Fouchier 2015; Hill et al. 2015; Munster et al. 2005; Chen et al. 2006).

In early 2014, the Republic of Korea reported the occurrence of an H5 clade 2.3.4.4 HPAIV in domestic poultry and wild waterfowl (Hill et al. 2015). Although the H5N8 virus was novel, the H5 gene of this virus was determined to be a descendent of the highly pathogenic H5N1 virus first detected in China in 1996 (Goose/Guangdong/96 lineage) (Lee et al. 2014). Between January and July of 2014 the H5N8 HPAIV infected domestic poultry at 212 farms in the Republic of Korea and was detected in numerous local wild birds (including both live and dead waterfowl) (Verhagen, Herfst, and Fouchier 2015; Lee et al. 2014; Lee et al. 2015; Jeong et al. 2014). Detections in domestic poultry in China, Japan, and Taiwan soon followed (de Vries et al. 2015).

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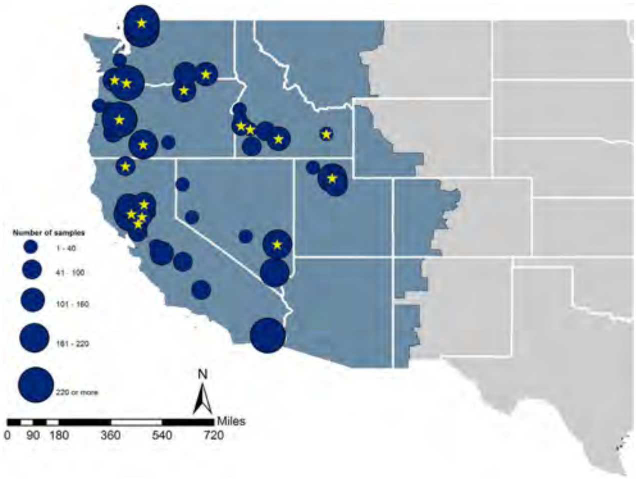
Figure 1. Circle diameter represents number of wild bird samples collected in that county; star denotes that at least one icA H5 clade 2.3.4.4 virus was detected from that set of samples. Background color represents the administrative boundary of the Pacific Flyway. Maps were produced using ArcGIS software by Esri, version 10.3.



In autumn 2014, H5N8 HPAIV was detected in a hunter-harvested Eurasian wigeon (*Anas penelope*) in northern Russia, more than 3,000 kilometers from the Republic of Korea but within the known breeding range of this species (World Organisation for Animal Health 2014c). Soon after this detection, HPAIV H5N8 was reported in either commercial poultry or wild bird species in Germany, the Netherlands, and the United Kingdom (World Organisation for Animal Health 2014a; World Organisation for Animal Health 2014b; Hanna et al. 2015). Genetic differences observed in viruses obtained from the European outbreaks, along with a lack of connection between the affected premises, suggest that, in most cases, there were multiple introductions of the virus rather than a single introduction followed by transmission between farms (FAO 2014).

In late November 2014, a reassortant HPAIV H5N2 subtype—with five gene segments similar to the Republic of Korea H5N8 and three gene segments from North American wild bird AIV lineages—was found in a British Columbia, Canada, poultry operation. Between November and December, the virus spread to 11 poultry farms in British Columbia and in December was found in a wild northern pintail (*Anas acuta*) in the United States. At the same time, and in close proximity to the positive pintail, a H5N8 that was greater than 99% similar to the H5N8 HPAIVs detected in Asia and Europe was found in a captive gyrfalcon (*Falco rusticolos*) that had fed on wild duck meat (Ip et al. 2015). This group of H5 clade 2.3.4.4 viruses—including European, Russian, Korean, Japanese, Chinese, and North American viruses—has been characterized as intercontinental group A (icA) (Lee et al. 2015).

The detection of these viruses on a global scale, combined with multiple detections in both live and dead wild birds, led to increased speculation that wild birds were involved in the movement of these icA H5 viruses between continents (Lee et al. 2015; Jeong et al. 2014; Hanna et al. 2015; Bouwstra et al. 2015; Verhagen et al. 2015). Following the detection of HPAIV in Canada and Washington, a multi-agency study was initiated to examine wild birds throughout the Pacific Flyway. This monitoring effort focused on sample collection from hunter-harvested wild birds in the Pacific Flyway of the United States combined with enhanced wild bird morbidity and mortality surveillance. The goals of this effort were (1) to identify the distribution of the Eurasian H5 clade 2.3.4.4 viruses in wild birds throughout the Pacific Flyway of the United States, which could aid in determining the risk these viruses posed to U.S. poultry producers and wild bird populations, and (2) to better understand what subtypes and what reassortant viruses were present in the U.S.

Results

Wild Bird Sampling

From December 20, 2014, through February 1, 2015, a total of 4,729 oral and cloacal swab were opportunistically collected from hunter-harvested birds. These samples were obtained from six states in the Pacific Flyway (Figure 1, Table 1) with 33% of samples coming from California, 9% from Idaho, 9% from Nevada, 19% from Oregon, 7% from Utah, and 23% from Washington. Sample locations were spread across 45 counties and nearly 100 sample locations. A total of 33 species were sampled, the majority of which were dabbling ducks, known reservoirs for AIVs (Munster et al. 2005; Hoye et al. 2011).

Of the samples tested, 469 (mean prevalence = 9.9%, 95% CL = 9.1–10.8) were influenza A positive (Table 2) as detected by real-time reverse transcriptase polymerase chain reaction (rRT-PCR). These 469 influenza A-positive samples came from 15 different species (Table 2). Of the influenza A-positive samples, 113 (mean prevalence = 2.4%, 95% CL = 2.0–2.9) tested positive for H5 by rRT-PCR; 55 tested positive for H7 (mean prevalence = 1.2%, 95% CL = 0.87–1.5). All H7 positive samples tested for pathogenicity (n = 35) were determined to be low pathogenicity viruses. Of the H5 positive samples, 63 were positive by molecular assays, including a highly specific Eurasian H5 clade 2.3.4.4 assay, for H5 icA viruses (mean prevalence out of 4,729 samples = 1.3%, 95% CL = 0.98–1.7) (D. Suarez, unpublished). No virus was isolated from 22 of the 63 positive samples and so the neuraminidase (NA) subtype was not determined. Isolates (n = 41) from the remaining positives were identified as H5N2 (n = 19), H5N8 (n = 19), H5N1 (n = 3). There were also two possible mixed infections with an H5 clade 2.3.4.4 positive and a LPAIV; however, the subtype was not definitively determined prior to publication. Species that were HPAIV positive were American green-winged teal (*Anas crecca*, n = 4), American wigeon (*Anas americana*, n = 31), Canada goose (*Branta canadensis*, n = 1), gadwall (*Anas strepera*, n = 1), mallard (*Anas platyrhynchos*, n = 15), northern pintail (n = 5), northern shoveler (*Anas clypeata*, n = 3), and wood duck (*Aix sponsa*, n = 3) (American Ornithologists' Union 1998).

Table 1. Date of first H5 clade 2.3.4.4 sample collection from hunter-harvested wild birds, by state, along with number of HPAIV positives collected between December 2014 and February 2015.

State	Date of First HPAIV	Number of Wild	Total HPAIV
Oregon	December 20, 2014	888	17
Idaho	December 22, 2014	413	6
Washington	December 23, 2014	1101	8
California	December 28, 2014	1563	30
Utah	January 2, 2015	350	1
Nevada	January 23, 2015	414	1
Total		4729	63

Table 2. Hunter-harvested wild bird surveillance rRT-PCR and highly pathogenic avian influenza virus (HPAIV) results for avian influenza matrix gene and hemagglutinin subtypes H5 and H7, Pacific Flyway, December 20, 2014 through February 1, 2015. Results shown as total positive and percent positive.

Species	n	rRT-PCR result			HPAIV icA
		Matrix Pos	H5 Pos	H7 Pos	
Mallard, Anas platyrhynchos	1410	163 (11.5%)	37 (2.6%)	9 (0.6%)	15
Northern shoveler, Anas clypeata	555	82 (14.7%)	11 (1.9%)	18 (3.2%)	3
Green-winged teal, Anas crecca	724	75 (10.3%)	6 (0.8%)	22 (3.0%)	4
American wigeon, Anas americana	777	66 (8.4%)	39 (5.0%)	1 (0.1%)	31
Northern pintail, Anas acuta	460	43 (9.3%)	7 (1.5%)	2 (0.4%)	5
Cinnamon teal, Anas cyanoptera	67	12 (17.9%)	0	1 (1.4%)	0
Wood duck, Aix sponsa	27	8 (29.6%)	6 (22.2%)	0	3
Gadwall, Anas strepera	185	5 (2.7%)	3 (1.6%)	1 (0.5%)	1
Canvasback, Aythya valisineria	68	4 (5.8%)	0	0	0
Ruddy duck, Oxyura jamaicensis	46	4 (8.6%)	2 (4.3%)	0	0
Bufflehead, Bucephala albeola	35	2 (5.7%)	0	0	0
Canada goose, Branta canadensis	148	2 (1.3%)	2 (1.3%)	0	1
Cackling goose, Branta hutchinsii	33	1 (3.03%)	0	0	0
Lesser scaup, Aythya affinis	14	1 (7.1%)	0	0	0
Ring-necked duck, Aythya collaris	65	1 (1.5%)	0	0	0
Common goldeneye, Bucephala clangula	39	0	0	1 (2.5%)	0
All other species sampled	76	0	0	0	0
Total	4729	469	113	55	63

There were no HPAIVs detected in the U.S. during a previous wild bird surveillance effort that occurred from 2006 to 2011, so a direct comparison between wild bird HPAIV prevalence before and after the arrival of the Eurasian H5 clade 2.3.4.4 cannot be made (Dusek et al. 2009; Bevins et al. 2014). We can, however, compare the H5 virus prevalence between the two time periods. The H5 prevalence in mallards and wigeons (two of the most commonly sampled dabbling ducks in both surveillance efforts) sampled between December 2014 and February 2015 in the Pacific Flyway reveal that prevalence of H5 viruses was significantly higher ($F = 44.30$, $p < 0.0001$) than in 2006 to 2011. The odds of these waterfowl being infected with an H5 are 11.9 times higher (95% CL 5.7–24.7) than they were from 2006 to 2011, with 3.5% (78/2186, 95% CL = 2.8–4.4) of mallards and wigeons currently testing positive for H5 versus 0.3% (8/2586, 95% CL = 0.1–0.6) during the previous surveillance effort. In contrast, prevalence of H7 viruses did not significantly differ ($F = 3.16$, $p = 0.08$) between mallards and wigeons sampled and tested for H7 from 2006 to 2011 and mallard and wigeons sampled in this current dataset (0.17%, 5/2890, 95% CL = 0.02–0.3 versus 0.46%, 10/2186, 95% CL = 0.1–0.7).

Morbidity/Mortality Sampling

From December 1, 2014, to February 28, 2015, a total of 150 (December = 83, January = 50, February = 17) sick or dead birds from the state of Washington were tested for HPAIV at the U.S. Geological Survey's National Wildlife Health Center. Four morbidity and mortality events involved multiple birds and accounted for 61 sick or dead birds, including 41 carcasses obtained from the index location (Wiser Lake, Whatcom County, Washington) and three other separate events with five, seven, and eight sick or dead birds examined. All remaining submissions were individual sick or dead bird investigations. Of the 150 sick or dead birds, 41 only had swab samples submitted. Full carcasses were received for the remaining 109 submissions (Table 3). Six out of 97 waterfowl samples (6.2%) were icA H5 positive (Canada goose, northern pintail, mallard, American wigeon) and four out of 35 raptor samples were icA positive (11.4%). Positive raptor species included peregrine falcon (*Falco peregrinus*), Cooper's hawk (*Accipiter cooperii*), and red-tailed hawk (*Buteo jamaicensis*). No HPAIV positive samples were identified from other water birds and no HPAIV positive samples were identified when only swab samples were submitted. Five of the icA H5 detections were made in waterfowl found dead at the index location from the ongoing morbidity and mortality event (Ip et al. 2015). In addition, four individual raptors found dead in four different Washington counties (Whatcom, Skagit, Grays Harbor, and Benton), and a single Canada goose found sick in Jefferson County, Washington, were icA H5 positive. None of the individual raptors or the single Canada goose that tested icA H5 positive were associated with morbidity or mortality events. H5N2 was detected in seven individual birds and H5N8 was detected in three birds (Table 4).

Phylogenetic analyses of the H5 clade 2.3.4.4 viruses detected as part of both the hunter-harvested surveillance effort and the morbidity and mortality surveillance reveal a high degree of relatedness (Figures 2 and 3). The H5N2, H5N8, and H5N1 viruses were co-circulating in wild birds sampled in the Pacific Flyway during the surveillance effort.

Discussion

The goals of this monitoring effort were to determine if Eurasian clade 2.3.4.4 viruses, newly introduced to North America, were present in U.S. Pacific Flyway wild bird populations and, if so, to better understand the extent to which they were circulating. The study was motivated by both the rapid spread of these H5 viruses in Asia and Europe and by the detection of these viruses in Canada (Lee et al. 2014; Lee et al. 2015; Pasick et al. 2015). Eurasian clade 2.3.4.4 viruses were detected in 1.3% (63 of 4,729) of hunter-harvested waterfowl sampled in the Pacific Flyway. Three different neuraminidase subtypes were detected, all of which were part of the H5 clade 2.3.4.4 lineage, including the wholly Eurasian lineage H5N8, as well as Eurasian-North American reassortants H5N2 and H5N1, all of which are greater than 99% similar across Eurasian gene segments to other icA H5 HPAIVs (Ip et al. 2015; Torchetti et al. 2015). The reassortant H5N2 (19/41, 46.3%), and the H5N8 (19/41, 46.3%) were equally prevalent in hunter-harvested birds. Three hunter-harvested samples also tested positive for the reassortant H5N1 (3/41, 7.3%). H5N2 ($n = 7$) and H5N8 ($n = 3$) were detected in samples from sick or dead birds.

The isolation of multiple reassortant viruses in wild birds is not surprising given the well-known occurrence of genetic recombination in influenza viruses, which occurs when more than one virus infects the same host cell. The segmented genome of influenza viruses allows segments from different viruses to be traded and, in this case, introduction of the Eurasian H5 viruses into the North American influenza gene pool appears to have generated multiple novel subtypes (Eurasian-American lineage H5N2 and H5N1) (Ip et al. 2015; Torchetti et al. 2015). Taiwan also identified novel reassortants after H5 clade 2.3.4.4 viruses were initially detected (Li 2015). Although it is not surprising to see reassortant viruses, their emergence in what is believed to be a relatively short time frame is intriguing. De Vries et al. (2015) noted that this emergence of new H5 combinations is unprecedented in H5N1 evolutionary history. In North America and in other places such as China and Taiwan, rapid reassortment of clade 2.3.4.4 viruses may be facilitated through encounters with a large and diverse population of LPAIVs in wild birds, although this pattern was not necessarily seen in Europe where the association of this novel virus with wild bird populations does not appear to have spawned similar reassortant events in the same relatively short time frame (Ip et al. 2015).

Interestingly, more than half of the H5 detections (63/113 samples, 60%) and 13% (63 of 469) of all influenza A detections from hunter-harvest surveillance samples were Eurasian H5 HPAIVs, suggesting that the H5 clade 2.3.4.4 viruses were a substantial part of the influenza A gene pool in U.S. wild bird populations during the winter of 2014 to 2015. Wild bird influenza surveillance efforts carried out from 2006 to 2011 found a significantly lower prevalence of H5 viruses in winter samples in the two most commonly sampled species (mallards and wigeon) from the Pacific Flyway when compared to this current effort (Dusek et al. 2009; Bevins et al. 2014). Samples collected from American wigeons accounted for almost half of all icA H5 detections (31 of 63) in wild waterfowl. American wigeons (n = 777) were the species most frequently infected with icA H5 despite mallards being the most frequently sampled species (1,410 mallard samples collected, 15 HPAIV detections). The high infection prevalence of icA H5 viruses detected during this wild bird sampling effort likely at least partially reflects the introduction of a new virus into a naïve population of birds that had no previous exposure to clade 2.3.4.4 viruses; however, it is unknown if these viruses will continue to circulate at high levels over time. In general, it is thought that HPAIV viruses are not maintained in wild bird populations. This is primarily based on HPAIV having rarely been isolated from wild birds prior to this emergence, even though prior research has found H5N1 outbreaks in domestic poultry to closely associate with known wild bird migration routes (Tian et al. 2015). Although this effort documented the widespread occurrence of HPAIV in wild bird populations, the possibility of long-term persistence is unknown. Our understanding of HPAIV dynamics in wild birds is still limited despite a substantial increase in research on influenza over the last decade and this highlights the need for continued consistent monitoring of HPAIV dynamics in wild birds over time.

Detection of icA H5 HPAIV in apparently healthy wild birds, combined with laboratory studies in avian species that demonstrate low morbidity and mortality, reinforces the likely role of wild waterfowl in the emergence and geographic spread of these viruses (Jeong et al. 2014; Verhagen, Herfst, and Fouchier 2015; Hill et al. 2015; Verhagen et al. 2015). Wild waterfowl infected with icA H5 viruses are likely capable of moving these viruses short distances, and possibly even long distances, along migration routes; however, the length of time that an infected bird sheds an influenza virus, which is typically up to 10 to 14 days in experimental infection with other goose/Guangdong/96 lineage isolates in ducks, also plays a role in the likelihood of virus introduction via long-distance migration (Pantin-Jackwood et al. 2007; Brown 2006).

Despite the widespread detection of clade 2.3.4.4 H5 viruses in wild birds sampled during this effort, only two commercial poultry facilities were infected in the Pacific Flyway of the U.S. during 2015, both with icA H5N8. Eight backyard poultry flocks were also infected in the Pacific Flyway (one with icA H5N8, the rest with icAH5N2). This is in contrast to the icA H5 outbreaks seen several months later in commercial poultry facilities in the Central and Mississippi flyways. By June 2015, there were 213 icA H5N2 outbreaks in commercial and backyard poultry within the Central and Mississippi flyways (USDA "Epidemiological and Other Analyses" 2015; USDA "Avian Influenza Disease" 2015). The mechanisms responsible for the different scale of commercial poultry outbreaks in the Pacific Flyway compared to the other flyways is largely unknown, although commercial outbreaks were shown to be a combination of both independent/point source introductions along with common source or lateral spread (USDA "Epidemiological and Other Analyses" 2015). The latter would be independent of wild bird influenza dynamics. Furthermore, the wholly Eurasian H5N8 virus accounted for almost 40% of HPAIVs in wild birds, but only four of the 223 documented domestic poultry outbreaks in the U.S. between December 2014 and June 2015 were caused by H5N8 (USDA "Epidemiological and Other Analyses" 2015). Laboratory studies suggest that these viruses were well adapted to the waterfowl host, with experimentally infected mallards remaining asymptomatic while easily transmitting the virus to conspecifics. This is in contrast to the less efficient transmission to contacts seen in infected chickens (Pantin-Jackwood et al. 2015). These differences may play a role in the different patterns seen in wild birds versus domestic poultry. Although the wild bird data reported here were collected between December 2014 and February 2015 in the Pacific Flyway of the U.S., most of the domestic poultry outbreaks in the U.S. occurred February to May 2015 in the Midwestern U.S., representing differences in both time and space and making direct comparisons difficult. Between March and June 2015, U.S. poultry producers lost nearly 50 million birds to these outbreaks (USDA "Avian Influenza Disease" 2015).

Table 3. Total number of free ranging wild birds found dead in Washington State with specimens submitted and tested for highly pathogenic avian influenza virus between December 1, 2014, and February 28, 2015 (Ip et al.).

Species	HPAIV Positive	Carcass	Swab Only	Total
Canada goose, *Branta canadensis*	1	1	0	1
Cackling goose, *Branta hutchinsii*		1	0	1
Mallard, *Anas platyrhynchos*	2	33	0	33
Northern shoveler, *Anas clypeata*		1	0	1
American wigeon, *Anas americana*	2	10	1	11
Northern pintail, *Anas acuta*	1*	2	0	2
Bufflehead, *Bucephala albeola*		1	0	1
Barrow's goldeneye, *Bucephala islandica*		1	0	1
Common goldeneye, *Bucephala clangula*		6	0	6
Trumpeter swan, *Cygnus buccinator*		3	36	39
Tundra swan, *Cygnus columbianus*		1	0	1
Double-crested cormorant, *Phalacrocorax auritus*		1	0	1
Bald eagle, *Haliaeetus leucocephalus*		9	0	9
Sharp-shinned hawk, *Accipiter striatus*		4	0	4
Cooper's hawk, *Accipiter cooperii*	1	8	0	8
Red-tailed hawk, *Buteo jamaicensis*	2	5	0	5
Peregrine falcon, *Falco peregrinus*	1	1	0	1
Marbled murrelet, *Brachyramphus marmoratus*		1	0	1
Cassin's auklet, *Ptychoramphus aleuticus*		7	0	7

Mew gull, *Larus canis*		0	2	2
Glaucous-winged gull, *Larus glaucescens*		0	2	2
Great Horned owl, *Bubo virginianus*		2	0	2
Barred owl, *Strix varia*		3	0	3
Long-eared owl, *Asio otus*		3	0	3
American crow, *Corvus brachyrhynchos*		4	0	4
Crow, Unidentified, *Corvus species*		1	0	1
Total	10	109	41	150

This effort focused on waterfowl because they are considered a primary influenza A virus reservoir, and while these data suggest that some waterfowl species are not negatively impacted by infections with Eurasian H5 clade viruses, it appears that other wild species may suffer severe morbidity and mortality. The first detection of icA reassortant H5N2 in wild birds in North America was obtained during a waterfowl mortality event at Wiser Lake, Whatcom County, Washington, although the cause of the mortality event was attributed to aspergillosis with the icA H5 infection reported as a secondary finding (Ip et al. 2015). Concurrent to this waterfowl mortality event, a captive-reared gyrfalcon died from icA H5N8 after being fed wild wigeon from the same area (Ip et al. 2015). From December through February, morbidity and mortality testing of wild birds in Washington increased; 150 additional waterfowl, other water birds, and raptors were tested as part of this effort. From these, icA H5 was detected in six waterfowl (five were ducks from Wiser Lake, the index location, and included the northern pintail reported by Ip et al. (2015) and one from a Canada goose in a second county). Four raptors from four different counties were also positive and represented 11% of all raptors (n = 35) tested. Lesions in the lung and heart consistent with highly pathogenic avian influenza (HPAI) infection were observed in all four raptors. The cause of death in the five ducks found dead at the index location was determined to be aspergillosis with a HPAI nonlethal coinfection. The cause of death in the single Canada goose is suspected to be due to HPAI, but the role of HPAI infection was difficult to interpret due to freeze artifact and a cobacterial infection in the lungs. Other sick and dead Canada geese and raptors testing positive for the icA H5 viruses have been reported in other states, suggesting they may be good targets for morbidity and mortality surveillance to identify presence of icA H5 viruses.

Table 4. Avian species detected with highly pathogenic avian influenza virus (HPAIV) by avian morbidity and mortality surveillance in Washington, December 1, 2014, through February 28, 2015 (Ip et al.).

Species	County	Date Found Dead	HPAIV Detected
Mallard, Anas platyrhynchos	Whatcom	12/8/2014	HPAIV H5N2
Northern pintail, Anas acuta*	Whatcom	12/8/2014	HPAIV H5N2
American wigeon, Anas americana	Whatcom	12/16/2014	HPAIV H5N8
American wigeon, Anas americana	Whatcom	12/16/2014	HPAIV H5N8
Mallard, Anas platyrhynchos	Whatcom	12/23/2014	HPAIV H5N2
Peregrine falcon, Falco peregrinus	Grays Harbor	12/29/2014	HPAIV H5N8
Cooper's hawk, Accipiter cooperii	Whatcom	12/29/2014	HPAIV H5N2
Canada goose, Branta canadensis	Jefferson	12/30/2014	HPAIV H5N2
Red-tailed hawk, Buteo jamaicensis	Benton	12/31/2014	HPAIV H5N2
Red-tailed hawk, Buteo jamaicensis	Skagit	1/9/2015	HPAIV H5N2

This surveillance effort that began immediately upon reports of HPAIV detection in British Columbia allowed early detection of clade 2.3.4.4 viruses in the U.S. wild bird populations. This rapid response to collect and test wild bird samples offered an unprecedented opportunity to better understand the dynamics of a novel virus introduced into a naïve wild bird population with its own endemic and diverse influenza A gene pool. Passive surveillance of apparently healthy hunter-harvested wild birds was used in conjunction with morbidity and mortality surveillance and both methodologies provided valuable data. Continued surveillance and characterization of influenza A in wild birds is suggested in order to monitor virus evolution, to understand risk pathways for introduction, and to assess the emergence of mutations that may be relevant for veterinary and public health (Hanna et al. 2015).

Methods

Sample Areas

Wild bird sample collection focused on the Pacific Flyway of the U.S. Waterfowl and water bird migration in North America generally consists of north-south seasonal movements between breeding grounds and wintering areas, and while the flyway boundaries are not biologically fixed or sharply defined, the flyways represent the prominent movement pathways of migratory waterfowl (Dusek et al. 2009). Band-recovery data on waterfowl species of interest show that migratory waterfowl move throughout this flyway. Ten priority sampling areas were chosen in the Pacific Flyway. These areas were chosen based on previous research that identified geographic clusters of low pathogenic AIV in wild birds and known high concentration wintering areas for waterfowl in the Pacific Flyway (Bevins et al. 2014; Farnsworth et al. 2012). Sample areas roughly corresponded to a broad watershed scale. Sample sizes were based on 95% confidence in detecting one positive bird out of a population of 10,000 or more birds

(Sargeant 2015). Expected prevalence was 1% based on previously published values of LPAIV, and sensitivity and specificity of the diagnostic assays was 86.3% and 100% respectively (Bevins et al. 2014; Janice Pedersen, personal communication).

Sample Collection

More than 99% of samples came from hunter-harvested waterfowl and less than 1% came from birds removed as part of permitted wildlife damage management activities. Sampling of hunter-harvested birds was voluntary on the part of waterfowl hunters and birds were either swabbed immediately in the field or shortly after if hunters called agency field personnel to arrange sampling. Samples collected at hunter check stations were collected in accordance with the guidelines and regulations set forth by the United States Fish and Wildlife Service (USFWS) and with the permission of participating hunters. For most birds, separate swabs were used to collect an oropharyngeal and cloacal sample. The two swabs were placed in a single uniquely labeled cryovial containing 4 milliliters of viral transport media (VTM) or 3 milliliters of brain-heart infusion media. In some cases, waterfowl carcasses were damaged and in those instances only one swab sample was collected. In four cases, a single swab was used to first swab the oropharyngeal cavity and then the cloacal cavity before being placed in the VTM. Used sample vials were held at 4°C for up to 48 hours or were placed in liquid nitrogen vapor and frozen before being shipped overnight to a reference laboratory.

Morbidity and Mortality Sampling

Between December 4, 2014, and February 28, 2015, we obtained swab samples or whole carcasses from waterfowl, other water birds, and raptors found sick and dead in Washington state. Collection protocols for wild bird morbidity and mortality events were approved under USFWS permit #MB084762-1. Birds that were swabbed only had a single combined oral and cloacal swab submitted to the U.S. Geological Survey’s National Wildlife Health Center for avian influenza testing as described previously (for the live bird surveillance). In cases where whole carcasses were submitted, separate tracheal and cloacal swabs samples were obtained at minimum. Additional tissues tested could include trachea, lung, combined trachea-lung, brain, heart, and others, as identified by pathologists conducting a cause of death necropsy on the submitted carcass and varied by individual case. Tissues were processed and tested as previously described for hunter-harvest surveillance swabs.

Figure 2. Phylogenetic comparison of hemagglutinin genes from highly pathogenic avian influenza A (H5N2, H5N8, and H5N1) detected in wild birds from the United States Pacific Flyway. Sequences were aligned using Clustal W. Evolutionary analyses were conducted in MEGA6 and the evolutionary history was inferred by using the Maximum Likelihood method based on the Hasegawa-Kishino-Yano (HKY) model (Tamura et al. 2013; Hasegawa, Kishino, and Yano 1985). The tree with the highest log likelihood is shown. Bolded samples were from wild birds sampled in the Pacific Flyway. The HA analysis involved 85 nucleotide sequences, 42 of which were from samples collected during this surveillance effort.

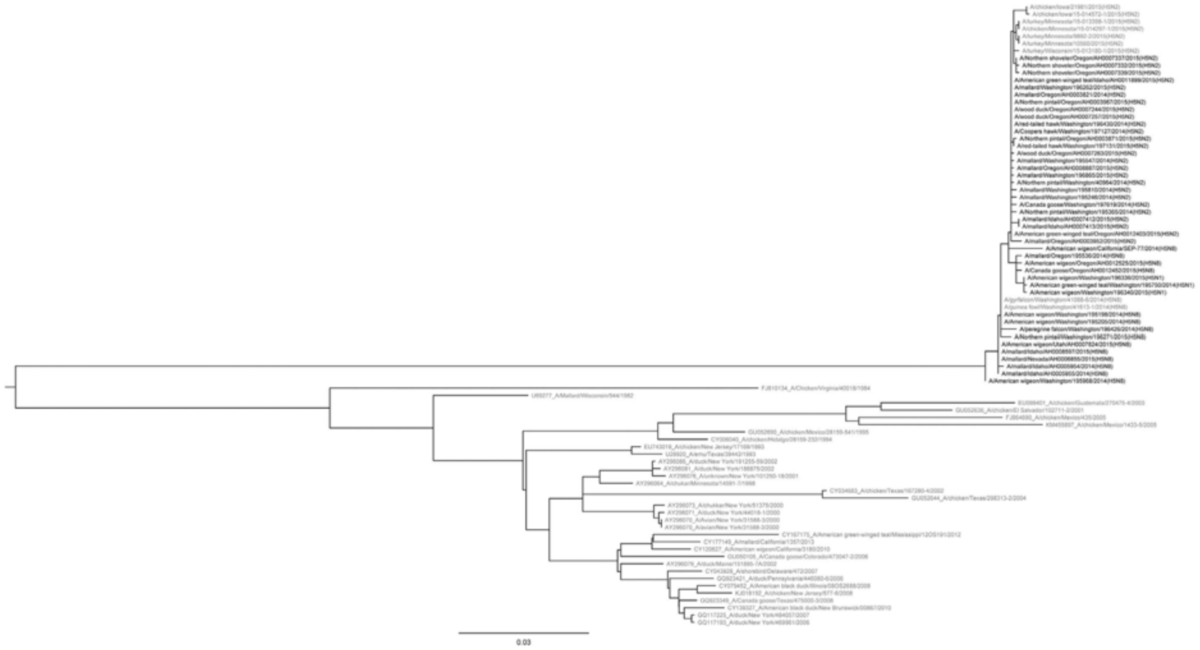
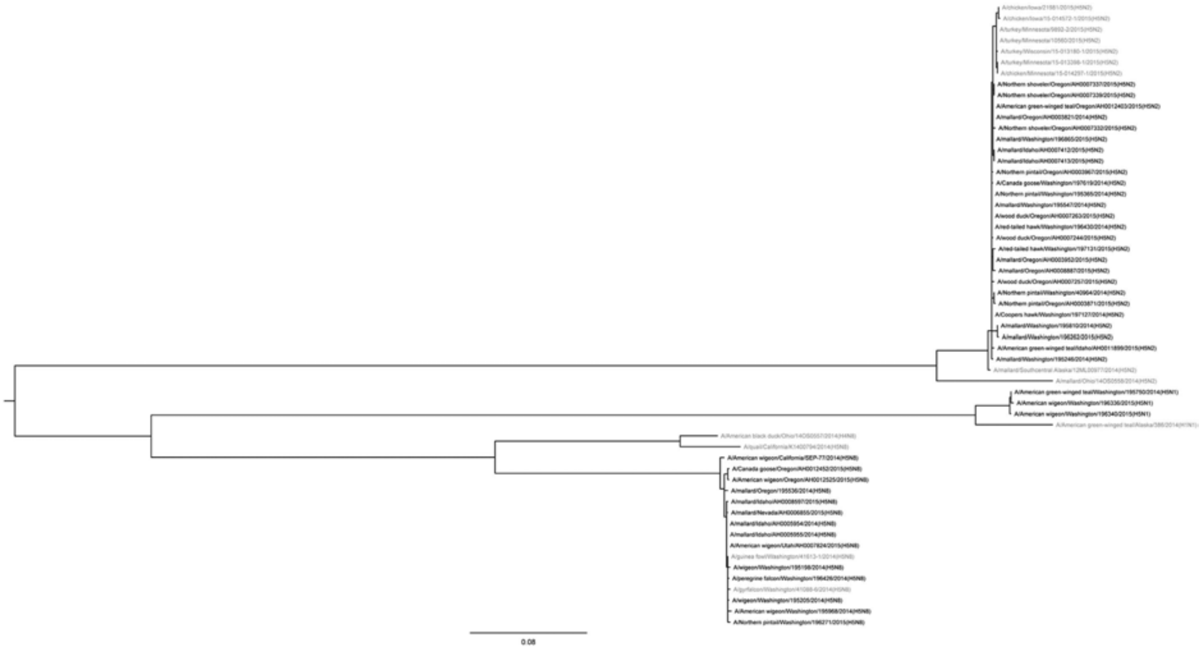


Figure 3. Phylogenetic comparison of neuraminidase genes from highly pathogenic avian influenza A (H5N2, H5N8, and H5N1) detected in wild birds from the United States Pacific Flyway. Sequences were aligned using Clustal W. Evolutionary analyses were conducted in MEGA6 and the evolutionary history was inferred by using the Maximum Likelihood method based on the Hasegawa-Kishino-Yano (HKY) model (Tamura et al. 2013; Hasegawa, Kishino, and Yano 1985). The tree with the highest log likelihood is shown. Bolded samples were from wild birds sampled in the Pacific Flyway. Analysis of the NA gene involved 57 nucleotide sequences, 43 of which were from samples collected during this surveillance effort.



Laboratory Analyses

Testing and analyses were conducted at laboratories in the National Animal Health Laboratory Network and at the Southeast Poultry Research Laboratory USDA-ARS. Presumptive positive findings were confirmed at the National Veterinary Service Laboratories-USDA-APHIS in Ames, Iowa, which is the U.S. reference laboratory for avian influenza. Samples were initially screened by rRT-PCR utilizing a test that targets the influenza matrix (M) gene using the USDA standard procedure (SOP-AV-0001) (Spackman and Lee 2014; Spackman et al. 2002). Further testing on M-gene presumptive samples was conducted using H5 and H7 subtype rRT-PCR assays as a general surveillance tool (Spackman et al. 2002). A highly specific H5 icA rRT-PCR was also run on M-gene positive samples to detect the Eurasian H5 clade 2.3.4.4 gene to distinguish icA-positive samples from those with the North American H5 gene (D. Suarez, personal communication). Virus isolation in embryonated chicken eggs was attempted on M-gene-positive samples by standard methods (Spackman 2014; Swayne, Senne, and Suarez 2008). Subtypes were identified by either serological assays (hemagglutination inhibition assay, neuraminidase inhibition assay) on isolates or by gene sequencing on swab material or isolates using standard methods (Spackman 2014; Pedersen 2014a; Pedersen 2014b). The pathotype classification was inferred from the HA gene proteolytic cleavage site sequence as defined by the World Organisation for Animal Health (OIE) (2015). Select viruses were processed for in vivo pathotyping in specific pathogen-free chickens at the NVSL in accordance with OIE guidelines (World Organisation for Animal Health 2015).

Analyses

Prevalence and 95% confidence limits were calculated using an exact binomial calculation. Comparisons between H5 prevalence during a prior wild bird surveillance effort and this current surveillance used a general linearized model with a binary distribution and a logit link function. Odds ratios were calculated using a Tukey-Kramer adjustment. All analyses were run in SAS (SAS v.9.2, Cary, North Carolina, USA).

Genetic sequences were assembled using Clustal W. Sequences were only available from a subset of samples. All positions containing gaps and missing data were eliminated. Evolutionary analyses were conducted in MEGA6 (Tamura et al. 2013). The evolutionary history was inferred by using the Maximum Likelihood method based on the Hasegawa-Kishino-Yano model (Hasegawa, Kishino, and Yano 1985). The tree with the highest log likelihood is shown. The percentage of trees in which the associated taxa clustered together is shown next to the branches. Initial trees for the heuristic search were obtained by applying the Neighbor-Joining method to a matrix of pairwise distances estimated using the Maximum Composite Likelihood approach. A discrete Gamma distribution was used to model evolutionary rate differences among sites. Analysis of the HA gene involved 85 nucleotide sequences; analysis of the NA gene involved 57 nucleotide sequences.

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The First Five (or More) Decades of Chronic Wasting Disease: Lessons for the Five Decades to Come

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Chronic Wasting Disease: Lessons Learned from the First Five Decades

Chronic wasting disease (CWD), an infectious prion disease of at least five cervid species, has run the gamut from minor scientific curiosity to national crisis since the syndrome's first recognition in the late 1960s (Williams and Young 1980; Williams 2005; Norwegian Veterinary Institute 2016). Moving forward, we believe this wildlife disease merits attention somewhere between those extremes. Collective experiences and observations made over the last five decades can serve—for better or worse—as a solid foundation for wildlife and animal health professionals to build upon in addressing anticipated challenges posed by CWD in the decades to come. Here we overview what we regard as the key lessons learned over the first five or more decades of North America's experience with CWD.

Longer Than You Think: Brief History and Known Distribution of Chronic Wasting Disease

That the duration of an outbreak often is underestimated seems perhaps the most important overarching lesson about CWD. Despite its likely occurrence in multiple locations since the 1960s or earlier (Williams and Young 1992; Miller et al. 2000; Wasserberg et al. 2009), many wildlife and animal health professionals, as well as our lay and media publics, perceive CWD as having emerged and spread rapidly only since the early 2000s (e.g., see Saunders, Bartelt-Hunt, and Bartz 2012). This perception has fostered the broader notion that newly discovered disease foci are truly "new" (i.e., very recent) occurrences. To the contrary, given imperfect surveillance approaches, incomplete or inaccurate knowledge about local exposure risks, and the insidious progression of an outbreak in its early stages, the first case *detected* in a locale is rarely *the* first case that has occurred. Consequently, on further investigation, "new" foci tend to have larger spatial dimensions and higher prevalence than expected, thereby perpetuating misconceptions about the speed of "spread." This lesson has been illustrated by experiences in Colorado and Wyoming, Saskatchewan, Wisconsin, and most recently Arkansas where expanded surveillance disclosed 79 additional cases within two months after their "first" case was diagnosed in February 2016 (Miller et al. 2000; Bollinger et al. 2004; Argue et al. 2007; Wasserberg et al. 2009; Holsman, Petchenik, and Cooney 2010; Arkansas Game & Fish Commission 2016).

Chronic wasting disease history (Table 1) remains incompletely documented. The "chronic wasting" syndrome first was recognized in captive mule deer (*Odocoileus hemionus*) held for research in Colorado in the 1960s, but unrecognized cases could have occurred in Colorado or elsewhere before that time (Williams and Young 1980; Williams and Miller 2003). Clinical cases also were recognized in captive mule deer in the Denver and Toronto zoos in the 1970s, and in captive Rocky Mountain elk ("wapiti" hereafter; *Cervus elaphus nelsoni*) in research and zoological collections in Colorado and Wyoming (Williams and Young 1992; Dubé et al. 2006). Undocumented involvement of other private collections or menageries during the 1960s and 1970s seems likely. Within little more than the first two decades after its characterization as a transmissible spongiform encephalopathy, CWD cases were diagnosed in wild mule deer, white-tailed deer (*Odocoileus virginianus*), and wapiti in northeastern Colorado and southeastern Wyoming (1980s to 1990s); in commercial captive wapiti facilities in

Saskatchewan (1996) and in South Dakota (1997); in commercial captive white-tailed deer facilities in several jurisdictions (2001 to 2002); and eventually in moose (*Alces alces*) (Williams and Young 1980; Williams and Young 1992; Spraker et al. 1997; Miller et al. 2000; Williams, Miller, and Thorne 2002; Williams and Miller 2003; Williams 2005). Cases from what have become recognized as large foci in Saskatchewan-Alberta and Wisconsin-Illinois also were first detected in the early 2000s (Williams, Miller, and Thorne 2002). As of April 2016, cases of CWD had been reported in captive and/or free-ranging cervids in 24 U.S. states (75 captive herds in 16 states and free-ranging cervids in 22 states), three Canadian provinces (including Ontario's Toronto Zoo in the 1970s), and South Korea (Figure 1) (Williams and Young 1992; Williams, Miller, and Thorne 2002; U.S. Geological Survey 2016; R. Pritchard personal communication). In addition, at the time of this writing in early April 2016, a single case in a free-ranging reindeer (*Rangifer tarandus*) in Norway in March 2016 had just been reported (Norwegian Veterinary Institute 2016). Based on experience to date, the true geographic distribution of CWD likely remains underestimated.

Two Good Stories: The Drivers of Chronic Wasting Disease "Spread"

A second overarching lesson—a corollary to the first—is that new CWD foci often can be explained by two or more equally plausible (and equally undeniable) "origin stories." Distorted temporal perceptions on the likely timing of introduction underlie the plurality of origin stories, as do sociopolitical motivations to deflect or lay blame elsewhere when "new" cases arise. But perhaps most pervasive is the lack of complete information on contributory events, particularly for outbreaks involving free-ranging cervids. Although the lack of a singular explanation can be dissatisfying, failing to consider plausible alternative timelines and exposure sources may be more problematic when disease prevention and control efforts are misinformed or misled. For example, the widely held belief that all CWD occurrences can be traced back to a single Colorado research facility has precluded wildlife and animal health professionals from considering that some outbreaks may be arising from unrecognized exposure events that occur repeatedly over time (e.g., Williams and Miller 2003; Greenlee et al. 2015). The recent Norwegian reindeer case may stimulate broader thinking.

In fact, both natural and anthropogenic factors have contributed to the geographic spread and persistence of CWD over the last five decades. Regardless of the ultimate origin, much of the geographic "spread" of CWD appears attributable to natural movements in some jurisdictions: Wyoming, for example, has only one private game farm and consequently commercial enterprise is unlikely to have driven the widespread distribution there. Alternatively, the role of commercial wapiti operations in CWD outbreaks in Saskatchewan and South Korea was well documented, with inadvertent spillover also giving rise to a large free-ranging focus spanning the Saskatchewan-Alberta shared border (Williams, Miller, and Thorne 2002; Kim et al. 2005; Argue et al. 2007; Bollinger et al. 2004). In Colorado, a combination of natural and anthropogenic factors likely contributed in different measures to separate outbreaks along the Front Range and on the Western Slope.

Natural factors contributing to persistence and geographic spread include prolonged incubation, multiple routes of agent shedding, the agent's environmental persistence, and movements of free-ranging cervids. Infected cervids likely shed prions for most of the disease course, thus affording ample opportunities for transmission within and among social groups (Tamgüney et al. 2009; Henderson et al. 2015). Migration movements also have potential for contributing to longer-distance jumps in distribution. Because infectivity can be harbored in some environments for an extended time, transmission occurs on overlapping ranges even in the absence of direct interactions between infected and uninfected animals. Indirect transmission also increases the likelihood of interspecies transmission.

The primary anthropogenic factor identified in the dissemination of CWD is human-facilitated movement of live animals (Williams and Miller 2003), and to date, this is the only confirmed contributing activity linked to CWD's spread between distant locations. These animal movements typically are fostered by other highly artificial wildlife management activities, such as captive wildlife propagation and high-fenced shooting enclosures (Fischer and Davidson 2005). Although spared from implication thus far, translocating free-ranging cervids from an infected source also would present a similar risk for spreading CWD. Local wildlife may be exposed to CWD if infected captive animals escape, or if there is ingress/egress of free-ranging cervids with exposure to infected captive animals or to contaminated environments. Fence-line contact offers another opportunity for direct transmission. (We note that these transmission opportunities are a two-way street, i.e., CWD can move in either direction between captive and wild cervids.) Other possible modes for the anthropogenic spread of CWD include transport of infected carcasses, products manufactured or contaminated with prion-laden deer or wapiti urine, saliva, or feces, and movement of hay or grain crops contaminated with the CWD agent. None of these has been documented in the field, although proof of concept has been demonstrated experimentally.

In addition, other anthropogenic factors can substantially increase the likelihood of establishing, maintaining, and disseminating CWD and other diseases in free-ranging wildlife. In particular, artificial management activities, such as wildlife baiting and feeding or other practices that congregate normally dispersed wild animals, enhance pathogen transmission opportunities (Fischer and Davidson 2005).

Things We Now Know: Chronic Wasting Disease Biology and Ecology

Many facets of CWD biology and ecology that were mysteries even into the early 2000s (e.g., see Williams, Miller, and Thorne 2002) now are well understood. For example, notable advances have been made in diagnostics and in our understanding of transmission routes and host factors modulating disease progression that have application in CWD detection and control. These and other advances have been reviewed thoroughly elsewhere (e.g., see Williams 2005; Sigurdson 2008; Smith, Booth, and Pedersen 2011; Saunders, Bartelt-Hunt, and Bartz 2012; Haley and Hoover 2015). We offer here only a brief synthesis of findings most relevant to detection and control, referring interested readers to the aforementioned reviews and numerous original papers referenced therein for greater details on and sources of specific points highlighted in our synopsis.

Chronic wasting disease appears to be caused by one or more strains of infectious prions. Although the ultimate historical origin never will be known with certainty, we regard exposure of native cervids to the sheep scrapie agent at one or more times and locations as a parsimonious explanation. Regardless of their origin(s), sustained outbreaks now occur as large and small foci and in captive wildlife facilities (Figure 1). Natural cases of CWD have occurred in five host species: mule deer, white-tailed deer, wapiti, moose, and reindeer/caribou. No immunity, recovery, or absolute resistance to infection has been documented in any of the susceptible species. However, natural variation in the host gene encoding for cellular prion protein (the *PRNP* gene) does modulate disease progression, thereby extending survival times and perhaps lowering infection probabilities for "relatively resistant" genotypes. The disease course typically is measured in years. Clinical signs—altered behavior initially, with body condition declining much later—become progressively apparent relatively late in the disease course. Infection can be detected in carcasses as well as in live animals, and diagnostic tests become increasingly reliable in individual animals as the disease progresses. Chronic wasting disease is infectious. Infected individuals shed prions from several routes during most of the disease course, exposing others either directly or through contamination of shared resources or environments. Shed prions can persist for years in the environment, and their binding to soil elements (e.g., clay) enhances persistence and infectivity. The uncoupling of transmission from the immediate presence of infected animals greatly complicates CWD control.

Looking Hard, Hardly Looking: Detecting Chronic Wasting Disease

A third key lesson relates to the difficulty in detecting CWD foci in captive and wild settings despite the considerable effort expended. Most North American jurisdictions have, at least for a time since the early 2000s, engaged in extensive if not intensive surveillance to seek out such foci. Although all of these efforts were well intentioned, many were too flawed or too short-lived to provide reliable information on disease absence. We briefly review common shortcomings of CWD surveillance as widely practiced to provide a basis for improving the efficiency and effectiveness of future efforts.

Preferred approaches for seeking out new foci (termed "surveillance" here) differ from approaches for following epidemic trends over time ("monitoring;" concepts reviewed in greater detail by Samuel et al. 2003). We recommend that CWD surveillance be an ongoing activity in jurisdictions or areas where foci have not been detected previously; monitoring may be a more episodic undertaking (e.g., at multi-year intervals) where support resources are limited because infection rates tend to change slowly compared to more conventional infectious diseases. Regardless of the purpose, CWD surveillance and monitoring should be undertaken at biologically relevant spatial scales and inferences drawn only in the appropriate spatial context in view of the highly patchy distribution of CWD in wild cervids. In our experience, statements exhorting that examination of a few hundred (or even a few thousand) harvested animals has proven a jurisdiction's freedom from CWD rarely are supported by the data in hand.

For surveillance in free-ranging settings, targeting sample sources known to have a relatively high probability of infection in endemic areas (e.g., clinical "suspects," vehicle- or predator-killed adult animals) can be a more cost-effective approach (Miller et al. 2000; Samuel et al. 2003; Walsh and Miller 2010). The effectiveness of so-called "targeted surveillance" assumes relatively even sampling effort over the geographic area of inference. However, this approach does have limitations. For example, clinical disease may not be observed in remote areas, vehicle-kills do not occur in roadless areas, and predator kills may be consumed before sampling can occur. In addition to clinical targeting, spatial targeting via risk-based assessments also may enhance the effectiveness and efficiency of CWD surveillance (Bollinger et al. 2004; Rees et al. 2012; Norbert et al. 2016).

For monitoring, random sampling (e.g., from harvested animals) provides relatively unbiased estimates of infection rates (Samuel et al. 2003). Comparisons over time or between locations should be based on a common denominator (e.g., harvested males aged 2 years or older) to assure that reliable inferences are drawn. Where available, data from lethal and nonlethal sampling can be combined for analysis provided sources are equivalent (e.g., see Geremia et al. 2015). Because foci emerge and grow so slowly, infection rates may be remarkably high on first detection when jurisdictions rely on random sampling for surveillance. Moreover, CWD tends to be unevenly distributed in the wild. The notion that a survey sample of 300 assures 95% probability of detecting at least one case where prevalence greater than or equal to 1% assumes infection is evenly distributed at that rate throughout the entire target population (Samuel et al. 2003). However, CWD distribution typically is uneven within an affected population, and the target population itself often is distributed unevenly.

Toward a Sustained and Sustainable Effort to Control Chronic Wasting Disease

The final overarching lessons learned over the past five decades relate to how wildlife and animal health professionals should (and probably should not) approach the control of CWD. In contrast to advances in our understanding of CWD biology and ecology, the available science informing effective management and control strategies remains relatively incomplete. However, recent insights and modest strides seem to offer a path forward. It follows that adaptive approaches for containing CWD foci and reducing infection and transmission rates deserve further attention.

Eradicating CWD from North America appears infeasible given its extensive distribution and other epidemiological attributes. With few exceptions—the small foci in New York and perhaps Minnesota—CWD in free-ranging cervids has persisted in reporting jurisdictions in the face of widely varied control attempts (New York Department of Environmental Conservation 2015; Minnesota Department of Natural Resources 2014). Faced with the dim prospects for eradication on scales large or small, some affected jurisdictions now seem to have abandoned any further consideration of disease management and some have effectively dismantled surveillance and monitoring as well. In light of myriad wildlife conservation needs and ever-dwindling resources, we appreciate the allure but believe this to be myopic. Instead, we strongly encourage affected jurisdictions to redouble efforts to collectively foster and develop sustained and sustainable approaches for CWD surveillance, monitoring, and control.

In contrast to the apparent success in eliminating New York's small free-ranging focus, well-publicized early attempts to control CWD in Colorado and Wisconsin yielded little evidence of progress and thus gave initial appearances of failure (e.g., see Conner et al. 2007; Holsman, Petchenik, and Cooney 2010). In recent years, however, evidence from several jurisdictions' control attempts applied across different geographic scales suggest that combinations of intensive deer removal focused around case clusters and more sustained suppression of the affected herd or population may offer some measure of effective disease suppression. A sustained culling program underway since 2003 has stabilized prevalence in northern Illinois white-tailed deer as compared to increasing trends in southern Wisconsin where disease control was suspended in 2007 (Manjerovic et al. 2014). Similar divergence in prevalence among white-tailed and mule deer harvested in Alberta and Saskatchewan may reflect the relative effectiveness of disease suppression approaches in Alberta but also could be an artifact of more recent epizootic emergence in Alberta (Norbert et al. 2016; Pybus 2012). In north-central Colorado, a combination of focal culling and broader, harvest-mediated population reduction (~25%) in the early 2000s appears likely to have contributed to reduced prevalence, whereas estimated prevalence in other Colorado mule deer herds has increased since 2002 (Conner et al. 2007; Colorado Parks & Wildlife, unpubl. data; Geremia et al. 2015).

One of the most common flaws in CWD control efforts to date has been initial underestimation of the affected area (often based on inadequate surveillance and erroneous assumptions about how long disease has been present). The outcome then gave the appearance that the control attempt had "failed" when in fact the approach was biologically sound but the application was either too small (spatially) or too short-lived. It follows that acquiring reliable distribution and prevalence data early in the planning and execution may improve the apparent efficacy of future CWD control efforts. To this end, we encourage jurisdictions to consider and set realistic disease control objectives and to use adaptive management approaches that incorporate existing and prospective field data to refine disease control objectives.

In addition to adopting and adaptively assessing approaches for stabilizing or suppressing CWD epizootics, we encourage jurisdictions to consider how recent trends in cervid management may be contributing to disease emergence. Modeling suggests harvest-based control of CWD may be most effective when focused on male deer, perhaps because infection rates among adult male deer tend to be higher than among adult females (Miller et al. 2000; Grear et al 2006; Rees et al. 2012; Jennelle et al. 2014; Potapov et al. 2016;). Conversely, then, harvest strategies intended to increase male-female ratios or adult male age structure could inadvertently facilitate CWD persistence. This may explain why in Colorado, for example, the dramatic increases in prevalence observed since 2002 in several affected mule deer herds coincide with statewide changes in harvest strategies that have increased male-female ratios over the same period (Bergman et al. 2011). Given the potential for unintended consequences, we encourage broader critical assessment of how this and other harvest strategies (e.g., season timing, baiting, "quality deer management") may be affecting CWD dynamics.

Such pursuits undoubtedly will be more difficult to champion and garner support for in sociopolitical climates ranging from apathetic to combative, particularly when control prescriptions impinge upon or conflict with commercial and sport hunting interests. The human dimensions of managing wildlife diseases in general and CWD in particular present a substantial challenge for those determining the management objectives and actions. For example, surveys of hunters and landowners in Wisconsin identified factors that contributed to hunter opposition to the state's CWD management plan including: opposition to deer population goals (initially zero), conflicts with traditions and consumption norms, uncertainty about the likelihood of success, questions about agency credibility, and no sense of urgency (Holsman, Petchenik, and Cooney 2010).

We believe there are two important motivations for responsible wildlife managers to make progress toward sustainable containment and control strategies for CWD in the coming decades. First, data from several sources suggest that heavily infected cervid populations will not thrive in the long-term (Miller et al. 2000, 2008; Almberg et al. 2011; Edmunds 2013; Monello et al. 2014; Williams, Kreeger, and Schumaker 2014; DeVivo 2015). Second, data on CWD prions and experience with other animal prion diseases suggest minimizing human exposure to these agents would be prudent (Raymond et al. 2000; Belay et al. 2004; Saunders, Bartelt-Hunt, and Bartz 2012; Cassard et al. 2014).

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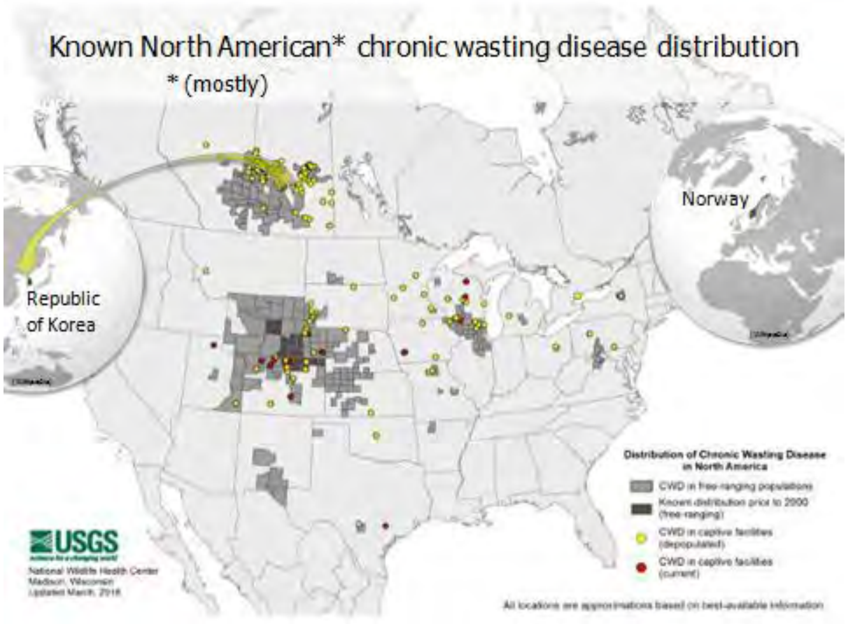
Table 1. An abbreviated timeline of select chronic wasting disease events. Adopted and from Williams, Miller, and Thorne (2002); updated and compiled by K. Niedringhaus, Southeastern Cooperative Wildlife Disease Study. See text for additional details and references.

Year	Events
1967	• Wasting syndrome observed in captive mule deer at a Colorado wildlife research facility
1975–81	• Wasting syndrome observed in Toronto Zoo mule deer that came from the Denver Zoo
1978	• Chronic wasting disease (CWD) diagnosed as transmissible spongiform encephalopathy (TSE)
1979	• Recognized in captive mule deer at Wyoming wildlife research facility
1981	• Detected in wild wapiti in Colorado
1985	• Detected in wild mule deer in Colorado & Wyoming
1996	• Detected in a captive wapiti farm in Saskatchewan; 38 other linked farms eventually found positive
1997	• Detected in captive wapiti facilities in South Dakota
1998	• Detected in captive wapiti facilities in Montana & Oklahoma • *Model Program for Surveillance, Control, & Eradication of CWD in Domestic Elk* presented at U.S. Animal Health Association to establish monitoring & control standards
1999	• World Health Organization indicates no evidence CWD is transmissible to humans, but advises that exposure should be avoided nonetheless
2000	• Detected in wild mule deer in Nebraska & Saskatchewan • Research: molecular studies compare host ranges for CWD, scrapie, & bovine spongiform encephalopathy prions; environmental contamination & subclinical infection contribute to transmission; prevalence estimates in wild populations in Colorado & Wyoming
2001	• Detected in captive wapiti in Kansas • Detected in captive wapiti in South Korea imported from Saskatchewan • Detected in wild white-tailed deer in South Dakota • U.S. Department of Agriculture (USDA) declares CWD emergency in captive wapiti; funds available for disease control
2002	• Detected in captive wapiti in Minnesota & captive white-tailed deer in Alberta • Detected in wild & captive white-tailed deer in Wisconsin • Detected in wild white-tailed deer in Illinois, mule deer in New Mexico, wapiti in South Dakota • Joint CWD Task Force of USDA/DOI/States/Universities develops *Plan for Assisting States, Federal Agencies & Tribes in Managing CWD in Wild & Captive Cervids* (National CWD Plan) • Colorado establishes guidelines to minimize transport of high risk carcass materials • 1st International CWD Symposium (Denver, Colorado) • Research: tonsil biopsy as a live animal test; improved high-throughput diagnostics
2003	• Detected in wild mule deer in Utah • APHIS funds available for CWD work in captive & wild cervids (through 2011) • USDA publishes a proposed rule for CWD herd certification & interstate shipping program (HCP) to eradicate CWD from captive deer & wapiti • Research: horizontal transmission of CWD likely important in CWD epidemiology
2004	• Detected in wild wapiti in New Mexico • National CWD plan progress report published & new priorities discussed • Research: environmental sources, decomposed carcasses can contribute to transmission
2005	• Detected in captive & wild white-tailed deer in New York • Detected in wild mule deer in Alberta, moose in Colorado, white-tailed deer in West Virginia
2006	• Detected in captive white-tailed deer in Minnesota

	- Detected in wild white-tailed deer in Kansas - USDA publishes Chronic Wasting Disease Herd Certification Program Final Rule (CWD Final Rule)—never implemented - Research: prions in muscles of infected deer; transmitted in saliva & blood
2007	- Research: prions in environment more infective in particular (clay) soil types
2008	- Detected in captive deer in Michigan - Detected in wild wapiti in Saskatchewan, moose in Wyoming - Research: CWD may be a plausible explanation for local deer population declines in Colorado
2009	- APHIS plans to withdraw 2006 CWD Final Rule, issue a new rule based on 2006 rule & 2009 proposed rule - Research: prions shed in feces from deer in early stages of CWD; prions in urine & saliva
2010	- Detected in captive white-tailed deer in Missouri - Detected in wild white-tailed deer in North Dakota & Virginia
2011	- Detected in wild white-tailed deer in Maryland - Detected in wild white-tailed deer in Minnesota - Severe reduction of USDA funds for CWD work
2012	- Detected in captive white-tailed deer in Iowa & Pennsylvania - Detected in wild white-tailed deer in Missouri - Detected in wild mule deer in West Texas - APHIS Interim Final Rule for CWD Herd Certification & Interstate Movement & CWD Program Standards published - Research: possible link between scrapie & CWD
2013	- Detected in wild white-tailed deer in Pennsylvania
2014	- Detected in captive deer in Ohio - CWD Program Standards revised - APHIS CWD Final Rule implemented - Research: plants may play role in CWD transmission & environmental maintenance; experimental aerosol transmission in white-tailed deer
2015	- Detected in wild white-tailed deer in Michigan - Detected in captive white-tailed deer in Texas - Research: plants can bind prions superficially & uptake prions from contaminated soil
2016	- Detected in wild wapiti & white-tailed deer in Arkansas - Detected in a wild reindeer in Norway

Figure 1. Current known distribution of chronic wasting disease (CWD). In addition to North America, cases have been reported in South Korea (captive only) and Norway (free-ranging only). North America map from U.S. Geological Survey (2016); global maps from Wikipedia.



Monitoring Hemorrhagic Disease: What Every Wildlife Professional Needs to Know

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Introduction

Hemorrhagic disease (HD) of wild ruminants is an arthropod-borne febrile disease caused by two closely related orbiviruses (family Reoviridae), epizootic hemorrhagic disease viruses (EHDV) and bluetongue viruses (BTV). Worldwide, seven EHDV serotypes and 27 BTV serotypes exist but historically only EHDV-1 and -2 and BTV-2, -10, -11, -13, and -17 were known to circulate in North America (Stallknecht, Howerth, and Gaydos 2002). These viruses are transmitted to ruminants by certain species of *Culicoides* biting midges, thus HD is closely associated with environmental conditions and has a predictable seasonality. Among wild and domestic ruminants in North America, the outcome of infection with BTV and EHDV varies within and between species (Howerth, Stallknecht, and Kirkland 2001). This diversity of viruses, ruminant hosts, and *Culicoides* vectors associated with HD makes for a very dynamic and complex epidemiology.

Hemorrhagic disease among white-tailed deer (WTD; *Odocoileus virginianus*) populations is not new, and reports of large-scale epizootic mortality of WTD consistent with HD date back to the late 1800s. Since discovery of the viruses that cause HD in the 1950s and '60s, documented HD outbreaks have occurred regularly in the U.S. (Stallknecht, Howerth, and Gaydos 2002). Considered one of the most significant infectious diseases of WTD, HD is well characterized in this species. The cyclical and explosive nature of local and regional HD outbreaks and high mortality among some WTD populations have made HD a well-known disease among wildlife biologists. Accordingly, HD has been a surveillance and research focus for many decades.

Because of the spatial distribution and cyclical nature of HD outbreaks, many biologists will not encounter this disease routinely. Our primary objectives are to 1) describe the two HD monitoring systems that have been used for decades; 2) review the basic field signs, necropsy findings, and diagnostic approach for HD related to utilizing these two monitoring systems; 3) highlight what we have learned from these surveillance efforts; and 4) discuss the importance of continuing these surveillance systems in order to monitor trends and address research gaps.

Long-Term HD Monitoring Activities at SCWDS

Many decades of research, comprising outbreak investigations, cross-sectional serological surveys, *Culicoides* surveys, and controlled experimental infections and laboratory studies, have laid the foundation for our current understanding of HD pathobiology and epidemiology in North America. This understanding has been greatly enhanced by two long-term surveillance projects conducted by the Southeastern Cooperative Wildlife Disease Study (SCWDS; University of Georgia): 1) annual questionnaire-based reporting from state wildlife management agencies that have provided data on the occurrence of HD in wild ruminants from 1980 to present, and 2) diagnostic virology on clinical case submissions from wild ruminants suspected of having HD from 1994 to present.

Annual HD Questionnaire-Based Surveillance

In 1980, the first annual post-outbreak HD questionnaire was sent to wildlife agency personnel in 16 southeastern states (Couvillion et al. 1981). In 1982, this was expanded to all state wildlife agencies and the annual questionnaire has operated since that time (Nettles et al. 1992). The questionnaire is based on the following four diagnostic criteria for reporting HD in a deer population and has remained unchanged since 1980:

- *Criterion 1*. Sudden, unexplained, high deer mortality during late summer/early fall
- *Criterion 2*. Necropsy diagnosis of HD by a trained wildlife biologist, a diagnostician at a state diagnostic laboratory or veterinary college, or by SCWDS personnel
- *Criterion 3*. Isolation or molecular-based detection of EHDV or BTV from an affected animal (does not include detection of serum antibodies)
- *Criterion 4*. Observation of hunter-killed deer that showed sloughing hooves, oral ulcers, or scars on the rumen lining

The questionnaire is completed annually by personnel in each state wildlife management agency, and these criteria are used to document the presence of suspected or confirmed HD at the county level. When possible, questionnaire participants include additional details, such as species and number of individuals reportedly affected, and virus detection results when labs other than SCWDS are involved. Numerous factors have contributed to the reliability of these data including: the diligence and continued support of state agency personnel, well-characterized and consistent field signs and necropsy lesions of HD in white-tailed deer, consistent criteria for reporting HD by state agencies, the relative visibility of deer to the public, and the value of deer as a natural resource. However, as with all surveys, potential reporting biases exist. For instance, over the extended period of time that this survey has been in place, the data have been obtained from different individuals and the specific methodology for data collection has varied between states. However, these potential biases are partially mitigated by a well-defined HD case presentation, consistency of the four criteria used in the case definition among years, and the large spatial and temporal scale at which the survey operates (Stallknecht et al. 2015).

The value of a field necropsy (criterion 2) and ancillary diagnostic testing (criterion 3) cannot be understated. Although field signs of HD are well characterized, not all deer mortalities during the late summer and early fall are caused by EHDV or BTV. A good field necropsy and diagnostic testing are important steps in not only confirming HD, but also in identifying other causes of deer mortality or identifying new or novel pathogens important to wildlife, human, or domestic animal health.

Annual Diagnostic Virology

Since 1994, SCWDS has provided virus isolation to support diagnostic investigations of sick and dead ruminants suspected to have HD. The vast majority of submitted samples are from WTD, although samples from a variety of other wild and domestic ruminants are also occasionally received. The isolation of EHDV or BTV by SCWDS personnel has relied on cell culture-based diagnostics. Although multiple cell lines can be used for virus isolation, cattle pulmonary arterial endothelial (CPAE; American Type Culture Collection, Manassas, Virginia) cells are used exclusively at SCWDS (Stallknecht and Howerth 2004). Submitted tissues are processed in the laboratory for isolation and identification of EHDV and BTV to the serotype, a process that can take two to three weeks (Allison et al. 2010; Stallknecht and

Howerth 2004). All EHD and BT viruses isolated are retained and stored at SCWDS, and currently, this collection includes more than 1,000 viruses spanning most of the U.S. from 1994 to present. These viruses routinely have been made available for research purposes and have become a valuable resource used by researchers in the U.S. and abroad.

While EHD and BT viruses are durable and can remain viable for long periods of time under proper storage, multiple factors can interfere with the success of virus isolation from field submissions. The amount of EHDV or BTV present in the tissues of an infected WTD varies overtime. For instance, the titer of EHDV in tissues typically peaks in a WTD with acute HD five to eight days after infection, after which virus titer sharply decreases (eight to 12 days after infection) and remains at very low levels until cleared (Ruder et al. 2012). Success of virus isolation typically is high when a deer dies early in the course of disease and tissues are collected from the carcass soon after death, promptly refrigerated, and shipped to the lab in a timely manner. However, deer dying greater than two to three weeks after infection likely have a low level of virus remaining in the tissues, which can complicate detection. Further, high temperatures during outbreaks can lead to fairly rapid decomposition, which limits virus isolation success. Therefore, a rapid field necropsy and refrigeration of tissue samples for submission greatly facilitate diagnosis.

The focus of the diagnostic virology effort at SCWDS is to achieve a herd-level diagnosis. While it is not practical to detect EHDV or BTV in all dead deer during an epizootic, it is important to achieve confirmation in one or more animals in order to have confidence in the suspected diagnosis, especially in the western U.S. where cervid adenoviral hemorrhagic disease occurs (Woods 2001). During large-scale or intense outbreaks, the recommended goal during a suspected HD mortality investigation is to submit tissue samples from a particular county for diagnostic virology until a virus is confirmed. Once HD is confirmed by one or more virus isolates, there is generally no need to continue virus isolation attempts from that particular area and resources can shift to confirm suspected cases in other counties, although it is important to continue to monitor confirmed counties to better understand the impact of the outbreak. However, additional virus isolation data may benefit specific management or research questions. Consultation with SCWDS may be helpful in determining the need for additional diagnostics.

What Should Every Biologist Know About HD?

Distribution and Host Range

As both EHDV and BTV are insect-transmitted, these viruses are distributed throughout temperate and tropical regions around the globe (~ 40-50ºN and 35ºS latitude) in climates supportive of the *Culicoides* spp. vectors. In the U.S., these viruses are broadly distributed and EHDV and/or BTV have been confirmed in all but the New England states (Massachusetts, Connecticut, Rhode Island, New Hampshire, Vermont, and Maine) (Ruder et al. 2015; Stallknecht et al. 2015). In Canada, BTV is rarely detected in ruminants in southern British Columbia and EHDV in southern British Columbia and Alberta (Pare et al. 2012; Pybus, Ravi, and Pollock 2014).

Despite the nearly global distribution of EHDV and BTV, HD has been reported in wildlife only in North America. Although disease is most common in WTD, disease associated with EHDV and/or BTV infection has also been reported in mule deer (*Odocoileus hemionus*), pronghorn (*Antilocapra americana*), bighorn sheep (*Ovis canadensis*), elk (*Cervus elaphus*), and bison (*Bison bison*) (Howerth, Stallknecht, and Kirkland 2001; Stevens et al. 2015; Ruder et al. 2015). Of these species, WTD are impacted most severely, although large outbreaks of BTV have occurred in the western U.S. in pronghorn, mule deer, and bighorn sheep (Thorne et al. 1988; Robinson et al. 1967). Both EHDV and BTV also are of concern to some livestock species, although outbreaks of severe clinical disease are relatively infrequent in the U.S. Cattle typically have subclinical infections with EHDV and BTV, although mild disease during large U.S. outbreaks occasionally occurs (Baldwin et al. 1991; Stevens et al. 2015). Sheep are very susceptible to severe disease with BTV infection but EHDV-related disease has not been reported (Miller et al. 2010).

Transmission and Epidemiology

Both EHDV and BTV are transmitted by *Culicoides* biting midges (Diptera: Ceratopogonidae), which are small (1 to 3 millimeters), primarily hematophagous flies that breed in a variety of semiaquatic habitats. Approximately 1,400 *Culicoides* species exist worldwide; however, only a small portion are proven vectors (Mellor, Boorman, and Baylis 2000). In North America, known competent vectors of BTV include *C. sonorensis* and *C. insignis*, whereas the only proven vector of EHDV is *C. sonorensis* (Gibbs and Greiner 1989; Ruder et al. 2015). *Culicoides sonorensis* populations are widespread in the western U.S. and smaller, more fragmented populations exist in the southeast, whereas *C. insignis* is abundant in Florida and occasionally is detected in adjacent states (Vigil et al. 2015). Although only these two species are confirmed vectors, other *Culicoides* spp. (e.g., *C. stellifer, C. debilipalpis*) are suspected vectors (Smith and Stallknecht 1996; Ruder et al. 2015).

Hemorrhagic disease is predictably seasonal, with outbreaks peaking in late summer to early fall and ending after the first frost (Couvillion, Nettles, and Davidson 1981). At southerly locations, this seasonal transmission also is typical, but virus transmission may occur throughout the year in locations where adults can survive cooling temperatures for extended durations (Mayo et al. 2014). The numerous environmental factors that influence insect populations also influence EHDV and BTV transmission cycles and disease outbreaks. For instance, some climatic variables (e.g., temperature and precipitation) can impact the life history of *Culicoides* spp., and populations can reach high densities under ideal conditions (Mullens et al. 2004; Lysyk and Danyk 2007). Additionally, replication of the viruses within *Culicoides* is temperature-dependent (Mullens et al. 2004). These climate-related factors, in addition to many habitat and landscape variables, may be important in creating ideal conditions for large HD outbreaks (Sleeman et al. 2009; Xu et al. 2012; Berry et al. 2013; Stallknecht et al. 2015).

The epidemiology of HD is complex, as the system involves multiple EHD and BT viruses, numerous ruminant hosts, and multiple *Culicoides* spp. that span a landscape with great ecosystem diversity. In the U.S., HD exists in enzootic and epizootic cycles, likely driven by interacting climatic, habitat, and landscape factors that in turn impact local and regional host and vector populations. In enzootic regions of the southeastern coastal plain where *Culicoides* activity can persist much of the year, virus transmission occurs annually and most cases are subclinical or occur as the chronic form. Moving inland into the Piedmont and Appalachian Mountains in the Southeast and in portions of the Midwest and Great Plains, epizootics with high mortality generally occur on multiyear cycles (e.g., three to five years). Historically, outbreaks are even more infrequent in northern latitudes and result in significant mortality when they occur. However, these spatial and temporal patterns are general trends, and isolated epizootics involving small numbers of animals likely occur regularly in both enzootic and epizootic regions. In addition to epizootic and enzootic cycles, it has been suggested that in certain regions of the U.S., such as parts of Texas, Kansas, and Florida, WTD coexist with EHDV and BTV in a state of enzootic stability (Stallknecht et al. 1996; Flacke et al. 2004). In these regions, seroprevalence among WTD may approach 100%; however, reports of clinical disease are rare. This enzootic stability likely is the result of acquired immunity via frequent exposure to the viruses, high subsequent passive immunity in fawns, and mechanisms of innate immunity via coevolution of the host and pathogen (Quist et al. 1997; Gaydos et al. 2002a, b, c). These mechanisms of immunity likely are absent in deer from nonenzootic regions and this potentially may explain high mortality rates sometimes observed in captive WTD imported to enzootic regions.

Clinical Signs and Necropsy Lesions

In WTD, diseases caused by EHDV and BTV are indistinguishable. The disease is highly variable in WTD, ranging from subclinical to rapid death without premonitory signs. Some animals recover after mild disease, whereas some succumb due to chronic sequela months after acute disease. Deer behavior makes it difficult to observe clinical signs in affected animals, especially when subtle. Deer often are simply found dead or moribund. However, common clinical signs initially include fever, loss of appetite, rough hair coat, lethargy, and reddening of mucous membranes and nonhaired regions of the skin. Salivation may occur, often associated with hemorrhages in the oral cavity that may progress to ulcers.

Additional clinical signs include lameness, bleeding tendencies, respiratory difficulty, bloody diarrhea, recumbency and terminal convulsions (Howerth, Stallknecht, and Kirkland 2001). Death from peracute and acute HD typically occurs within two weeks of infection.

Necropsy lesions also are variable and interpretation can be complicated by decomposition often encountered in the field. Three forms of HD have been described: peracute, acute, and chronic (Howerth, Stallknecht, and Kirkland 2001). The peracute form may include effusions in the thoracic cavity and pericardial sac, pulmonary edema, and subcutaneous edema, especially in the fascial planes of the head, neck, and ventrum. However, necropsy findings are variable and can be very subtle when animals die peracutely. As the disease progresses to the acute form and a bleeding disorder ensues, widespread hemorrhages in various organs are common, especially in the gastrointestinal tract and heart. When present, two gross necropsy findings nearly indicative of HD in WTD are hemorrhage at the base of the pulmonary artery and hemorrhage on the serosal surface of the abomasum. With time, erosions and ulcers frequently are observed in the oral cavity, especially on the dental pad. Deer surviving acute HD may present with lesions of the chronic form, including open or healing ulcers of the tongue, scarring of the rumen mucosa and cracked or sloughing hooves in multiple limbs subsequent to interruption of growth of the hoof wall. The ulcers in the oral cavity and cracked hooves sometimes are associated with secondary bacterial infections that contribute to the poor nutritional condition of these animals. Often, these animals may present as over-winter mortality subsequent to malnutrition and secondary problems. The chronic form does not represent active infection but rather sequelae after recovery from acute HD.

Diagnostic Sampling

Epizootic mortality in a herd from July through October should lead to a suspicion of HD. Gross necropsy findings can support this suspicion but a confirmed diagnosis of HD must be based on virus isolation from the affected animal. Preferred diagnostic samples include fresh (not frozen) spleen and lung, although lymph node and whole, unclotted blood (i.e., EDTA, heparin, or citrate) also are suitable. Since subclinical infection of WTD can occur, positive test results must be supported by field or necropsy findings consistent with HD. This consideration is especially true when testing domestic ruminants or other less susceptible wildlife species. Field diagnosis of the chronic form of HD typically is based on consistent field and necropsy findings because the virus typically has been cleared from the body and cannot be isolated at this stage. Circulating antibodies against EHDV and BTV are common in WTD throughout many portions of the U.S., thus serology should not be relied upon for diagnosis of recent infection but can give an indication of virus activity within a region.

What We Have Learned From Long-Term Monitoring

These long-term datasets have been fundamental to our understanding of HD and have been essential to capturing numerous changes in disease patterns over the past three decades. The monitoring of HD among state agencies in the U.S. is a good example of the power of long-term cooperative surveillance of a wildlife disease.

Understanding Basic Patterns of Disease

Our basic understanding of the descriptive epidemiology of HD has been greatly enhanced through long-term monitoring. Since 1994 when annual diagnostic virology was initiated at SCWDS, 1,150 viruses have been isolated from tissues submitted from sick and dead ruminants. From 1994 to 2015, the majority of viruses (91%, 1,043/1,150) have been isolated during a three-month period (August to October) (Figure 1) and most (92%, 1,081/1,150) have been isolated from WTD. However, a total of 69 viruses have been isolated from other ruminant species in the U.S. including: domestic cattle (34), domestic sheep (8), pronghorn antelope (6), mule deer subspecies (6), elk (5), bison (5), bighorn sheep (4), and alpaca (1).

Of the viruses isolated from 1994 to 2015 from WTD, 94% (1,016/1,081) were EHDV, 89% (902/1,016) of which were EHDV-2. While regional or localized epizootics may be caused by other viruses in a given year, EHDV-2 clearly is the predominant cause of HD outbreaks in WTD in the U.S. The mechanisms driving this are unknown but likely are related to complex vector-host-virus interactions. Although BTV is far less common among viruses isolated by SCWDS (104/1,150), BTV appears to be a more common isolate among the species other than WTD. Specifically, BTV represented 57% (39/69) of viruses isolated from these species, compared to only 6% (65/1,081) BTV for WTD. However, BTV is more common in the western U.S. as 76% (79/104) of BTV isolates were from submissions coming from west of the Mississippi River. This may explain much of the species-related variability.

The annual HD surveillance questionnaire also has contributed to our collective understanding of the distribution of HD. Figure 2 shows the distribution of reported HD among wild ruminants in the U.S. from 1980 to 2014. It is noteworthy that this does not represent a distribution of viruses but rather a distribution of disease. The viruses are more broadly distributed, especially in portions of the Southwest where infection of ruminants with EHDV and/or BTV may be common but disease is rare (Stallknecht et al. 1996; Ruder et al. 2015). Additionally, in the western U.S., primarily west of the Rocky Mountains, a cervid adenovirus may account for some historical HD reports, as this disease has lesions similar to HD and is common among populations of mule deer subspecies in some states (Sorden, Woods, and Lehmkuhl 2000; Woods 2001). This underscores the importance of ancillary diagnostic testing in this region to confirm presumptive field diagnoses. Within the overall distribution of HD, marked regional variation occurs in the frequency of HD reporting. Figure 3 shows the proportion of years from 1980 to 2014 that HD was reported by state wildlife management agencies. Although an oversimplification, this state-level information provides insight into the regional variation in HD frequency during a 34-year period and helps shape our understanding of where enzootic and epizootic regions exist in the U.S.

Detection of Multiple Exotic Viruses in the U.S.

Bluetongue virus and EHDV first were isolated in the U.S. in the 1950s, although historical accounts suggest these viruses likely circulated prior to this time (Nettles and Stallknecht 1992). For the next 50 years, there was consistency in the viruses known to circulate in the U.S. (EHDV-1 and -2, and BTV-2, -10, -11, -13, and -17) (Howerth, Stallknecht, and Kirkland 2001). However, since 1999, 11 exotic BTV serotypes (1, 3, 5, 6, 9, 12, 14, 18, 19, 22, and 24) and an exotic EHDV serotype (6) have been detected in the U.S. (Gibbs et al. 2008; Ostlund 2010; Allison et al. 2010). Some of these exotic viruses (EHDV-6, BTV-1, -3, -12, and -18) have been isolated by SCWDS from WTD suspected to have died from HD based on field signs and necropsy findings. These viruses would not have been detected without routine investigation (necropsy and sample submission) of wildlife mortality. The importance of many of these exotic viruses to wildlife and livestock is not fully known but continued surveillance has made the picture clearer for EHDV-6, particularly for wildlife. Since it was detected in 2006, EHDV-6 has been associated with large epizootics and has been isolated annually from dead WTD throughout the central and eastern U.S., indicating it likely is established in the U.S. (Allison et al. 2010; Stallknecht et al. 2015). The source and route of introduction for these exotic viruses are not fully understood and it is not clear which BTV serotypes may be established; however, the emergence of these new viruses serves as an indication that the vector-host-virus system in the U.S. is changing. In the midst of such change, it is important to investigate suspected HD mortality events and submit tissues for diagnostic testing.

Northern Expansion and Increasing Frequency and Intensity of HD

Perhaps the biggest benefit of the annual HD surveillance questionnaire has been our ability to use it as a semiobjective tool to measure change over time. In particular, it has been critical in documenting the apparent northern expansion of HD, as well as the increasing frequency and intensity of outbreaks in the Midwest and Northeast since 1980 (Stallknecht et al. 2015). Historically, this region largely has been free of HD other than infrequent outbreaks (Nettles, Davidson, and Stallknecht 1992; Stallknecht, Howerth, and Gaydos 2002), but recent analysis suggests patterns are changing and reports of northern HD outbreaks are becoming increasingly common. For instance, EHDV outbreaks confirmed by virus isolation have occurred in New Jersey in 1955, 1975, 1999, 2007, and 2010 to 2012; Michigan in 1955, 1978, 2006, 2008 to 2013; and in New York in 2007, 2010, and 2012 (Stallknecht et al. 2015;

Ruder et al. 2015). In addition, the intensity of outbreaks appears to be increasing, as the number of counties annually reporting HD from 1980 to 2012 in the Midwest and Northeast increased over time (Stallknecht et al. 2015). The mechanisms driving these changes and whether these trends will continue remain unknown and continued monitoring will be critical.

While the drivers of HD outbreaks are not well understood, multiple studies using these long-term datasets have identified numerous factors (e.g., land cover, drought, temperature, precipitation, wind) that may be involved and should be explored further (Sleeman et al. 2009; Xu et al. 2012; Berry et al. 2013; Stallknecht et al. 2015). The interaction of these potential variables with ruminant and vector populations and how they impact transmission at the landscape and local scale likely are complex and there may be significant regional variation.

Why Should We Continue to Monitor HD?

Hemorrhagic disease was once considered a potential threat to deer restoration efforts in the eastern U.S., but WTD populations proved resilient and have thrived despite decades of periodic HD outbreaks. However, the recent detections of new viruses, expanding range of HD, and increasing frequency and intensity of outbreaks, are all indicators that changes are occurring in this dynamic disease system. Accordingly, it is important to continue to monitor HD if we hope to better understand the drivers of outbreaks and the impact on WTD populations and potentially on other susceptible wild ruminants (e.g., pronghorn, bighorn sheep). White-tailed deer in North America likely have lived with HD for more than a century, and that will not change. However, if the above epidemiological patterns continue to change, so too could the impact of HD on deer populations. In a changing environment (e.g., climate change, growing human populations, changing land-use patterns), the future pressures on WTD populations are difficult to predict. If HD cycles increase and expand north in a sustained manner, and HD becomes a more prominent and frequent nonhunting mortality factor, will future populations continue to recover after outbreaks and will management goals be maintained? As trends in disease patterns shift, so too must our perception of the potential for HD to impact populations. Therefore, an important area of future research is the impact of HD on WTD populations, which has not been well documented. Estimated population losses of 6 to 16% in Missouri and 20% in West Virginia have been documented during local EHDV outbreaks and losses in penned WTD can be much higher (Fischer et al. 1995; Gaydos et al. 2004). Future HD outbreak investigations should aim to document regional and local mortality rates, their short-term and long-term impact, and the effectiveness of reduction in legal deer harvest following large-scale HD outbreaks (essentially the only current management tool for populations experiencing high HD mortality).

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Figure 1. Bar graph showing number of successful epizootic hemorrhagic disease virus and bluetongue virus isolations by SCWDS 1994 to 2015 (n = 1,150). The predominance of virus isolates August to October (91%, 1,043/1,150) demonstrates the strict seasonality of HD in most of the U.S.

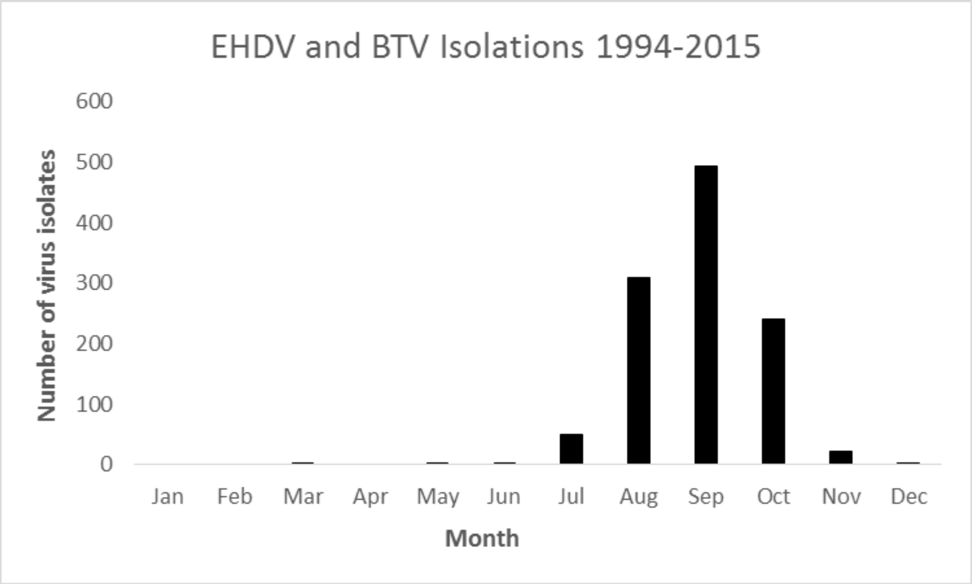


Figure 2. Map showing the distribution of reported HD morbidity and/or mortality among wild ruminants, primarily white-tailed deer, in the U.S. from 1980 to 2014. Results are based on a long-term annual survey of all state wildlife management agencies to report HD occurrence on a county basis.

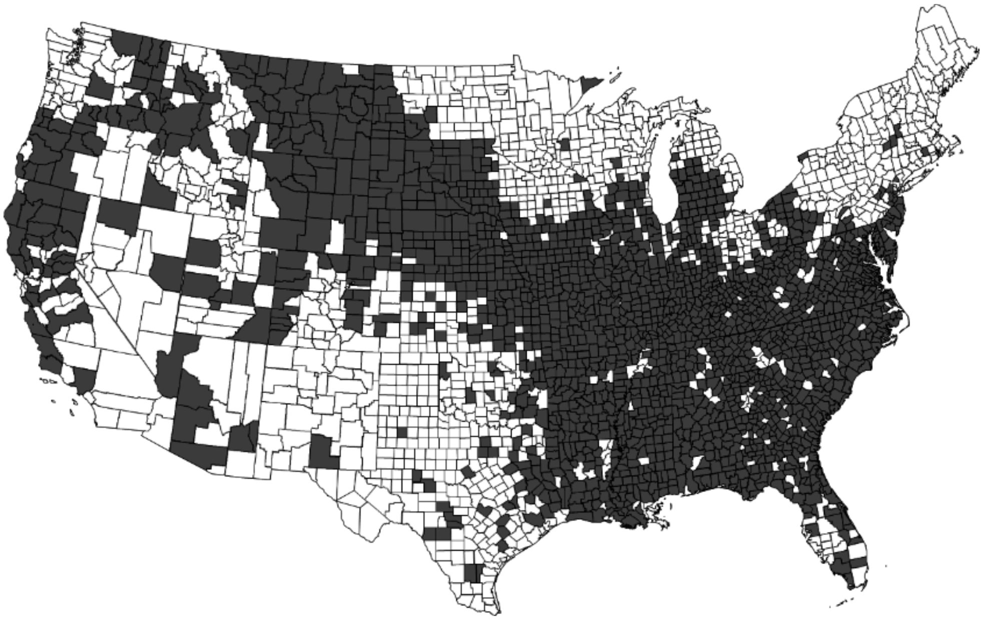
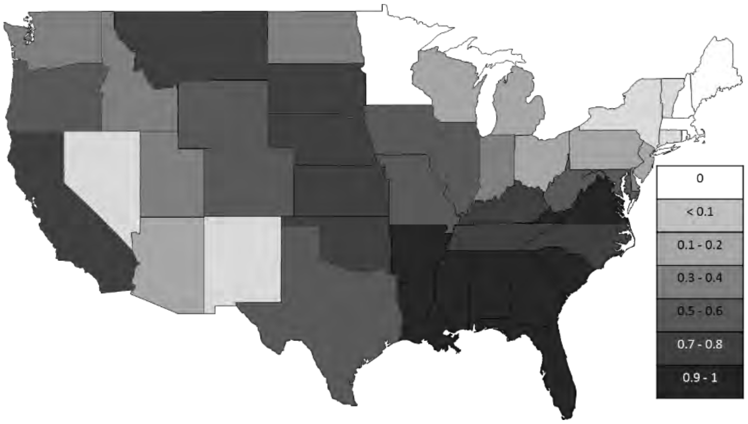


Figure 3. Map showing the proportion of years from 1980 to 2014 in each state that HD morbidity and/or mortality was reported among wild ruminants, primarily white-tailed deer, in the U.S. Results are based on a long-term annual survey of all state wildlife management agencies to report HD occurrence on a county basis.



Infectious Salmon Anemia (ISA), Infectious Hematopoietic Necrosis (IHN), and Bacterial Kidney Disease (BKD) as Case Studies for Disease Management in Farmed and Hatchery-Reared Salmonids

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Introduction

Infectious diseases can cause significant losses among both farmed and natural populations of aquatic animals. In the wild, disease is considered a component of natural mortality, but the effects of disease on wild populations are often difficult to measure or manage. However, there are documented cases of severe mortality in wild populations caused by both endemic and exotic diseases. For example, endemic strains of infectious hematopoietic necrosis (IHN) virus cause losses in wild Pacific salmon on the West Coast of North America, and an introduced strain of viral hemorrhagic septicemia (VHS) virus has affected several wild populations of fish in the Great Lakes region (Kurath et al. 2003; Faisal et al. 2012). Nevertheless, much of what we know about aquatic animal diseases comes from farmed or hatchery-reared stocks in facilities owned or managed by federal, state, tribal, and private sector entities. Among these farmed fish, the consequences of disease can range from decreased production to large-scale mortality and, in cases where a disease is caused by regulated pathogen, may include the complete depopulation of all stocks and disinfection of the facility. However, disease outbreaks among these hatchery populations are more amenable to study and may provide management options for their control. The management of disease in farms and hatcheries has important benefits for not only the health of the farmed stocks, but because farmed and wild fish are closely linked by a common aquatic environment through which pathogens can readily transfer, the management of hatchery diseases may have important benefits to the health of wild stocks as well (Kurath and Winton 2011).

In recent years, outbreaks of infectious salmon anemia (ISA) and spring viremia of carp (SVC) in private U.S. aquaculture operations have resulted in losses of more than $10 million. Although the management of infectious disease in wild populations is often not feasible, disease management in hatchery and aquaculture facilities has proven successful in many cases. These management strategies typically include strict biosecurity measures, improved husbandry practices, vaccination, and use of chemotherapeutics. The choice of appropriate management strategies is largely dependent on the epizootiological features of the disease, including the presence of reservoirs or vectors, how the causative agent is spread, and the most susceptible life stage of the target host. Therefore, having a sound understanding of the host-pathogen relationship for a given disease is critical to developing effective management strategies. Here, we review the successful management of ISA in commercial salmon aquaculture in Maine, IHN in a federal hatchery, and bacterial kidney disease (BKD) in Idaho state hatcheries to demonstrate how research and improved knowledge of the factors controlling the epizootiology of each disease informed highly variable but effective management strategies for these three viral diseases.

Infectious Salmon Anemia Management in Maine

Infectious salmon anemia virus (ISAV) is a member of the family *Orthomyxoviridae*. The virus primarily infects Atlantic salmon (*Salmo salar*) and has caused severe morbidity and mortality in Atlantic salmon farming industries in eastern North America, Norway, Scotland, the Faroe Islands, and Chile. The

Quoddy region of Maine and New Brunswick, Canada, is characterized by extensive tidal mixing and close proximity between commercial farms rearing Atlantic salmon (Gustafson et al. 2007). This region is also prone to recurrent appearances of ISA, resulting from the spillover of wild-type strains of ISAV from a reservoir among wild stocks and the subsequent selection of mutants with high virulence that rapidly spread within the farm and are transported to nearby farms. Although control measures might limit the spread and severity of the virulent forms of ISA within or among farms, eradication of the wild-type virus in the natural reservoir was not possible.

Initially, control measures in Maine consisted primarily of enhanced biosecurity, single year-class farming, and instituting somewhat arbitrary bay management zones. However, the extensive mixing of waters and close proximity of farms in the region was shown to link these salmon farms epidemiologically. Hydrographic studies demonstrated that the strong currents in the region were able to drive the exchange of water, and potentially waterborne pathogens, between as many as seven farms within a single tidal cycle in this region (Chang et al. 2005).

Epidemiological studies by Gustafson et al. (2007) indicated that new outbreaks of ISA that soon followed the institution of a control program that included depopulation and disinfection were spatiotemporally clustered, with new outbreaks on farms occurring one tidal excursion away. This finding had important repercussions for the management of ISA in the Quoddy region and differed from the management of ISA in other countries. For example, in Norway, the passive movement of virus particles in water is not nearly as important for disease spread as is the movement of potential reservoirs or vectors such as naturally occurring brown trout and sea lice.

Subsequently, the bay management zones in the Quoddy region were redrawn based on tidal excursion patterns. These changes in the shape of bay management zones, in conjunction with the biosecurity measures and single year-class farming, resulted in the elimination of clinical ISA outbreaks in the region since 2006. However, the wild-type virus continues to be detected through the ongoing ISA surveillance program.

Improved Survival of Steelhead Trout at the Dworshak National Fish Hatchery

Infectious hematopoietic necrosis virus (IHNV) is a species of single-stranded negative-sense RNA virus in the family *Rhabdoviridae*. The virus infects Pacific salmonids, primarily sockeye salmon (*Oncorhynchus nerka*), Chinook salmon (*O. tshawytscha*), and steelhead and rainbow trout (both *O. mykiss*). In these hosts, the virus typically causes acute disease in juvenile fish and asymptomatic infection in adults. Both juvenile and adult fish can transmit IHNV horizontally through water. Transmission from infected adults to progeny has also been observed via egg-associated virus, but this is greatly reduced or eliminated in fish culture facilities by egg disinfection with iodophor.

In North America, infectious hematopoietic necrosis virus occurs as three phylogenetic genogroups designated U, M, and L (Kurath et al. 2003). The IHNV field isolates from Alaska, western Canada, Puget Sound, and coastal Washington collected prior to 2007 are in the U (upper region) genogroup while isolates from Idaho trout farms in the Hagerman Valley are in the M (middle region) genogroup. California isolates are all in the L (lower region) genogroup, which is also detected in the southern Oregon coastal region. In addition to geographic differences, there is some degree of host specificity associated with the IHNV genogroups: U genogroup viruses cause high morbidity and mortality in sockeye salmon but have little disease impact in rainbow and steelhead trout; M genogroup viruses cause high levels of mortality in rainbow and steelhead trout but not sockeye salmon; and L genogroup viruses cause mortality in Chinook salmon (Garver et al. 2006; Kelley et al. 2007). This host specificity is not absolute, and all three primary host species (as well as other more refractory species) can be infected by virus isolates from each genogroup.

The steelhead program at the U.S. Fish & Wildlife Service's Dworshak National Fish Hatchery has an annual production goal of 2 to 2.5 million steelhead smolts but has suffered significant mortality from IHNV in young fish for decades. The worst such case in recent years was in 2009 when 50% of juvenile steelhead died from IHNV infections, costing the program more than $1.5 million in lost investment alone, not counting the additional and very substantial value of the future adults to tribal or sport fisheries.

Researchers at the U.S. Geological Survey Western Fisheries Research Center (WFRC) performed genetic analysis on more than 200 isolates of IHNV from the region to demonstrate that the IHNV isolates causing losses in young steelhead trout originated from infected adults upstream of the hatchery water supply (Breyta et al. 2016). The genetic data was sufficiently compelling that Dworshak staff, together with the Army Corp of Engineers, undertook a multimillion-dollar redesign of a portion of the hatchery water system to obtain water from above Dworshak Dam that did not contain adult steelhead. In the four years since the redesign, no significant IHNV mortality has occurred in Dworshak steelhead, allowing the facility to regularly meet production goals and leading to significantly increased economic impacts.

ELISA-Based Management of Bacterial Kidney Disease in Salmon

Bacterial kidney disease caused by *Renibacterium salmoninarum* is an important disease in salmonid species worldwide and has been implicated in declines of adult Pacific salmon returns in the Pacific Northwest, including threatened and endangered populations of Chinook salmon in the Columbia River Basin. The causative agent of BKD can be transmitted both horizontally (fish to fish) and vertically (from female parent to progeny within eggs) and is one of the most difficult bacterial fish diseases to control.

Scientists at the WFRC developed an enzyme-linked immunosorbent assay (ELISA) for detection of BKD-specific proteins produced during infection (Pascho and Mulcahy 1987). Transfer of the technology to staff at the fish disease diagnostic laboratories of federal, state, and tribal agencies in the Pacific Northwest has led to extensive use of the ELISA for screening spawning female salmon for BKD. Eggs of females that test positive for the highest levels of BKD are culled or segregated from the rest of the population to reduce vertical and horizontal transmission of BKD within the population.

A multiyear study implemented by the Idaho Department of Fish and Game for ELISA-based management of BKD in Chinook salmon at several agency hatcheries clearly illustrates some of the benefits that have resulted from this strategy (Munson, Elliott, and Johnson 2010):

- Prespawning mortality as well as BKD prevalence and infection intensity have significantly decreased in adult fish. For example, at Rapid River Hatchery, annual prespawning mortality was 19 to 30% prior to ELISA-based BKD management and has since declined to 3 to 8%, resulting in a significant increase in available gametes.
- Mortality of juvenile fish from BKD during hatchery rearing has significantly decreased.
- The strategy allowed reduction or elimination of antibiotic use for BKD control in hatcheries with a cost savings in excess of $100,000 per year in Idaho alone.
- The survival of returning adult Chinook salmon has increased sufficiently to allow resumption of regular tribal and sport fisheries for Chinook during their upriver migration. Prior to implementation of ELISA-based BKD management, these fisheries were rarely allowed, but since 2000, tribal and sport fisheries have occurred each year, bringing millions of dollars into the nearby communities and helping to maintain traditional tribal fisheries.

Implementation of a similar program by fisheries managers in states surrounding the Great Lakes is largely credited with helping to restore the exceptionally valuable (estimated more than $2 billion annually) recreational salmon fishery following widespread losses of Chinook salmon in the lakes due to BKD during the early 1990s.

Conclusion

Natural resource managers are increasingly faced with complex management decisions that cross the boundary of social, political, and biological science. Infectious disease is one of the factors that can limit management options for improved fish production or restoration of important stocks. It will be increasingly important for managers to understand the science behind approaches that may help in the eradication or control of disease among captive populations and the subsequent benefits to both user groups and natural stocks that share their waters.

Acknowledgments

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Special Session Four.
Wildlife Governance Principles: Guidance for More Effective Wildlife Management

Opening Remarks

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Good morning, ladies and gentlemen, and welcome. My name is Dan Decker; I'm a professor in the Human Dimensions Research Unit at Cornell University and moderator for this session dedicated to the topic of wildlife governance. On behalf of the session organizers and speakers, I thank you for joining us for what we hope will be an interesting, informative, and thought-provoking set of presentations.

Those of you who have been attending North American conferences regularly for some time recognize that the themes of transforming the wildlife management institution and agency adaptation have been present in special sessions and workshops for several years. Throughout the years, the story line has evolved, from describing the sociocultural and ecological drivers of change to articulating the need for agencies to transform strategically to remain relevant and valued to considering tools and techniques available to enable change.

With the causes, need, and process tools articulated, the next step is to address the question: Change to what? The set of presentations we have lined up this morning address this question in a broad way that we hope captures your interest. There won't be any prescriptive models presented, but instead you will be offered ideas intended to provide guidance.

Our purpose during the next couple hours is to share and partially critique a recently published set of principles that promise guidance for consistent yet adaptable governance of public wildlife resources. Governance refers to the practices and procedures that determine how decisions are made and implemented and how responsibilities are exercised. We believe adoption of the governance principles you will hear about this morning will contribute to perpetually relevant and valued wildlife management.

We recognize that's a high hope. And clearly adoption of governance principles alone is not sufficient to fulfill it. But arguably, aligning governance practices of the institution with these principles may be necessary for wildlife resource trust administration to be relevant and valued by society.

Here's what we have in store for you. Starting with a brief review of the evolving context for wildlife management in the U.S., 10 wildlife governance principles will be described that might guide the evolution of effective wildlife conservation in current and anticipated circumstances. These principles are derived from the combination of public trust thinking and good governance norms. The presentations will describe why and how the wildlife governance principles were developed. They will explain how applications of these principles help government agencies fulfill their public trust obligations. The speakers collectively argue that the principles offer the wildlife management institution a framework for considering stakeholder-engagement behaviors and decision-making processes that will result in better informed and consistent governance of public trust wildlife. Furthermore, applying governance practices that align with the principles is expected to elevate the importance of wildlife management among all public trust beneficiaries—all citizens.

Taken together, our speakers will provide practical considerations for successful application of the wildlife governance principles by a state agency and its partners. They'll also identify limitations to applying the principles and share ideas about how limitations might be overcome.

As leaders and key players in the wildlife management institution, we know you have already thought a great deal about the ideas presented in the session, but you might not have seen or heard the ideas organized in one place as a set of principles. In any event, we hope the session will contribute to your thinking about how best to lead the institution into the future. We sincerely hope the session and any subsequent conversations about it will be useful to you.

I want to thank session co-chairs Ann Forstchen (Florida Fish and Wildlife Conservation Commission) and Chris Smith (Wildlife Management Institute) for their efforts in organizing this session. I also want to thank our speakers, who in aggregate reflect key sectors in the wildlife management institution. They represent state and federal wildlife agencies as well as the NGO (nongovernmental organization) and academic communities. And of course, we are indebted to the Wildlife Management Institute for providing this venue for sharing ideas about wildlife conservation and management.

Genesis of Wildlife Governance Principles: Need and Response

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Darragh Hare
Cornell University
Ithaca, New York

Introduction

The history of modern wildlife conservation in the United States includes many accomplishments. Nevertheless, and with no disrespect intended regarding those accomplishments, our wildlife heritage on the whole is being depleted. There are many reasons for this situation. Among them is the historically narrow approach to governance of public trust resources applied by state and federal wildlife management agencies, focusing much of their attention on harvested, "pest," and high-profile imperiled species. Once unquestioned because the articulated needs of active stakeholders in wildlife management were largely met, this set of foci is now broadly recognized as inadequate given current ecological and sociocultural conditions vis-a-vis wildlife, including contemporary public expectations for wildlife management performance in particular situations and for overall governance of wildlife resources (Decker et al. 2016; Jacobson et al. 2010; Treves et al. 2016).

Tectonics of Institutional Change

Many events in the 1960s and 1970s signaled the changing stance of Americans toward management of all wildlife (not just species valued for hunting and trapping) as public trust assets and a change in how wildlife might fit in the national policy agenda (e.g., publication of *Silent Spring* (1962), Earth Day (1970), Clean Water Act (1972), and Endangered Species Act (1973)). In 1980, the Fish and Wildlife Conservation Act ("Nongame Act") authorized financial and technical assistance to the states for the development, revision, and implementation of conservation plans and programs for nongame fish and wildlife. With growing public interest in the environment generally, many wildlife management agencies realized that people in addition to their traditional user groups were interested in a broader set of wildlife species and management contexts. National surveys sponsored by the U.S. Fish & Wildlife Service since 1980 have repeatedly confirmed the magnitude of nonconsumptive wildlife interests. Concurrently, environmentally focused groups were growing in number and in political activity, many expecting greater voice in the wildlife conservation institution (Tarlock 1992).

Changes in the distribution of the human population and resulting wildlife habitat modifications at local and landscape scales, together with changes in the distribution of several wildlife species, have resulted in conflictual human-wildlife interactions where many people do not have the knowledge or capacity to handle problems with wildlife on their own. These people have increasingly turned to government to reduce or mitigate negative impacts of human-wildlife coexistence. Additionally, the decline of some species of wildlife, greater abundance and distribution of others (e.g., expansion of ungulate and large carnivore populations), and impacts from nonnative species have led to increased public expectations for wildlife to be managed by federal, state, and local governments. Wildlife governance has responded but not quickly or in a consistent and directed manner across the wildlife institution in the U.S. Governance refers to practices and procedures that determine how decisions are made and implemented (Decker et al. 2016).

In the 1970s, a new discipline in support of wildlife management emerged, which has become known as the human dimensions of wildlife management. Focusing initially on social science research to understand “client” opinions and attitudes, its scope broadened during the 1980s, with several state and federal agencies seeking to better understand a wider suite of stakeholder interests. Human dimensions inquiry came to include: identifying and mitigating negative human-wildlife interactions in a variety of contexts; improving stakeholder engagement for wildlife governance, especially at the local community level; understanding risk perceptions regarding wildlife-associated disease (e.g., Lyme disease) and large carnivores in close proximity to humans (e.g., bears and mountain lions); and advocacy for rare or imperiled species (Decker et al. 1996). As some state agencies faced the need to be responsive to new problems in new areas, they employed social science to understand the interests, needs, and management preferences of the broader suite of stakeholders. From shaky beginnings, social science applied to wildlife management has become more widely used and sophisticated.

In addition to the rising application of social science to inform wildlife decision-making, public input in wildlife governance has expanded in recent decades. Since the 1990s, stakeholder involvement has broadened from traditional stakeholders (such as hunters, trappers, and anglers) providing input to decision makers to public wildlife agencies engaging diverse stakeholders more directly in wildlife management decision-making processes. Although often portrayed as a recent phenomenon, diverse stakeholder interests in wildlife conservation and management have existed for as long as the wildlife conservation movement has existed in the U.S. Citizens with interests other than a desire to harvest wildlife have been organized and seeking a voice in wildlife management for a long time. These diverse values are evident in the 100-year history of national parks protecting wildlife and providing for nonconsumptive uses as well as the network of national wildlife refuges ensuring, among other things, that wildlife are available for harvest. What is relatively new is the increasing attention being given to nonconsumptive interests during the last two to three decades by public wildlife professionals. But change in wildlife management like most other institutions comes slowly. These interests continue to seek fair consideration in wildlife decision-making because acceptable and consistent responses from the wildlife institution to diverse interests is still lacking, stifled by outdated institutional cultures and rigid organizational structures and procedures and captured by traditional allegiances with stakeholders who have invested heavily in financial, political, and other support of the institution.

Institutional Change is Inevitable and Necessary

Arguments for reform of the wildlife institution that enable it to address broad stakeholder interests more effectively have been presented in previous North American Wildlife and Natural Resources conferences and professional journals (Jacobson, Decker, and Carpenter 2007; Jacobson et al. 2010; Forstchen and Decker 2014; Forstchen and Wiley 2015). Arguably, recognition of the need for change has been achieved throughout most, if not all, major components of the wildlife institution. Tools for change (techniques and practices) have been enumerated (e.g., Decker, Jacobson, and Organ 2011), and cases demonstrating their application have been expounded upon in special sessions or workshops at the 2012, 2013, 2014, and 2015 North American Wildlife and Natural Resources conferences (Decker, Jacobson, and Organ 2011). Yet strategic, institution-wide change has been elusive. What seems to have been missing is consensus around an answer to the question: Change to what? Certainly the answer is not a simple prescription or a cookie-cutter model with step-by-step instructions for overhaul of the current model. Sociocultural and ecological variations between state jurisdictions will prevent such an approach from working. Given the central role of state wildlife agencies in our wildlife institution, a vision of the traits and practices of a wildlife institution led by state wildlife agencies that are sensitive to the diverse needs and interests of stakeholders is a possible answer to: Change to what? One way to express such a vision is through a set of wildlife governance principles that reflect the public trust thinking (PTT) that has evolved through the ages and the more contemporary norms of good governance aspired to by liberal democracies worldwide.

A PTT orientation emphasizes the role of government in ensuring that natural resources are managed for the benefit of current citizens and conserved for future generations of citizens without privileging any particular individuals or groups (Hare and Blossey 2014). Key concepts of public trust thinking include:

- natural resources are an endowment that must be stewarded to sustain benefits for current and future generations;
- certain natural resources are not suited to exclusive private ownership;
- all citizens deserve fair consideration in allocation of benefits from the trust;
- current decisions should avoid foreclosing future options;
- trust administrators (agency staff and their elected/appointed commissioners or board) must be transparent and fulfill their duty; and
- citizens (beneficiaries of the trust) are entitled and obligated to hold trustees accountable (Hare and Blossey 2014).

While emphasizing the role of government, beneficiaries are crucial to PTT. Beneficiaries can communicate their interests (values, needs, preferences) through direct dialogue with trust administrators. Social science research is also required to understand how the interests of beneficiaries who participate in such dialogue compare with the interests of beneficiaries who do not. Since trustees are required to give equitable consideration to the interests of all beneficiaries, they cannot base decisions solely on the most readily available information but must actively seek a more complete understanding of the interests of all beneficiaries.

Good governance (GG) is a more modern development and reflects the expectations of citizens in liberal democracies regarding the roles and relationships of government to those governed. Among the most important elements of good governance are transparency and accountability, equity and inclusiveness, efficiency and effectiveness, responsiveness, and participation (Lockwood et al. 2010). PTT and GG respond to the growing attention to public trusteeship of wildlife (Jacobson et al. 2010; Smith 2011; Decker et al. 2014a; Hare and Blossey 2014; Wood 2014).

The dialogue around transformation of wildlife management during the past 10 to 12 years indicates that some parts of the institution (i.e., customs, practices, organizations and agencies, policies and laws with respect to wildlife) have been evolving to more fully embrace elements of PTT and GG (Jacobson et al. 2010; Decker, Jacobson, and Organ 2011). However, that evolution has not been uniform across all state wildlife agencies, and it has been insufficient overall. Movement from governance practices privileging narrow special interests towards broader, more inclusive GG has not been strategic (i.e., collectively planned by the consortium of key organizations, then widely adopted and evenly applied). The institution has been urged to adopt changes that will better position it to remain relevant to and, more importantly, valued by a larger, broader segment of the public (Forstchen and Decker 2014). Being strategic is key to avoiding the vagaries of being buffeted by external pressures (Jacobson and Decker 2008). For some time now, most agency leaders have not doubted the need to change governance of wildlife resources and recognize the tools needed for such change to occur, but the persistent question has been: Change to what?

It is essential that agencies are *adaptable*, given the diversity and ever-changing priority of interests in wildlife (Decker et al. 1996; Riley et al. 2002; Jacobson et al. 2010; Decker, Jacobson, and Organ 2011; Forstchen and Decker 2014). Since rigid rules are not in order, what is? We propose that an answer is the adoption of high-level guidance that is consistently applied at all levels of the institution. A set of principles that reflect the contemporary expectations for PTT and GG could provide such guidance.

Wildlife Governance Principles

To summarize: the wildlife institution urgently needs to adopt a more effective, strategic approach to address contemporary social values relative to wildlife and changes in land use and ecological conditions (Jacobson et al. 2007, 2010; Decker, Jacobson, and Organ 2011). Such an approach must be grounded in principles that encompass roles and responsibilities of all players in the wildlife institution: trustees (elected and appointed officials), trust managers (conservation professionals in state and federal government), nongovernment entities (such as for-profit organizations and nonprofit organizations), and beneficiaries (all members of the public) (Smith 2011; Wood 2014). A set of 10 wildlife governance principles (WGPs), proposed by Decker et al. (2016) are intended to integrate the key ideas of PTT and GG (Hare and Blossey 2014; Lockwood et al. 2010). The WGPs are specific enough to give general guidance and general enough to accommodate the inherent variability of state-level conditions and governance possibilities and constraints.

The WGPs arose from a group of wildlife practitioners and scholars who have been thinking about the need for and designing activities to help state agencies better understand the full spectrum of stakeholders in fish and wildlife management and modernize their management processes to improve the delivery of benefits from the wildlife trust. During the past decade, their thinking was informed through interactions with researchers and managers at federal and state wildlife management agencies, academics, professionals in nongovernmental organizations, legal scholars, and many more. Multiple workshops at state agencies, sessions at national conferences, and a workshop focused on public trust policy and practical applications of public trust thinking helped them coalesce a set of high-level principles for ecologically and socially responsible wildlife conservation.

The WGPs should not be surprising to those within the institution, and most agencies can point to many practices that align with the WGPs. However, it is also likely, in some situations, some WGPs are "common sense but not common practice" (consistently, broadly, and adequately applied).

1. **Wildlife governance will be adaptable and responsive to citizens' current needs and interests, while also being forward-looking to conserve options of future generations.** Wildlife decisions will consider future scenarios and allow for adaptation to social and ecological change. Options must be retained for future citizens whose values, interests, and needs are unknown, while addressing expectations of current beneficiaries (i.e., decision-making should respond to present interests without precluding future needs).

2. **Wildlife governance will seek and incorporate multiple and diverse perspectives.** Wildlife resources will be managed with consideration given to all citizens' values and interests. Attending only to the interests of narrowly focused or vocal stakeholders is inconsistent with both PTT and GG.

3. **Wildlife governance will apply social and ecological science, citizens' knowledge, and trust administrators' judgment.** Trust administrators will apply well-informed, evidence-based, sound judgment in decisions about allocation of benefits produced by wildlife resources. This will require credible, salient, and legitimate social and ecological science, local knowledge, and professional expertise, enabling conservation practitioners to effectively meet conservation goals.

4. **Wildlife governance will produce multiple, sustainable benefits for all beneficiaries.** Wildlife resources will provide sustainable ecological, aesthetic, economic, and recreational benefits. Trust administrators must allocate benefits equitably and avoid systematically privileging some beneficiaries over others.

5. **Wildlife governance will ensure that trust administrators are responsible for maintaining trust resources and allocating benefits from the trust.** Trust administrators are stewards of an

intergenerational inheritance. Responsible trust administrators must be efficient, effective, and adaptive to ensure the quantity, quality, and sustainability of wildlife resources.

6. **Wildlife governance will be publicly accessible and transparent.** A mutually respectful and productive relationship between beneficiaries and trust administrators is fundamental to wildlife governance. Transparency and broad accessibility are crucial to this relationship.

7. **Wildlife governance will ensure that trust administrators are publicly accountable.** Appropriate and accessible mechanisms must be in place to allow beneficiaries to hold trust administrators accountable.

8. **Wildlife governance will include means for citizens to become informed and engaged in decision-making.** Citizens have the responsibility to be both knowledgeable about and to participate in wildlife governance to ensure their needs are recognized; one trait is insufficient without the other. Holding wildlife trust administrators accountable requires citizens be informed and engaged.

9. **Wildlife governance will include opportunities for trust administrators to meet their obligations in partnerships with nongovernmental entities.** Efficient, effective, and adaptive trust administrators will recognize when the capacity they control or direct is inadequate for sustaining the wildlife trust. Enhancing capacity to meet trust management goals may require partnerships with other individuals and organizations including private landowners; such partners essentially become trust managers and must adhere to WGPs.

10. **Wildlife governance will facilitate collaboration and coordination across ecological, jurisdictional, and ownership boundaries.** Wildlife resources and beneficiaries' interests do not neatly fall within existing ecological, jurisdictional, and ownership boundaries. Collaboration and coordination across all types of boundaries improve the effectiveness and adaptability of wildlife governance.

Conclusion

The wildlife institution in the U.S. needs to take many actions to reduce the decline of species and habitats; key among them is to shift from operating under a framework focused predominantly on a narrow set of wildlife interests and species to a sociocultural and ecological paradigm and concomitant approach to wildlife governance that embraces the interests and participation of a broader public (Jacobson et al. 2010; Decker et al. 2014b). The WGPs highlighted in this paper and special session support the evolution of this paradigm by offering guidance on behaviors, processes, and decisions that embody PTT and GG. Alignment of organizational practices with WGPs will almost certainly result in a more focused, cohesive, and informed institution that is sensitive to sociocultural and ecological realities and can elevate the importance of wildlife conservation to all beneficiaries.

The driving force for change in the wildlife institution is the need for contemporary relevance (value *and* support) from a broad suite of stakeholders. This is essential for sustained, responsible wildlife conservation. We believe that the WGPs provide a framework for changes to institutional practices that will result in improved delivery of public trust and good governance expectations. They help guide the objectives of the institution without being prescriptive in how specific entities in the institution achieve those objectives. Practices adopted to apply WGPs will be cognizant of each organization's culture, history, and desire and capacity for improvement. In any event, the WGPs can help conservation organizations be more strategic in their responses to contemporary wildlife management challenges. Improved alignment to the WGPs is expected to result in a more focused, cohesive, and informed wildlife institution that can stop the decline of wildlife and elevate the importance of wildlife conservation to all beneficiaries.

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Public Trust Responsibilities and Wildlife Governance Principles

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Fish and wildlife agencies at federal, state, and provincial levels are directed by legal mandates in the exercise of their duties. These legal mandates effectively function as public trust responsibilities. The manner in which these responsibilities are acknowledged, prioritized, and exercised is a function of governance. We outline the nature and breadth of public trust responsibilities, and precepts of trusteeship. We evaluate barriers and shortcomings in adoption and implementation of these responsibilities. We explore the linkage between fulfilling public trust responsibilities and governance models. We describe how adoption and implementation of wildlife governance principles can overcome barriers to fulfillment of public trust responsibilities and help achieve biodiversity conservation and sustainability of wildlife interests and pursuits that are an important part of the fabric of North American natural and cultural heritage and essential for conservation.

Public Trust Responsibilities

The public trust doctrine (PTD) is the common law basis for ownership and conservation of wildlife in the United States (Sax 1970; Horner 2000; Batcheller et al. 2010). The PTD assigns wildlife ownership to state governments except for conditions whereby the Constitution directs ownership to the federal government (Geist and Organ 2004; U.S. CONST. art. IV, § 3, cl. 2.). Under trust law, wildlife resources are public property held in trust for the benefit of current and future generations of Americans by the government (Organ and Batcheller 2009). State and federal governments have statutory laws derived from this common law basis to further define trust responsibilities for wildlife resources (Bean 1983; Musgrave and Stein 1993). These legal mechanisms collectively form the foundation for the wildlife conservation and management institution in the United States.

The manner and degree to which state and federal governments fulfill their responsibilities under the PTD vary widely and comprehensive description of this situation is beyond the scope of this paper. Nevertheless, there are a number of basic responsibilities governments must meet, derived from trust law (Wood 2014; Scott 1999).

Trustee Responsibilities

Organ et al. (2014) summarized trustee responsibilities as:

- Prudence: careful management; exercise of good judgement
- Risk aversion: conservative management; economically responsible decision-making
- Loyalty to beneficiaries: avoidance of favoritism and conflict of interest; fairness and equitability
- Corpus protection: balancing current benefits against the sustainability of trust resources
- Application of expertise: use of special skills and knowledge relative to trust resources in decisions
- Adaptability: information on trust status and beneficiaries' interests should be regularly updated to allow for adjustments in objectives and actions

We describe each of these in the context of a trustee exercising them in the governance of trust resources.

Prudence

Uncertainty to varying degrees is inherent in natural resource decision-making (Conroy and Peterson 2013). Prudence is required of trustees in exercising decisions because the consequences of poor decisions will be borne by the intended beneficiaries. Scott (1999) observes that both case and statutory law require trustees to manifest the care, skill, prudence, and diligence of an ordinary, prudent man. This requires care in the management of assets and sound judgement regarding the certainty of intended results. For example, a decision regarding approval or denial of a land and water development project could potentially have unintended consequences leading to a species extinction—a permanent loss to society. Similarly, decisions on allocation of harvest in the short term could potentially deprive future generations of equal opportunities. Therefore, trustees must exercise prudence so as to assure trust resources are maintained and benefits can be allocated indefinitely.

Risk Aversion

Trustees are required to make decisions regarding assets for the benefit of others. Trust law stipulates that decisions trustees make for others need to exercise greater risk aversion than those they make for themselves (Scott 1999). Trustees should exercise the precautionary principle in decision-making to guard against unintended consequences of management actions taken under uncertainty (Perrings 1991). Economic principles hold that diversifying investments acts as security against risk (Gupta and Sapienza 1992). Wildlife trustees are advised to invest broadly in management actions to conserve biological diversity so that a robust portfolio of wildlife resources will guard against vulnerability associated with dysfunctional ecosystems (Rodiek and DelGuidice 1994). The exercise of risk aversion is essential to fulfillment of a trustee's responsibility to maintaining trust resources.

Loyalty to Beneficiaries

Loyalty to all beneficiaries and avoidance of both favoritism towards particular beneficiaries and actions that may constitute conflicts of interest is considered a standard for trustees (Horner 2000). For example, the constitution of Louisiana requires conservation and management decisions to be "fair and equitable to all people of the State and implemented in such a manner that no individual, corporation, or other entity acquires an excessive share of such rights and privileges" (Horner 2000). Fortman (1990) describes three theories on trustee-beneficiary relationships (agency-client relations) that illustrate how favoritism and conflict of interest can be cultivated in a trustee. Capture theory suggests the trustees come to identify with a homogeneous constituency and abandon their proper impartial role and adopt the views of the special interest. Cooptation theory is a process where the trustees manipulate the institutional environment to their advantage. This can occur when the trustees, in attempting to appease hostile interests and avoid conflict, establish relations with interests that result in the trustees being manipulated. Whereas capture theory connotes takeover, cooptation connotes trade-offs. Trustee obligations to the coopted beneficiaries may inhibit new beneficiaries being recognized. Agency resource theory suggests that trustee power is based on both the expertise and resources held and the ability to mobilize support. Trustees would cultivate beneficiaries they could mobilize for support to protect or expand their power base when needed. This would suggest that the willingness to embrace a broader suite of beneficiaries depends on the instrumental value of those beneficiaries to the trustees (Clarke and McCool 1985). Any of these scenarios violates the inherent responsibility of the trustee to show loyalty, fairness, and equitability towards all beneficiaries and avoid conflict of interest.

Corpus Protection

Trustees are expected to seek the most balanced means of both protecting the trust and providing benefits from it (Scott 1999). However, gains in a trust are not valued to the same extent that losses are disdained. This asymmetrical standard establishes the main goal of trusteeship to be the protection of the corpus of the trust (Sagarin and Turnipseed 2012). Further, trust law requires profits derived from a corpus to be reinvested and current beneficiaries entitled only to dividends (Scott 1999). If we consider wildlife trust resources to be intergenerational—that is, to be conserved for the benefit of current and future generations—it follows that investment and distribution of trust assets would be approached with utmost conservatism. The responsibility of the trustee is, then, to take every precaution to ensure the corpus of the trust is protected and not squandered.

Application of Expertise

Trustees with greater knowledge or skill have a duty to apply it in their trust responsibilities (Bogert 1987). Scott (1999) cites several state laws that explicitly require trustees to use special skills or expertise they hold. Trustees can be held liable for losses if they are found to be negligent in applying those skills. Both skilled and regular trustees are advised to solicit expert advice and take precautions to assure that advice is sound (Bogert and Bogert 1993). Wildlife trustees, in adhering to this standard, would be expected to seek information from professional agency staff, and from a variety of experts when warranted, and consider multiple perspectives. This would likely necessitate the integration of both ecological and social science in decision-making. Trustee responsibility also includes accountability for actions (Scott 1999).

Adaptability

Sax (1970) identified adaptability to contemporary concerns as one of the key elements necessary for a public trust to be effective. Adaptability in trust management requires knowledge of the corpus and the trends, threats, and future scenarios associated with it, as well as knowledge of the needs and desires of the beneficiaries and dynamics associated with the breadth, scope, and nature of the beneficiaries. Trustee responsibility then would include not only seeking information from experts but also providing transparency in decision-making and opportunity for beneficiaries to become engaged in the process. Decker et al. (2015) identify a potential conflict between the need to engage beneficiaries in decision-making and the need for trustees to keep beneficiaries at arm's length in order to avoid inappropriate influence. They offer a number of recommendations, including providing beneficiaries information about decision-making processes so they can more effectively participate, and ensure accountability measures are evident and available to beneficiaries in case they have grievances with the trustees. Trustee responsibility is to assure decision-making processes are readily available to the public, the implementation and results of the processes are transparent, and beneficiaries have opportunity for observation and engagement.

Do Wildlife Governance Principles Reflect Trustee Responsibilities?

Decker et al. (2016) proposed wildlife governance principles (WGPs) for ecologically and socially responsible wildlife conservation. Do these align with the trustee responsibilities outlined by Organ et al. (2014)? Figure 1 depicts the direct interrelationships between WGPs and trustee responsibilities.

WGP1—adaptability and responsiveness—involves the current needs and interests of all citizens, as well as conserving options for future generations. This relates directly to trustee responsibilities to be loyal to beneficiaries and avoid favoritism and conflicts of interest; protecting the corpus of the trust for sustainability; and adjusting actions and objectives to reflect beneficiaries' interests.

WGP2—incorporating multiple and diverse perspectives—relates directly to trustee responsibilities to be adaptable and to apply expertise. Adaptability requires the trustee to gather information on trust status and beneficiary interests and adjust objective and actions if warranted. Applying expertise requires the trustee to utilize any special skills he or she has, or to seek outside expertise, in order to ensure the best knowledge is brought forth in decision-making.

WGP3—applying social and ecological science—involves using the best science in combination with citizen knowledge and trustee judgment in decision-making. This relates directly to the trustee responsibility to apply expertise in making decisions.

WGP4—produce multiple, sustainable benefits for all beneficiaries—relates directly to trustee responsibilities to be loyal to beneficiaries and adaptable to trust status and beneficiary needs.

WGP5—responsibility for maintaining trust resources and allocating benefits—relates directly to trustee responsibilities to exercise prudence, avoid risk, and protect the corpus of the trust. These essentially hold the trustee responsible for exercising good judgment in the careful management of trust resources so as to make economically responsible decisions that protect the corpus.

WGP6—accessibility and transparency—relates directly to trustee responsibility to be loyal to beneficiaries. Being open and accessible to the public is essential to avoiding conflicts of interest and promoting fairness and equitability.

WGP7—public accountability—relates directly to trustee responsibilities to be loyal to beneficiaries and protect the corpus. If trustees violate these essential responsibilities, they must be held accountable, otherwise the public trust will not be viable (Sax 1970).

WGP8—informed and engaged citizenry—relates directly to trustee responsibility to be adaptable. Beneficiary engagement is a valuable means for trustees to understand whether or not beneficiary interests are dynamic or static.

WGP9—partnerships with nongovernmental entities—relates to trustee responsibilities to apply expertise and be prudent and adaptable. Partnering with nongovernmental entities can bring in additional expertise in terms of understanding the current and forecasted future status of the trust, as well as the interests of the beneficiaries. This can add prudence to decisions regarding adjustments in objectives and actions.

WGP10—collaboration across ecological, jurisdictional, and ownership boundaries—relates to trustee responsibilities to apply expertise and be adaptable. Similar to partnerships, collaboration across boundaries enhances the level of expertise that can be applied and provides more robust information on trust status and beneficiary interests.

Our comparison shows strong alignment of wildlife governance principles with trustee responsibilities.

Barriers to Fulfilling Public Trust Responsibilities

A number of factors can collectively become barriers to implementation of public trust responsibilities. We focus here on four of those factors and how adoption and implementation of the WGPs proposed by Decker et al. (2016) can help overcome them. These include: the scope of wildlife agency jurisdictions, agency funding, public understanding of trust-based governance, and trusteeship.

Scope of Wildlife Agency Jurisdictions

Wildlife conservation is widely recognized as involving three basic elements: wildlife populations (especially the size, structure, or distribution of populations), habitat that supports wildlife, and human interactions with wildlife and habitat. The scope of state and federal wildlife agencies' jurisdictions varies widely but generally is limited to regulatory control of at best two of these three elements: wildlife populations and direct human interactions with wildlife (Bean 1983; Musgrave and Stein 1993). Few, if any, state wildlife agencies have jurisdiction over factors that affect habitat except on lands owned or managed by the agency such as wildlife management areas. Federal agencies have somewhat more ability to affect land use, particularly on larger federal land areas in the western states and Alaska or under specific statutes such as the Endangered Species Act. However, even under these powerful federal statutes, the ability of wildlife agencies to regulate use, modification, or destruction of habitat is limited.

Given these limits in jurisdiction, state and federal wildlife agencies alone cannot fulfill the government's public trust responsibilities. They must influence decisions of others who exercise control over land use or other factors that affect habitat. WGP8 calls for an informed and engaged citizenry, and WGP7 calls for trustees to be publicly accountable. By increasing public understanding of the PTD, including the trust responsibilities of elected and appointed officials at all levels of government, agencies can increase the potential that trustees will be held accountable by voters when making decisions that can impact the corpus of the trust. WGP9 calls for trustees to meet their obligations in collaboration with others, and WGP10 calls for conservation to work across ecological, jurisdictional, and ownership boundaries. These WGPs foster the type of landscape-scale, cooperative conservation required to meet today's challenges (NASEM, in press).

Agency Funding

Jacobson et al. (2010) identified dependency on a narrow funding base as a barrier to some state agencies' ability to embrace a broader suite of stakeholders and expand programs to a more diverse suite of programs and interests as required by the PTD. They found that those state agencies that had implemented programs designed to meet needs and interests of nontraditional stakeholders in spite of initially narrow funding were ultimately more successful in securing expanded funding. In other states, however, efforts to broaden programs or stakeholder participation led to a political backlash that further constrained the agency (Moore 2014).

Federal agencies are mainly funded from the national treasury and do not face the same perceived obligation to specific interests that state agencies do. However, federal wildlife agencies must compete with other obligations of the federal government including defense spending and entitlement programs that consume a significant portion of the federal budget. Thus, both the nature and amount of funding constrain the ability of state and federal agencies to fulfill their PTD responsibilities.

By seeking and incorporating multiple diverse perspectives and producing multiple, sustainable benefits for all beneficiaries as called for in WGPs 2 and 4, agencies can broaden public recognition for the value of the work they do. This will likely increase public support for broader funding. Agencies can also use the mandates to engage and serve all beneficiaries in WGPs 2, 4, 6, and 8 to counter arguments against expanding funding sources for state agencies out of misplaced perception that agencies are beholden to those interests that fund them.

Public Understanding of Trust-Based Governance

Smith (1980) identified the need for the public to be aware of their rights relative to public ownership of resources in order for public trust to become an effective tool. Organ and Batcheller (2010) further suggest that agencies should strive to link programs they provide to ecosystem services that benefit a broad spectrum of society. This would ensure ongoing relevancy of agencies to all beneficiaries.

Smith (2011) emphasized that more effective application of trust-based governance is critical to the future of wildlife conservation and management. Key to this is understanding roles and responsibilities in trusteeship. The WGPs that promote broader information gathering, information sharing, and public engagement all contribute to greater understanding of public trust responsibilities. WGP7 works to ensure that trustees—the elected or appointed governing officials, not just wildlife agencies—understand and apply their responsibilities broadly, equitably, and inclusively with information and input by trust managers and stakeholders.

In many jurisdictions, guidelines prescribe trustee appointments along narrow or special interest parameters (Nie 2004). This may lead both the public and trustees, themselves, to believe those interests deserve special consideration in administration of the trust. WGPs 1 through 8 make clear the obligation of trustees to treat all beneficiaries equitably.

Trusteeship

Jacobson et al. (2010) stressed that separation of essential components of trust oversight from political process was necessary for trust-based governance that strictly adhered to care of the trust's assets, not those associated with external interests. Organ and Fritzell (2000) and the Wildlife Management Institute (1987, 1997) showed that trends in state fish and wildlife agencies are moving towards less autonomy in decision-making and greater partisan political influence and control. As with the barrier of public understanding of trust-based governance, the WGPs that foster broader public engagement in decision-making, consideration of the needs of all beneficiaries, and accountability of trust administrators can be an effective counter to the trend toward increased politicization.

Conclusions

Adoption of WGPs would establish a desired framework for execution of trustee responsibilities. This, in turn, would help place focus on addressing barriers to fulfillment of trustee responsibilities. The scope of agency jurisdiction would be clarified, and this could help mobilize efforts to address other barriers. Broad-based funding initiatives would be aided by assurances that all citizens are indeed beneficiaries and will receive dividends from the trust. Active public engagement would lead to greater public understanding of trustee responsibilities and the limitations of funding and decision space. A broader beneficiary base can hinder interference in execution of trustee responsibilities by narrow political or special interests. Adoption of WGPs will help assure an enduring trustee-beneficiary relationship that conserves wildlife resources for posterity.

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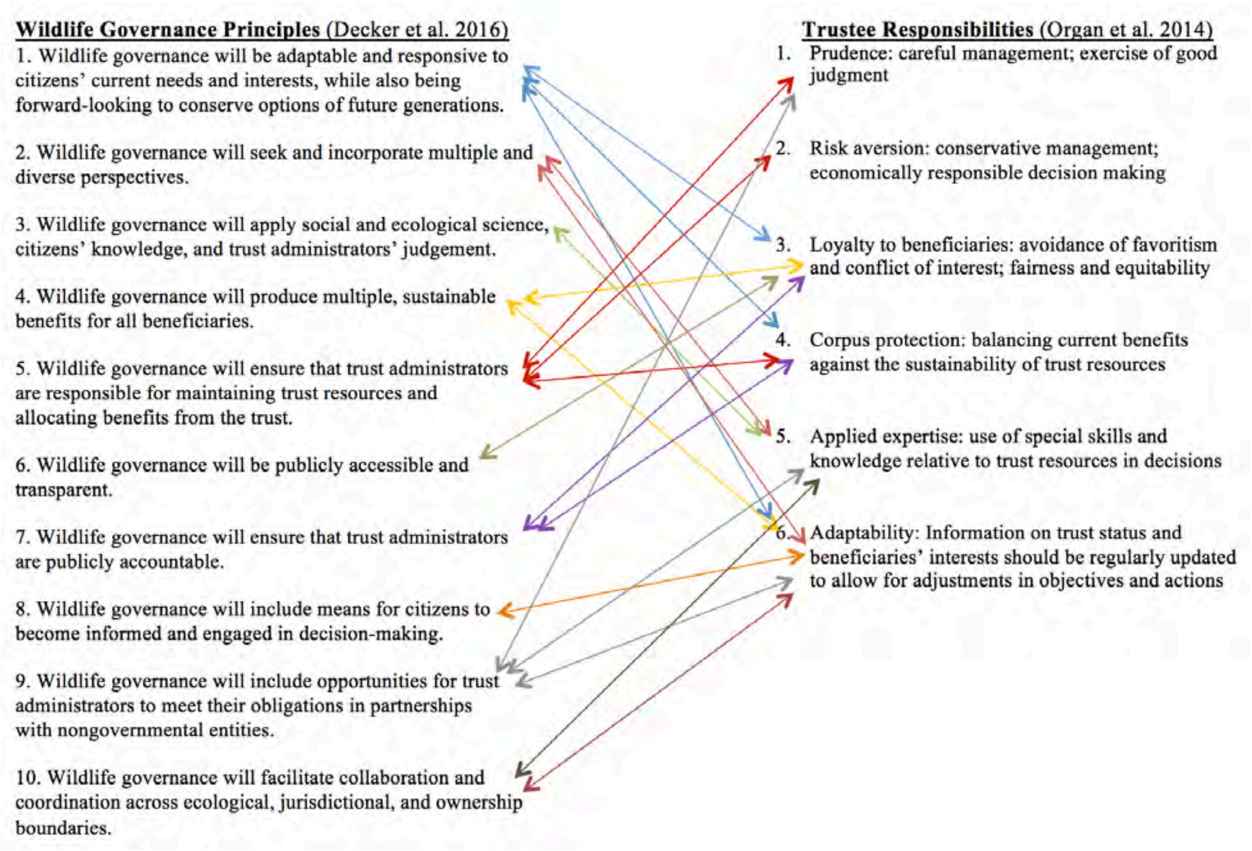
Figure 1. Interrelationship of wildlife governance principles to trustee responsibilities.



Wildlife Governance Principles (Decker et al. 2016)

1. Wildlife governance will be adaptable and responsive to citizens' current needs and interests, while also being forward-looking to conserve options of future generations.
2. Wildlife governance will seek and incorporate multiple and diverse perspectives.
3. Wildlife governance will apply social and ecological science, citizens' knowledge, and trust administrators' judgement.
4. Wildlife governance will produce multiple, sustainable benefits for all beneficiaries.
5. Wildlife governance will ensure that trust administrators are responsible for maintaining trust resources and allocating benefits from the trust.
6. Wildlife governance will be publicly accessible and transparent.
7. Wildlife governance will ensure that trust administrators are publicly accountable.
8. Wildlife governance will include means for citizens to become informed and engaged in decision-making.
9. Wildlife governance will include opportunities for trust administrators to meet their obligations in partnerships with nongovernmental entities.
10. Wildlife governance will facilitate collaboration and coordination across ecological, jurisdictional, and ownership boundaries.

Trustee Responsibilities (Organ et al. 2014)

1. Prudence: careful management; exercise of good judgment
2. Risk aversion: conservative management; economically responsible decision making
3. Loyalty to beneficiaries: avoidance of favoritism and conflict of interest; fairness and equitability
4. Corpus protection: balancing current benefits against the sustainability of trust resources
5. Applied expertise: use of special skills and knowledge relative to trust resources in decisions
6. Adaptability: Information on trust status and beneficiaries' interests should be regularly updated to allow for adjustments in objectives and actions

Applying Wildlife Governance Principles: Opportunities and Limitations

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Introduction

The wildlife governance principles (WGPs) recently articulated by Decker et al. (2016) combine deeply held ideals and a vision for reinvigorating and modernizing wildlife conservation and management in North America. Rooted in the recognition that wildlife is a public resource, WGPs emphasize the legal obligations of trustees (elected and appointed officials) and trust managers (public wildlife professionals), collectively referred to as trust administrators, and the centrality of public wildlife agencies in leading and coordinating wildlife conservation (Blumm and Paulsen 2013; Hare and Blossey 2014; Smith 2011). WGPs recognize the important conservation activities of nongovernmental entities and see partnerships across sectors and scales as essential to achieving comprehensive conservation success. One of the most important dimensions of WGPs, therefore, is a vision for harmonizing wildlife conservation activities, uniting the goals and efforts of public wildlife agencies, individual landowners, nonprofit organizations, and for-profit organizations. Successfully embracing WGPs will require a significant shift in how conservation in the U.S. is directed and coordinated and will likely involve a difficult period of transition as the institution adjusts (Decker et al. 2016). WGPs are intended to support the work of wildlife professionals and policymakers, but as with any set of norms for guiding an institution or professional endeavor, application of WGPs will likely take advantage of some opportunities, as well as surface limitations of the wildlife institution (i.e., all customs, practices, organizations and agencies, policies, and laws with respect to wildlife).

Opportunities for implementing WGPs abound. WGPs promote collaborative partnerships, which in many places already exist. Application of WGPs can occur through formal recognition of the important roles partnerships play including the ability to address issues that transcend jurisdictions, integrate diverse perspectives, transfer knowledge across disciplines and sectors, and increase accountability to beneficiaries (all members of the public and future generations). These opportunities allow for alignment and mobilization of resources to address critical challenges now and in the future.

Efforts to implement WGPs can also be expected to reveal limitations. These include uncertainty regarding roles, lack of trust, or historic disputes over jurisdiction between partners; administrative and bureaucratic barriers to sharing or reallocation of resources; historic allegiances to particular interests; opaque decision-making; and reluctance to engage in partnerships. Although such limitations may constrain implementation, they should not be viewed as rationale for rejection of WGPs.

We explore opportunities and limitations and describe how collaborative relationships between trust administrators and others can help all participants in the institution. We provide case studies from state wildlife agency and nongovernmental organization (NGO) perspectives that elucidate the need for WGPs and how practices consistent with WGPs can engender conservation success.

Opportunities for Application of Wildlife Governance Principles

Application of WGPs provides opportunities to engage in new practices and enhance relationships with all beneficiaries. Trust administrators are currently limited in their ability to meet biological and social demands. Depending on the specific situation, they may lack capacity, relevancy and credibility, and internal and external support (Decker et al. 2013). Partnerships among various governmental and nongovernmental entities will catalyze collaborations that could help overcome these limitations. Such partnerships already exist but, as evidenced by the case studies, are not guaranteed to work smoothly. WGPs could guide, enable, and facilitate partnership consistently throughout the wildlife institution to improve conservation. Moreover, closer alignment with WGPs will likely increase formal or informal support of management decisions by beneficiaries.

Promote Collaborative Opportunities

Formal and informal partnerships between the public sector and nongovernmental entities such as academic institutions, business, industry, and nonprofit organizations can enable the wildlife institution to better address increasingly common "wicked" conservation challenges (Balint et al. 2011). These issues are often difficult to define and transcend jurisdictions, requiring a larger landscape perspective. Partnerships have practical applications such as efficient collection and analysis of data, leveraging of resources (e.g., people, funding), and promoting exchange of diverse expertise and ideas that reflect an array of interests and can achieve broader public support and enhanced credibility. Collaboration does not mean that trust administrators abdicate their public trust responsibilities; adherence to WGPs by all partners will allow them to better fulfill those responsibilities.

Transcend Jurisdictions

No single entity has the authority or resources to effectively abate stressors such as climate change or the impact of human development on the landscape (National Academy of Sciences, Engineering, and Medicine). Collaboration that transcends jurisdictional boundaries and leverages the combined resources of public and private parties is essential to fulfilling public trust responsibilities (Decker et al. 2016). Partnerships more formally established through application of WGPs will have wider geographic reach that crosses town, state, and in some cases national boundaries. By calling for government to meet its obligations in partnership with nongovernmental entities, WGPs offer guidance for more integrated and effective conservation across multiple jurisdictions.

Integrate Diverse Perspectives

WGPs challenge the institution to incorporate diverse perspectives at multiple levels, creating opportunities for beneficiaries to provide input, and for public wildlife agencies to engage a broad audience. Integrating diverse viewpoints and values into planning and decision-making will ultimately augment trust administrators' ability to achieve meaningful conservation (Wondolleck and Yaffee 2000). Beyond opportunities for public input, integration of diverse perspectives includes hiring staff from different economic and social backgrounds representing many types and users of wildlife resources and partnering with organizations exhibiting diverse viewpoints, experience, and expertise. Augmenting capacity through partnerships (rather than hiring new staff) may be an effective and realistic strategy given decreasing budgets and periodic hiring freezes for state and federal agencies. Collaboration between agencies and traditional and nontraditional partners with shared purposes could accomplish more than if partners acted alone (Wondolleck and Yaffee 2000). A sense of shared responsibility among partners will allow the wildlife institution to be future-looking, strategic, and considerate of ecological and sociocultural conditions. Partnerships consistent with WGPs recognize the important contributions that nongovernmental entities can make in public trust wildlife conservation but require that oversight and ultimate accountability remain with trust administrators. By employing an interdisciplinary approach that incorporates a wide range of ideas and values, trust administrators may be viewed as more relevant and credible than under a "traditional" management paradigm focused on a limited suite of species or interests.

Facilitate Knowledge Transfer

Collaborative conservation partnerships stimulate information sharing and transfer of knowledge, leveraging the strengths of all partners. For example, an agency may excel at "on the ground" monitoring and management but lack proficiency in social science inquiry or effective communication techniques. Partnerships facilitate evaluation of management actions and an adaptive approach to management that may not be possible with agency personnel alone (Wondolleck and Yaffee 2000).

Increase Accountability

For the institution to function effectively, trust administrators and beneficiaries must understand and fulfill their respective roles (Smith 2011; Wood 2014). Increased collaboration among these parties will stimulate discussion on delineating responsibilities and instituting accountability. By determining clear authority for trust administrators, informed and engaged beneficiaries, and transparent, inclusive decision-making processes, WGPs offer the potential to clarify roles and create mechanisms that ensure trust administrators consider the needs of all beneficiaries and allocate benefits equitably. When societal needs for wildlife management and conservation are unmet, responsibility for needed changes or adaptations will be easier to assign if WGPs are implemented consistently with clarity and transparency. Cooperative agreements can provide a mechanism for partners to hold each other accountable and to adapt, learn, and "try again." Such changes in accountability and transparency may inspire broader public participation in and benefits from wildlife governance that could also lead to more comprehensive financial, political, and public support for the institution.

Limitations for Application of Wildlife Governance Principles

While WGPs offer significant promise for increasing the effectiveness of the institution, limitations must be overcome for implementation to succeed. Limitations are rooted in patterns of behavior, historic relationships, and administrative structures that must be objectively examined and adapted to improve alignment with WGPs.

Uncertainty and Lack of Trust

Broadening the number and type of partners in wildlife conservation projects will generate uncertainty about each partner's roles and responsibilities. While it will be possible to allocate responsibilities at the outset, uncertainties could arise as projects develop and generate unforeseen challenges. This will be especially relevant in partnerships where one party is expected to share responsibility for activities it has traditionally performed alone and could manifest in a sense of loss or a distrust of partners to perform an adequate job, especially if those partners are as yet "untested." Such difficulties might abate as partners establish a history of successful collaboration and learn to trust and value one another's contributions. Nevertheless, strong leadership and guidance will be essential in the early stages to make sure that partners focus on the responsibilities they have accepted and allow others to do the same. A change in institutional mindset that sees partners not as "outsiders" but important collaborators in the larger endeavor of wildlife conservation will be essential. However, exactly which organizations and individuals can be partners is not settled. This reflects uncertainty about which public agencies and nongovernmental entities comprise "the wildlife institution." It is clear that public wildlife agencies and wildlife NGOs are members of the institution, but it is not so clear for other entities such as universities, public transportation, agriculture or planning agencies, and nonwildlife environmental NGOs. WGPs' vision for inclusive governance suggests a dynamic, flexible interpretation of the institution and potential partners—malleable according to time, location, and the specific issue at hand.

Administrative and Bureaucratic Obstacles

Requirements under WGPs, such as inclusivity, need significant dedication, mobilization, and transfer of resources (e.g., information, funding, liability) to be successfully implemented. Collaborations to acquire and use these resources to benefit conservation will need to be formalized contractually. Devising and administrating such arrangements carry costs. While public wildlife agencies and large nongovernmental organizations may be accustomed to bureaucracy and have structures and expertise to accommodate it, overcoming bureaucratic hurdles for large and small organizations will create limitations for adoption and implementation.

Effective partnerships require long-term commitments to collaboration that might be difficult to establish between organizations with little or no shared history. Sustaining commitment to partnership may also be difficult for some public wildlife agencies due to the broad nature of their responsibilities and the diversity of public demands; reacting to political, social, or ecological emergencies; and unforeseen changes in policy direction. Reacting to incidents such as human-wildlife conflicts or wildlife die-off events, as well as responding to specific issues raised by trustees or beneficiaries, often requires urgent attention and can carry significant costs. Changing priorities at higher levels of public administration can trickle down through the system, requiring adjustments to programs and priorities in the field. These are realities of public wildlife administration and are essential for agencies obligated to respond to the public even when immediate public desires do not necessarily reflect long-term needs or objectives. Nevertheless, they are sources of uncertainty and instability that could inhibit the confidence in long-term planning necessary for effective partnerships. Long-term planning could be inhibited further by the rhythms of public sector election and funding cycles.

Ties to Special Interests

State fish and wildlife agencies (SFWAs) derive a significant proportion of their revenue from consumptive wildlife activities and have close and long-established relationships with consumptive wildlife users (Nie 2004). Many NGOs rely on support from individuals with specific interests, such as certain taxa, land protection, hiking, or birding, and perform advocacy roles that are essential to the deliberative governance system envisaged by WGPs. For both agencies and NGOs, transitioning to operations more reflective of the full suite of societal interests in wildlife is essential to implementation of WGPs but will be a significant challenge (Jacobson et al. 2010).

SFWAs will need to learn not only how to incorporate the interests of individuals and groups that they have not traditionally engaged but in some cases will have to partner with them. NGOs will also have to learn to work with SFWAs whose values and activities they might previously have seen as orthogonal to their own. Learning to put differences aside and to reconcile diverse viewpoints will be important and could be facilitated by processes of collaboration, dialogue, and identification of shared goals. Nevertheless, such processes take time and could exceed planning and funding cycles. Decisions will have to be made during periods of adjustment, and how they are made will shape their quality and the feasibility of subsequent partnerships.

Opaque Decision-Making

Historically, management of wildlife resources often involved “the experts,” such as agency staff, deciding the appropriate course of action with limited external accountability regarding sources of data or decision-making processes. That is no longer the case. Increased public skepticism toward government generally and science in particular requires greater transparency and scrutiny of data used in decision-making (Pew Research Center 2015). Political pressure to know where and how limited public funds are spent and an actively litigious society also require more transparency and justification for decisions. In addition, if beneficiaries perceive that decisions are made without their input, particularly if the outcome is controversial, they could withdraw support or consent and agency credibility and effectiveness would suffer. Decision-making processes among partners within the institution may face challenges associated with sensitive data, election cycles, or the wishes of private funders, making it difficult to change. Under WGPs, transparency and accountability are incorporated into the decision-making process, not only to preclude possible litigation but also to deliver WGPs' commitment to inclusive, participatory wildlife governance. Currently the wildlife institution lacks the capacity and in many cases the expertise to clearly document and communicate such processes.

Reluctance to Engage in Partnerships

Given these obstacles, questions arise as to whether nongovernmental entities would be willing to partner with public wildlife agencies. Formally contracting with public wildlife agencies could increase oversight and accountability, for example transparency requirements such as freedom of information legislation. While these are necessary aspects of public administration and required by WGPs, they could introduce unfamiliar and perhaps unwelcome obligations in terms of data sharing and financial disclosure, generate unwanted additional work, and compromise the financial anonymity nongovernmental entities often require. Furthermore, NGOs whose priority is a single species, community, activity, or issue might see partnerships with public wildlife agencies as generating diversions from the activities that their donors willingly support. NGOs may hesitate to commit often-limited financial resources or relinquish independent choices for broader public benefit.

Relatedly, formal partnerships between public wildlife agencies and nongovernmental entities could create perceptions that blur the distinction between beneficiaries and trust administrators. Partnerships with nongovernmental entities would help increase management capacity, augmenting the activities of public wildlife agencies. Ultimate oversight and accountability would remain with trustees, but if a nongovernmental partner takes a prominent role in management, it could be perceived as having oversight of the resource. Nongovernmental partners would presumably wish to avoid the possibility of being exposed to legal challenges, and public wildlife agencies would unlikely be willing to assume full liability for the activities of partners and their employees. Further complications could arise when landowners or NGOs believe that public wildlife administrators breach their public trust obligations. Their roles as partners in public trust administration could inhibit their willingness to challenge public wildlife agencies, and their roles as beneficiaries or representatives of beneficiary interests could inhibit their willingness to enter into such partnerships in the first place. Similarly, a history of or potential for legal disputes with potential partners could dampen willingness for partnership.

Case Studies

The following case studies demonstrate the need for WGPs and how application of practices consistent with some elements of WGPs can overcome limitations related to entrenched institutional difficulties that impede conservation. In the first case, we demonstrate how transparent decision-making and interdisciplinary approaches improve accountability, but achieving inclusivity can be a challenge without dedicated resources and a commitment to WGPs. In the second, we provide an example of how a well-run collaboration can efficiently lead to clear conservation outcomes and an example of how collaboration, impeded by bureaucracy, can delay conservation action underscoring the importance of embracing WGPs to formally recognize and facilitate the role of partnerships in conservation.

Towards Transparency in Decision-Making: A State Agency Perspective

Wild turkey populations in New York State have been declining during the last 15 years causing concern among agency biologists, hunters, and the general public (NYSDEC 2015; Robinson et al. 2015). While changes in harvest regulations can address this decline, such changes must reflect the values of stakeholders to maximize acceptance of the changes and maintain agency credibility among all beneficiaries. In this situation, trust administrators sought to sustain viewing and biodiversity interests related to turkeys while also attempting to yield some benefits to turkey hunters. How to achieve this balance created a challenge. Here we demonstrate how partnership between the agency and academic institutions enabled improved transparency and accountability.

The agency faced several limitations that needed to be overcome in this decision-making process including: 1) using a transparent process that identified an optimal solution that met competing objectives; 2) focusing on identifying the problem and its component parts in a holistic manner rather than focusing solely on alternatives; and 3) uniting specialists in various fields that allowed the agency to overcome its capacity limitations and the challenges associated with understanding a complex social and biological system.

To tackle this challenge the New York State Department of Environmental Conservation (NYSDEC) partnered with the New York Cooperative Fish and Wildlife Research Unit and the Human Dimensions Research Unit at Cornell University to employ structured decision-making (SDM). SDM is a systematic framework to describe the values of stakeholders (in this case, turkey hunters) and formally evaluate the consequences of management options on these values (Keeney 1992; Robinson et al. 2015). Wildlife managers and stakeholders identify objectives to guide the decision and evaluate trade-offs among competing objectives (e.g., turkey abundance and harvest opportunity). The final goal of SDM is to help determine the optimal management alternative that best meets the objectives (Clemen 1996; Gregory et al. 2012). This approach produces an outcome that is more defensible than "top down," impulsive, or instinctual methods that lack systematic thinking and comprehensive analysis of ecological, social, and economic factors. Moreover, the transparency associated with SDM is an important trait for holding decision makers accountable, a key aspect in the application of WGPs (Decker et al. 2016).

Wildlife managers took a multidisciplinary approach to determine the optimal fall season structure that balanced turkey populations and stakeholder satisfaction. While agency staff were intimately familiar with turkey biology, trends in abundance and productivity, and harvest data, they lacked expertise in modeling turkey population response to the interactions of landscape-scale habitat and weather, population modeling, and understanding hunter values. State agency staff worked closely with social scientists, ecologists, and decision analysts from academia and the federal government to better understand the dynamic ecological and social system in which turkey populations and hunters operate, and SDM provided a systematic method for incorporating environmental parameters and stakeholder values that varied across the landscape to evaluate how successful various harvest alternatives were at satisfying each objective. The group participated in a rigorous objective-setting exercise to identify and connect the myriad of biological, social, and economic factors that influence turkey populations. This exhaustive process described a turkey management system that was much broader in scope than the decision about the fall hunting season. They identified objectives that were most salient to the decision and remained sensitive to their obligation to all beneficiaries to provide self-sustaining turkey populations for current and future generations of New Yorkers. The SDM process requires that decision makers weight each objective relative to its importance in the decision outcome. Decision makers put more weight on the fundamental objective of "turkey abundance" rather than on "hunter satisfaction," thus acting as a surrogate for a broader suite of stakeholders more interested in wildlife viewing, photography, and intrinsic wildlife values than just the hunting community. Ultimately, SDM identified an optimal season structure that reduced hunting in most of the state; however, the thorough process made the decision palatable to hunters by conspicuously incorporating their concerns and attitudes into the decision (Robinson et al. 2015).

The agency-academic partnership to employ SDM provided the context for improved transparency and accountability. Scientists and managers from multiple entities and disciplines worked together to identify the optimal fall harvest recommendation for ecologically distinct regions of New York State. By involving experts from academia and the federal government, the state agency was able to develop a more robust way to evaluate and make a management decision than it would be had it operated alone. Furthermore, the SDM process and its values-focused approach increased support for the recommended season reduction at multiple levels within the institution, from stakeholders to trust managers to trustees.

While SDM enables improved transparency and accountability in decision-making, full adoption of WGPs could yield additional opportunities. The inclusivity requirement of WGPs would incorporate multiple and diverse perspectives. In this case, the agency sought values and attitudes of fall turkey hunters through surveys and participation in the process while the agency represented the views of other stakeholders that value higher populations of turkeys. This process focused on the input and values of hunters due the specific nature of the decision outcome (i.e., selecting the optimal fall hunting season structure given competing beneficiary interests). WGPs call for decision makers to be broadly inclusive across a range of public interests; however, the need or ability to include all beneficiaries (or their representative) in all decisions is not practical, nor is it always necessary. A more inclusive approach would have included surveys of the general public or other beneficiaries such as birdwatchers who enjoy turkeys, landowners who may not enjoy turkeys visiting their yards, and even public servants like the police who may have to address community concerns about turkeys (e.g., more turkeys in roads). These groups would have also been invited to participate at the SDM deliberations. The real challenge for application of WGPs is defining what inclusivity means and mobilizing the resources to ensure inclusivity can be met.

Attempting to more closely align agency practices with WGPs highlights a drawback of the SDM approach. SDM required a significant commitment of time and resources by the state agency, trustees, and stakeholders. Stakeholders, in particular, may have preferred more immediate action but were willing to let the process play out, which is itself a testament to the value of a structured approach; however, many conservation issues require decisions be made relatively quickly, with high rates of uncertainty, under tremendous political pressure. In these cases, engaging in practices that are closely aligned with the WGPs becomes even more challenging. Not all SDM approaches need be as resource-intensive as the one described here. We suggest that having a decision framework and associated partnership network in place before a "brushfire" occurs is a mechanism by which trust managers can become more closely aligned with WGPs and buffer against the inclination to engage in purely reactive or top-down decisions.

Transfer of Resources to Facilitate Collaboration: NGO Perspective

Much of the work conducted by the Wildlife Conservation Society (WCS) occurs through partnerships and collaborative arrangements with state and federal wildlife agencies as well as other NGOs, businesses, and private landowners. However, establishing these partnerships and, in particular, facilitating the transfer of resources (e.g., funding, personnel, information/data) across the various entities involved has often led to complicated bureaucratic negotiations, increased costs for administration, confusion and frustration for individuals involved, and ultimately delays in conservation action. These challenges could be overcome under a future scenario in which WGPs are consistently applied and adhered to across the wildlife institution thus creating a more formal recognition of partnerships. For WCS collaboration is indispensable; however, efficiencies or inefficiencies in the transfer of resources can influence conservation outcomes, as illustrated by two examples below.

The Path of the Pronghorn (POP) is an example of successful collaboration and successful transfer of resources across diverse partners to achieve conservation (Berger and Cain 2014). WCS and the National Park Service conducted research on pronghorn movements around Grand Teton National Park starting in 2003, which identified an important travel corridor for pronghorn. Once the science on the migration corridor became known, many organizations and agencies joined the effort to enact the First National Migration Corridor. Among the public agencies with authority to manage wildlife, National Park Service, U.S. Fish & Wildlife Service (USFWS), U.S. Forest Service (USFS), and Wyoming Game and Fish Department (WGFD) provided resources to WCS in the form of permission to conduct research (animal capture permits) and logistical support. In this case, WCS had outside support from a foundation, so the transfer of funds occurred only from WCS to WGFD for the installation of signage to promote POP. Importantly, public agencies were willing recipients of the data, analyses, and findings of an NGO (i.e., a transfer of knowledge) and were willing to use the science to influence decisions that resulted in protection of the corridor. These groups, along with a myriad of other federal agencies, NGOs, private businesses, and local governments, worked with the Wyoming governor's office on communicating a unified request for protection of the corridor. Ultimately, the USFS established the first federally protected migration corridor as an amendment to Bridger-Teton National Forest Plan (ENS 2008).

Just as successful transfer of resources can lead to strong conservation outcomes, unsuccessful transfer of resources can create problematic delays for NGOs operating on smaller budgets with fewer staff. In the case of POP, science to on-the-ground action happened in five years (2003 to 2008). By comparison, some contracting processes that arrange for the transfer of financial or other resources can take more than half of that time just to be executed.

In May 2014, the USFWS awarded the California Division of Fish and Wildlife (CDFW) a state wildlife grant to examine the effects of recreation on sensitive wildlife species in the Natural Community Conservation Planning reserve system in San Diego County. CDFW lacked the resources to accomplish this work internally, so turned to a university and WCS (a subcontractor to the university). Contract negotiations between the state agency and the university broke down over legal issues and CDFW was unable to work directly with WCS, leading to a protracted contracting process that has delayed the start of the project by more than 20 months. These types of process delays are not unique to any one state (e.g., Kretser, Glennon, and Smith 2014).

The difficulty of transferring resources often arises out of state or federal requirements or limitations on how tax dollars are disbursed, accounted for, and spent. The issues surrounding the transfer of resources often do not stem from the wildlife agency staff but rather from the larger state and federal bureaucracies. State and federal agencies with responsibility for budgets and contracts have a different set of priorities and obligations than conservation agencies and NGOs, and these priorities and obligations often have little obvious overlap with the conservation of public trust resources. Larger institutions may be able to support work via other sources, as was the case with the highly visible Path of Pronghorn work that earned support from several foundations. Larger institutions may also be able to supply emergency funds, budgets permitting. But in some instances, for large and small organizations, whole programs may be cut if the transfer of resources is delayed. Such delays may be perceived as a lack of commitment to an issue or project, jeopardizing a long-term partnership.

The POP example is a window to a future where WGPs are adopted and applied consistently. That case exemplifies the benefits of collaboration to result in a societal change that benefits future generations. However, bureaucratic inefficiencies will need to be addressed for effective collaboration and adoption of WGPs as envisioned by Decker et al. (2016). This may mean developing strategies to streamline state and federal contracting processes while being sensitive to the obligations of government budgeting agencies to safeguard public monies. An approach to streamlining bureaucratic inefficiencies could be to articulate the optimal conditions for a successful agency-NGO relationship and then create processes by which organizations meeting these criteria can engage in formal collaborations or perhaps even a comanagement relationship. Some possible conditions include: 1) the NGO mission should be compatible with agency obligations; 2) the NGO should be able to improve agency capacity in accordance with other WGPs (e.g., broadly inclusive, enabling citizens to be informed); 3) the NGO and agency agree to resolve disagreements through formal or informal arbitration rather than through litigation; 4) the agency and NGO must strive to embrace WGPs and a willingness to engage in a collaborative relationship; and 5) the agency and NGO need to clearly define the terms of the relationship regarding transparency, communication, and acknowledgements. Other opportunities undoubtedly exist and the processes by which state and federal agencies adopt WGPs will need to explore the systems that lead to the most effective deployment of resources to meet natural resource management needs.

Conclusion

Cross-sectoral partnerships are central to WGPs' vision for reinvigorating and modernizing wildlife conservation and management in North America. Such partnerships exist and can be central to embracing adoption of WGPs. However, adoption of WGPs also brings challenges. The opportunities and limitations we present, as well as the case studies we describe, are intended to help anticipate and avoid potential difficulties and to support participants throughout the wildlife institution adopt processes and practices consistent with WGPs.

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Implementation of Wildlife Governance Principles in a State Agency

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Introduction

With few exceptions, wildlife conservation in the U.S. is losing ground. The fish and wildlife management paradigm (the combination of professional values and norms, structures and processes, relationships with citizens and stakeholders, and our management practices) is struggling to keep up with modern expectations (Forstchen and Decker 2014). Additionally, changing citizen values and expectations have created a new political zeitgeist, which stimulates greater skepticism of government (Dalton 2005). And yet, globalization, greater connectedness through technology, and increased advocacy of nongovernmental organizations have contributed to making citizens more aware of their rights and therefore more demanding of their governments (Eccles 2015).

Fish and wildlife in the U.S. are public property held in trust by the government for the benefit of current and future generations (Batcheller et al. 2010). Public trust *thinking* offers a broad philosophical orientation toward natural resources and a means of addressing persistent and emerging challenges in environmental conservation (Hare and Blossey 2014). In addition to public trust thinking, present-day expectations for wildlife governance include incorporating objectives of good governance, which seek to establish fairness and transparency in decision-making; policy formation; and implementation processes (Lockwood et al. 2010). The wildlife governance principles (WGP) proposed by Decker et al. (2016) provide a framework for state fish and wildlife management agencies to fulfill their public trust obligations and meet contemporary expectations of good governance. Adoption of WGPs will result in a more focused, cohesive, and informed institution that can elevate the importance of wildlife conservation to all beneficiaries (Decker et al. 2016). Implementing actions that improve agency alignment with the WGPs will require self-reflection, assessment, and a commitment to change from all parties in the conservation institution: trustees (elected and appointed officials), trust managers (agency leaders and staff), nongovernmental partners (including private landowners, community organizations, nontraditional and traditional interest groups, industry, academia, and nonprofit organizations involved in wildlife conservation), and beneficiaries (i.e., all members of the public). Changes in strategic orientation; cultural adaptability; transparency; accountability; increased reliance on multiple forms of information and insight; increased inclusiveness of diverse stakeholder perspectives; and agency capacity need to be explored and addressed. WGPs reflect the evolution of this necessary paradigm shift by offering guidance on behaviors, operational routines, and decision-making processes to improve the quality and quantity of input from a broad suite of stakeholders.

While all agencies employ the practices and exhibit the behaviors embodied by the WGPs at some level, wide scale application has not been adequate or consistent. Agencies generally recognize the need to transform, diversify, and broaden their scope of conservation services and stakeholder engagement efforts, but the path forward is not easy with some agencies making more progress in this regard largely depending on the political, economic, and social climate in each state. Applying guiding principles and any strategic management process is about understanding what changes are needed, designing processes to implement those changes, and then sustaining those changes that lead to desired performance and outcomes.

To facilitate agencies in determining how they are aligned to the WGPs, several authors of the WGPs and their colleagues developed an assessment instrument to help agencies evaluate their traits and practices with respect to the WGPs. Traits are broad descriptors or characteristics of an agency, and practices are identifiable actions or activities. The instrument, administered by Cornell University's Human Dimensions Research Unit, was first tested by a small group of senior staff from the Florida Fish and Wildlife Conservation Commission (FWC) in December 2015. The assessment focuses on specific traits and practices that either support or impede achievement of the WGPs, organized into five broad themes: strategic orientation and adaptability, evidenced-based and broadly informed decision making, transparency and accountability, inclusiveness and diversity, and capacity for conservation. Traits and practices are more actionable than the WGPs, which provide high level guidance for desired conditions.

A two-day workshop also was created to promote dialogue and reflection on the assessment results. The discussions were designed not to focus on the absolute numbers from the assessment but to spark discussion about what structures, conditions, or behaviors exist that resulted in any less-than-desirable ranking. The same group of FWC staff who provided input in the agency assessment volunteered to participate in this pilot workshop in January 2016. One outcome of the workshop was a list of practices that the group thought FWC should focus on for improvement (e.g., communication about accomplishments and performance, collaboration across boundaries for planning and implementation, and increasing the scope of information applied to decisions). Another outcome was a successful test using the WGPs to frame a critique of a current conservation issue to assess how well FWC applied the practices and traits of the WGPs.

The FWC has been on a deliberate transformative journey since its creation in 1999, focusing on efforts to broaden our understanding of the interests of our residents and visitors in fish and wildlife and our management of these pubic trust resources. Like other agencies, FWC has gradually changed from being a traditional hierarchy with limited responsibilities to a broader institutional actor negotiating multiscale policies, navigating complex relations with stakeholders, building interdependencies among partners, and working across multiple jurisdictions on shared conservation responsibilities. Yet, we sometimes operate in traditional ways as if the ecological and sociopolitical landscape has not substantially changed.

Fish and wildlife management agencies, like other public sector organizations, are influenced by political cycles dominated by short-term budgeting cycles and planning horizons and are often pressured to add programs that stretch the scope of stakeholder vetted and agreed upon conservation priorities. Characteristically, wildlife management agencies are very responsive to immediate conservation issues, especially those involving humans. They have a hard time "saying no" and have insufficient capacity to perform everything asked of them. They are risk-averse to ensure long-term well-being of fish and wildlife and are comfortable working in this arena. But conservation issues are rarely simple; they often are long-term endeavors, frequently involving opposing stakeholder interests and values in a context characterized by institutional complexity and scientific uncertainty—situations becoming increasingly difficult to navigate with traditional tools (Head and Alford 2015).

Systemic changes to institutional structures, practices, allocation of resources, and behaviors will need to occur and may require somewhat of a revolution in organizational thinking and learning, capacity calibration, resource allocation, and administrative routines. This will result in more externally focused management practices, increased partnerships, new ways to deliver conservation benefits to stakeholders, increased attention to building relationships with beneficiaries, more diverse staff, and a strong focus on conservation impacts and outcomes. This may require significant realignment, which takes time and may be costly in the short term but promises to have long-lasting benefits to society and wildlife.

Implementation

Montjoy and O'Toole (1979) provide a classic definition of implementation—the strategic mobilization and application of human, financial, and technological resources to alter routines. The WGPs provide a framework for increased understanding of stakeholder preferences and improved distribution of conservation benefits to all citizens. Each of the 10 principles may require specific structures, processes, or behaviors but running through the principles are five overarching themes (strategic orientation and adaptability, evidenced-based and broadly informed decision-making, transparency and accountability, inclusiveness and diversity, and capacity for conservation) that can help identify actionable steps for agencies to adopt or to evaluate and improve their current practices. We'll describe these themes, offer some examples from FWC, and suggest some areas for improvement FWC is pursuing that may be helpful to other agencies.

Theme: Strategic Orientation and Adaptability

Managing strategically involves looking to the future but also understanding and meeting current demands. Fish and wildlife need to be managed for current use and enjoyment but also for future generations to use and enjoy, perhaps in ways currently unimaginable. Agencies should position themselves to be adaptable to unknown future ecological and sociopolitical conditions. It's important to understand the broad social, demographic, political, technological, and ecological trends that may impact delivery of wildlife trust benefits but also to understand internal organizational characteristics (i.e., mandates, capacity, expertise, traditions, and structures) and their impacts. Adaptive organizations are inquisitive and test their assumptions; have robust evaluation processes (outcomes are monitored relative to goals and objectives); have "real" partnerships that share goal setting and ownership; create, accept, and embrace change as an opportunity; are continual learners; and are reflective and forward-thinking. Adaptive organizations embrace experimentation in order to keep pace with incessant change, guiding their organizations through a process of managed evolution in which activities and strategies continuously evolve in response to change (Kamener, Reeves, and Chua 2010).

Long-term planning may be one area where government can fulfill an essential role in bringing various players and voices together while mediating the longer-term public interest (Wanna 2015). After a complete revision of Florida's imperiled species rule in 2012, which included an in-depth review of how we manage imperiled species from a systems perspective, FWC has completed its Imperiled Species Management Plan—a plan to conserve 57 species that includes species-specific action plans and conservation strategies that benefit multiple species. The plan guides FWC and its partners to prioritize actions to conserve these important species.

Like other agencies, FWC holds periodic meetings of specific stakeholder groups to gather their input and provide updates on issues we're working on. In fall 2015, FWC's Marine Fisheries Management Division held 18 workshops around the state to better understand their concerns and needs. Additionally, in January 2016, they held a Snook Symposium in Orlando to engage with snook anglers (snook fishing is a very popular, mostly catch-and-release fishery on both coasts of Florida). These engagement efforts inform our short- and long-term strategies to research, monitor, and develop regulations to conserve and manage our marine fisheries. FWC also conducts a large number of "user satisfaction"-type polls and surveys to better understand the benefits that stakeholders want from the resource.

Areas for Improvement

- Use a variety of planning tools (i.e., environmental scanning, scenario planning, predictive modeling) to better detect trends that will impact conservation or management actions
- Periodically seek information on public attitudes, opinions, and behaviors towards fish and wildlife
- Adopt rigorous evaluation methods to measure our progress on conservation outcomes as well as the effectiveness of stakeholder engagement practices and processes
- Thoughtfully consider and communicate the short- and long-term consequences when pressured to stray from adopted conservation priorities
- Make resource allocation decisions based on current and predicted ecological and sociopolitical conditions, not last year's or last decade's priorities
- Embrace planning as a critical element of wildlife management
- Embrace innovation, learn from missed opportunities or mistakes, and "fail faster"

Theme: Evidence-Based and Broadly Informed Decision-Making

Conservation is part of a continuous process in which management activities are implemented in spite of uncertainties about their effectiveness. Priority setting in conservation will always reflect human-oriented values and be forever changed and contested, as values regarding fish and wildlife shift and other societal priorities change. Nevertheless, science can be a potent guiding force in informing decision-making and can help improve the cost effectiveness of conservation practice. Conservation science is just one component of the overall decision-making process. Economic, social, and political considerations also play a role and may determine the outcomes (Pullin et al. 2013).

Decision processes require relevant, sufficient, and accessible information. Agencies need to continually acquire new knowledge and not rely on hunches or dated research. Information used in decision-making needs to be credible and come from many disciplines (i.e., ecological, social, economic) and sources (i.e., academic research, government or citizen science monitoring, professional judgment, local experiential insight). Information should be shared widely among staff, partners, stakeholders, and citizens in an understandable format to inform opinions and contribute to the formation of potential recommendations for management action. Data gaps should be identified and any limitations caused by these gaps clearly acknowledged. Stakeholders who may be affected by the decision should be identified and included in the decision-making process and the impacts on those affected fully understood.

To respond to local stakeholder preferences FWC has used a regional management approach for some species. Red drum (*Sciaenops ocellatus*), a popular recreationally targeted marine fish, has different harvest regulations in different areas of the state. FWC also manages some freshwater lakes for a trophy catch experience and others for those who value catching quantities of largemouth bass (*Micropterus salmoides*). A strong relationship between FWC and marine life collectors (for the aquarium trade) bring experiential knowledge and professional judgment into our decision-making process. They alert FWC about their observations of changing conditions in the Florida Keys (i.e., an increase in harvest of sea cucumbers), which have instigated or informed regulations that sometimes restrict their own industry. Properly deployed, citizens with their local knowledge, wisdom, commitment, authority, and even rectitude can address serious failures of legitimacy, justice, and effectiveness in representative and bureaucratic institutions (Fung 2006).

Areas for Improvement

- Use *all* available information from a variety of disciplines and sources (ecological, social, professional judgment, local knowledge)
- Science should be relevant and credible
- Fully understand impacts of decisions on affected stakeholders
- Identify and fill ecological and social science data gaps

Theme: Transparency and Accountability for Decisions and Actions

Wildlife management agency boards or commissioners (trustees) have legal mandates for managing trust resources and are directly accountable to beneficiaries (citizens). Trust managers are civil servants employed by agencies in various capacities; they are directly accountable to trustees but are only indirectly accountable to beneficiaries (Hare and Blossey 2014). The natural resource trust exists to provide benefits to current and future generations of citizens; therefore, trust administrators (trustees and staff) are obligated, to the extent possible, to equitably distribute benefits from the resource (Organ et al. 2014). The processes of this distribution are expected to follow norms of good governance—fairness, transparency, and participatory decision-making.

The only way to guarantee good governance is by institutionalizing powerful accountability mechanisms that hold every public official responsible for his or her actions as a public servant (Ackerman 2004). The public sector administration literature provides considerable support for new governance models that include: 1) governing *with* citizens instead of *for* citizens; 2) organizational networks instead of silos; 3) flexible, purpose-driven organizations; 4) government serving as facilitators or brokers rather than as providers or directors; 5) greater community involvement in direction setting; 6) evaluations based on outcomes rather than outputs; and 7) collaboration based on trust (Wanna 2015). These align well with the WGPs for wildlife management.

Transparency and accountability are key to full application of the WGPs, characteristics demonstrated by openness and stakeholder inclusion in decision processes. Research on stakeholder inclusion in government processes has been found to enhance accountability, efficiency in decision-making, and good governance (Ackerman 2004). Being transparent and accountable in the wildlife management arena means that all staff can engage with citizens, not just spokespeople or senior leadership.

Florida has very broad open records and rigorous records retention laws. All available information is shared, and FWC helps partners, stakeholders, and citizens understand it. We provide multiple avenues for citizens to provide input, demonstrate how that input was considered, and are responsive to their requests. Citizens can email the FWC commissioners and senior staff directly via links on our website. Commission meeting agendas, along with an issue overview document and the staff presentation to be given at the meeting, are posted on the website several weeks prior to the meeting. We have a web portal that archives answers to commonly asked questions (ask FWC—e.g., "How do I become a law enforcement officer?"), in addition to our topical hotlines to report events (e.g., fish kills, avian mortality, invasive species), regional call centers, regional Wildlife Assistance Biologists, and a work unit dedicated to understanding and reducing negative human-wildlife interactions. We encourage citizen reporting of wildlife interactions or sightings such as our Florida panther sighting web page. We hold many public meetings, but we could hold more of them at times that are more convenient for the public to attend and increase our use of webinars and webcasting meetings. We might also increase citizen knowledge about fish and wildlife management by increasing opportunities to view commission meetings remotely.

Areas for Improvement

- Allow and promote citizens access to wildlife managers (i.e., all agency staff)
- Share *all* available information about conservation issues
- Improve awareness and understanding of agency decision-making processes
- Increase awareness of and provide specific mechanisms for citizens to hold the agency accountable (i.e., administrative hearings, "file a complaint" web page, Inspector General's Office)
- Carefully weigh input from traditional stakeholders and highly engaged organizational representatives relative to social science and other input from the broader interests and public
- Clearly communicate the rationale for our decisions (including analysis of alternative options)
- Communicate effectively about performance, accomplishments, and the benefits and value we provide to citizens—not just popular interest items
- Evaluate and improve the effectiveness of communications
- Evaluate efforts to seek out and include diverse stakeholders

Theme: Inclusiveness and Diversity

Inclusiveness and diversity in this context refers to the traits and practices that broaden the perspectives and voices in conservation and in our decision-making processes. Traditional stakeholders and those most closely engaged in decision forums that determine the distribution of trust benefits are important to the process. We need to be more open and welcoming, however, to new voices in our conservation processes that bring new information, new ways of understanding issues, and motivation to address problems and elevate agency attention to these issues. They can be used to uncover new understandings, generate better projects and policies, secure buy-in for decisions, and limit delays, mistakes, and lawsuits (Burby 2003).

The fear of agencies giving up their decision-making authority to overly powerful citizens is easing but still exists among some agency staff. The argument that stakeholder engagement creates unrealistic public expectations and takes too much of our limited resources is still heard. The purpose of stakeholder engagement is not just to ask citizens what they prefer but also to explore which ideas are likely to work and have durability. It's a cost-effective means to clarify expectations and sideboards, communicate what and why we selected specific actions, and ensure selected alternatives meet users' needs.

Florida is the third largest state in the U.S. with more than 20 million people and has the highest percentage of residents over the age of 65. About 23% of Floridians are Hispanic and 26% of Floridians speak a language other than English at home (U.S. Census 2010). FWC is struggling to translate these statistics into impacts to and demands on fish and wildlife conservation.

We need to increase our workforce diversity to help us identify and connect with latent or underserved stakeholder groups. We need to explore new methods of stakeholder engagement to ensure those connections are productive and build long-term relationships. FWC is working to provide benefits that satisfy all interests. Our Office of Public Access Services manages an extensive statewide birding and wildlife viewing trail and, with our Office of Boating and Waterways, designed a growing system of paddling trails to accommodate growing participation in paddling. Many of our wildlife management areas have hiking, biking, or horseback riding trails. We are building our social science capacity to better understand attitudes, opinions, behaviors, and motivations of all our citizens.

Areas for Improvement

- Critically evaluate communication practices to ensure all stakeholders are reached
- Evaluate processes and practices to ensure they demonstrate we value public input
- Evaluate and improve practices that gather input from all stakeholders affected by our management actions
- Evaluate policies to reduce barriers to engaging with stakeholders
- Use multiple methods to engage with stakeholders
- Engage stakeholders often, not just when we want their opinion about a specific issue (i.e., develop relationships)
- Assess agency programs to ensure benefits are successfully being distributed to all beneficiaries
- Expand workforce diversity to better reflect state demographics and actively seek to reach and engage a broader cultural diversity of stakeholders

Theme: Capacity for Conservation

Governmental agencies were created to ensure that societal values for wildlife resources were attended to, laws enforced, and management undertaken (Decker, Riley, and Siemer 2012). Governance is effective to the extent that governance arrangements are capable of solving the substantive problems they are meant to address (Fung 2015). Capacity is often translated into the availability of resources (time, talent, and treasure).

We need to hire staff and partner with people with a diverse range of expertise and values to meet modern expectations of wildlife conservation. In Florida, we are heavily invested in partnerships (e.g., landscape cooperatives, joint ventures, landowner assistance programs) but don't invest enough in the skills that foster productive partnerships. We cannot overemphasize the importance of personal relationships that staff build with stakeholders—we need staff that create credibility and trust through one-on-one interactions with the beneficiaries. The knowledge and application of information and insight from the social sciences (e.g., sociology, social psychology, economics, communications, and education) in wildlife conservation is increasing and will improve collaborative governance of wildlife resources. FWC is increasingly hiring social scientists and other experts to complement the work of wildlife management professionals.

Adequate and reliable funding for conservation remains elusive. Agencies need to better demonstrate the societal value of conservation to all citizens to build support that will translate into broad-based funding at all levels. Designing and implementing processes that increase and improve citizen engagement in the shared development of desired conservation benefits will lead to increased support for conservation in general. FWC is moving beyond the traditional public meeting format and using listening sessions, focus groups, webcasting, and webinars to improve citizen engagement. FWC has a diverse funding structure where only about 23% of the budget is from direct hunting and fishing license sales. We receive funding from eight conservation-related vehicle license plates, a check-off box to donate to youth programs on hunting and fishing license sales, a portion of documentary stamp revenue from home sales, and a wildlife surcharge on speeding tickets.

Areas for Improvement

- Evaluate policies and practices that promote collaboration and information sharing
- Increase staff skills in collaboration, communication, negotiating, mediation, partnering
- Assess vacancies with respect to agency skill set needs
- Partner with others to increase management capacity
- Increase our influence and exercise our authority to protect and regulate habitat
- Explore novel ways to fund conservation (don't wait for national policy changes—start local)

Conclusion

The past and current fish and wildlife management paradigm is not sufficient for the challenges of today or for the future. The broad management system—people, landscape, wildlife populations, interactions between these components, and the formal and informal processes to manage them—has changed. Wildlife management agencies not only need to be relevant to society, they need to be valued by society (Forstchen and Decker 2014). Decker et al. (2016) have provided a framework to create or improve practices, processes, and behaviors that will result in increased citizen awareness, engaged stakeholders, improved wildlife conservation outcomes, and increased value and support for conservation.

Nothing happens in a predictable, sustainable way unless you build mechanisms that cause it to happen in a predictable, sustainable way (Joiner 1994). Changing our practices, processes, and behaviors will take time and resources; pressure to maintain the status quo may be high. We need to build on our existing good social capital as we challenge some widely held assumptions. We'll need to be creative and experiment with new ideas and refine them as we learn. We'll need to engage others to make progress and be clear in our purpose. We'll need to engage and energize others around our common purpose—improving conservation outcomes for all citizens.

Involving the public more effectively in administrative decision-making promises a number of benefits for both public agencies and the public. For agencies, benefits can include 1) better information, as citizens contribute ground-level knowledge, that otherwise would be unavailable to decision makers; 2) greater likelihood of the public accepting any decision it helps make, which can facilitate program implementation; 3) improved governmental performance; and 4) increased citizen trust. For current and future citizens, the benefits can include a better fit of public policies and programs to community preferences, improved community capacity for other joint efforts, and ultimately better quality of life (Thomas 2013).

Wildlife conservation is best understood as a complex adaptive system with a wide variety of actors, ever-changing sociopolitical conditions, and changing ecological forces. WGPs can facilitate the evolutionary process of this social-ecological system in its adaptation to modern expectations. For practical purposes, the unit of analysis for implementing WGPs is a single state agency, but they need to be applied at the conservation institution scale to be effective. We are a collection of codependent organizations that need to use common standards and practices to improve the distribution of conservation benefits with minimal barriers, and create value and support from wildlife trust beneficiaries across large landscapes. The challenge is to create and improve practices, procedures, and programs that are well designed; satisfy stakeholder needs; and provide products and services the public values and supports. We have the opportunity to become more attuned to the needs and influence of all wildlife interests by understanding their priorities and determining how best to engage and gain their affiliation, ultimately leading to more successful program impact. By necessity, some changes will need to be incremental (implement, observe, evaluate, modify, re-implement), while others may need to be more transformative. We'll need to distinguish what processes, practices, and programs are critical and which are optional and allocate our resources accordingly.

The current structure, processes, and practices have served us well, and we can build on those historical conservation successes. We constrain ourselves by our cultural norm of focusing more narrowly on fish and wildlife *management* rather than focusing on delivering fish and wildlife *benefits* to all citizens (Forstchen and Wiley 2015). We need to focus on immediate contemporary conservation issues but also strategize for bigger-picture future scenarios. WGPs provide some certainty—simple rules to facilitate interaction, help people make trade-offs, and set the boundaries within which they make decisions. WGPs are a conscious, intentional, and purposeful intervention to modernize the wildlife conservation management paradigm.

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Increasing Capacity for Conservation: Do the Wildlife Governance Principles Enhance or Hinder Partnerships?

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Introduction

Governance principles for wildlife conservation were introduced to encourage adoption of a combination of public trust thinking and conceptualizations of good governance to improve wildlife conservation (Decker et al. 2016). Conservation, regardless of where it occurs in the world, is accomplished through management, which in most cases is a governance activity (Rudolph, Schechter, and Riley 2012). Governance is an emerging concept applied to conservation that describes the processes, instruments, and mechanisms available to collectively steer a society or organization toward a desired end state, including how decisions are made and implemented and how responsibilities are exercised (see Armitage, Loë, and Plummer 2012 for descriptions and comparisons of environmental governance and management) (Lemos and Agrawal 2009; Bäckstrand et al. 2010).

Governance and government are not necessarily synonymous. Governance includes actions initiated by "the state" (e.g., public trustees or trust managers in the case of wildlife conservation), yet also includes actions of civil society (e.g., nongovernmental organizations (NGOs) or groups of organizations and beneficiaries of public trust management such as individuals), as well as actions of the private sector, such as corporations who might not be direct beneficiaries (Smith 2011). Partnerships are common arrangements in governance structures, yet definitions of partnerships vary widely in literature and in practice (Delmas and Young 2009). In the simplest sense, partnerships are arrangements where sharing of goals, power, risks, and responsibilities occurs between two or more participating actors, normally to achieve a common goal or mutual interest (Schäferhoff, Campe, and Kaan 2009).

This essay addresses the question: Does application of wildlife governance principles (WGPs) enhance or hinder partnerships? Our thesis is that in a future of wildlife conservation characterized by more active public participation, continued declines in numbers of traditional stakeholders (i.e., hunters and agricultural interests), and subsequent decreases in conventional funding (i.e., revenue from hunting license sales), capacity to achieve objectives may be increased and sustained through partnerships. We use "capacity" to mean having requisite resources for governance systems to adapt, learn, and conduct actions necessary to achieve desired outcomes while remaining resilient to change (Brown and Westaway 2011). In light of declining funding situations related to decline in hunter populations, state wildlife agencies (SWAs) who effectively engage in strategic partnerships are more likely to increase capacity and achieve mutual interests in wildlife conservation (Winkler and Warnke 2013; Kretser, Glennon, and Smith 2014).

Partnerships

Partnership arrangements are important to clarify before assessing whether the application of the WGPs helps or hinders partnerships. A typology of partnerships within a governance framework (Figure

1) includes three different sectors engaged in at least four types of relationships. There are myriad ways agencies or groups partner *within* their respective sectors. For instance, SWAs frequently partner with state forest agencies to help ensure wildlife values are taken into account when managing forests. Similarly, two private companies might partner with one another to manufacture a product that could not be produced by one company alone. Arrangements between the public sector (government agencies), civil society (public trust beneficiaries, NGOs), and the private sector (corporations, developers) exist in many forms (Delmas and Young 2009).

Public/Social Partnerships

In natural resources management, public/social partnerships are generally the most common and easily recognized. For example, in the mid-1980s, Safari Club International (SCI) partnered with the Michigan Department of Natural Resources (MDNR) to reintroduce moose in Michigan. Support in the form of lobbying, direct purchases of equipment, and fixed-wing and helicopter flights increased capacity of the state wildlife agency to a point where plans could be finalized and implemented. Today, there is a small moose population in the central Upper Peninsula of Michigan that contributes to the local economy through wildlife-related tourism, a situation that would not exist without capacity-building partnerships. In the years following the moose introduction, the partnership has continued and 10 chapters of SCI in Michigan formed a 501(c)(3) nonprofit corporation to provide additional support annually for MDNR research projects and graduate student scholarships, thus contributing sustained capacity for long-term conservation efforts.

Another public/social partnership involves bighorn sheep, whose distribution and abundance declined with the European settlement of the West and was estimated to be less than 20,000 animals in 1960 (Buechner 1960). Since then, partnerships between state, federal, and provincial agencies, the Western Association of Fish and Wildlife Agencies, and NGOs such as the Foundation for North American Wild Sheep have engaged in research, education, reintroduction programs, and habitat improvement projects such as water developments, resulting in increasing population abundance now thought to exceed 80,000. The Nevada Division of Wildlife has conducted more translocations of sheep than any other agency, yet those efforts would not have been possible without long-term partnerships with Nevada Bighorns Unlimited, Fraternity of the Desert Bighorn Sheep, and other organizations that resulted in increased capacity to conduct the necessary and expensive work of animal translocations vital to the overall increase in bighorn sheep distribution and abundance across the western states (Nevada Division of Wildlife 2001; Wild Sheep Working Group 2015).

Public/Private Partnerships

These partnerships may include contractual arrangements between an agency and the private sector to provide services that achieve a conservation objective. Resources, risks, and rewards are shared throughout the process. Business arrangements, such as those between state agencies and local businesses to sell hunting licenses, are needed for the convenience of license buyers and to keep costs to the state contained. Yet, there are other subtle benefits accrued from these relationships. For example, a single corporation in Michigan accounts for 19% of all fishing and hunting licenses sold in the state. Although there is no formalized partnership other than the agreements necessary to host point-of-sale terminals in their approximately 100 locations across the state (and the selling commission of 7.5% per license), these stores represent a portal into outdoor recreation experiences because they also sell equipment, ammunition, and supplies. Monies from license sales and excise taxes on ammunition are tangible benefits to promote capacity that can be measured and would be the same if sold by any other store. Nonetheless, the convenient access to equipment and supplies to a high proportion of license buyers, including purchases of outdoor gear that promotes hunting, fishing, wildlife watching, water sports, and camping (to name a few), results in the more intangible benefit of easier access to those desiring to connect with the natural world. Participation in these recreational activities creates the potential to increase awareness and appreciation of natural resource issues and potentially a more informed citizenry through involvement. These sorts of public/private partnerships have not garnered much attention in the literature, yet may indirectly increase the capacity of SWAs to perform more effective trust management and thus warrant additional consideration.

Another example of public/private partnerships is an agency providing financial and tax incentives and partnering with corporate landholders to develop conservation easements that help support ecosystem services resulting in clean water, increased biodiversity, erosion control, or increased recreational opportunities (Gustanski and Wright 2011). Because conservation easements provide similar levels of ecosystem services yet are far less expensive than fee simple land transactions, partnerships of this sort increase the capacity of SWAs to promote these positive outcomes with excellent value to public trust beneficiaries (Villamagna, Scott, and Gillespie 2015).

Private/Social Partnerships

Private/social partnerships have little or no direct involvement by the public sector, yet increase the overall capacity of the conservation institution. One example is the nonprofit organization Ducks Unlimited (DU) Corporate Partner Program. Purchases of DU-licensed products or services by individuals result in a portion of each sale being earmarked for wetlands and waterfowl conservation programs. Similar partnerships occur between the nonprofit National Wild Turkey Federation (NWTF) and dozens of corporate sponsors who contribute annually to the management and educational work conducted by NWTF to promote wild turkey habitat and populations

Another example is the nonprofit Defenders of Wildlife, which in the past provided financial compensation to livestock producers who experienced losses from wolf and grizzly bear depredation and now provide resources and supplies used to minimize or prevent carnivore depredation on livestock. Those efforts are argued to increase tolerance for large carnivores on the landscape, yet evaluations of effectiveness are lacking (Nyhus et al. 2003).

Similarly, the Bobolink Project started in Rhode Island in 2007 provided funds collected from local residents to pay local farmers to delay or stop haying of fields during critical nesting times, thus protecting ground nesting birds. Farmers benefitted from only haying once instead of twice and local conservationists benefitted because the birds they valued were protected. This partnership increased capacity for conservation efforts over the years and now includes many more farms and Audubon organizations in Massachusetts, Vermont, and Connecticut (Mass Audubon, Audubon Connecticut, and Audubon Vermont 2016).

Public/Private/Social Partnerships

The Federal Agriculture Act of 2014 (i.e., the Farm Bill) provides more than six billion dollars in funding over 10 years for conservation programs often delivered through multidimensional partnership programs. Specifics of partnerships vary depending on the program, yet include federal, state, and tribal government agencies, NGOs, the private sector, and individual landowners where the conservation actions take place. As one example, the Conservation Reserve Program (CRP) administered by the U.S. Department of Agriculture Farm Service Agency (FSA) is a 30-year-old program that has resulted in more than 20 million acres currently enrolled in projects designed to protect water quality, prevent soil erosion, and improve wildlife habitat. Grassland birds species, in particular, benefit from the CRP program, including a positive relationship between ring-necked pheasant abundance and the amounts of CRP acreage in a nine-state area and increases in abundance of five targeted species in Pennsylvania (Nielson et al. 2008; Pabian, Wilson, and Brittingham 2013). Whereas Farm Bill funding provides financial incentives to landowners, actual project implementation is unlikely without positive capacity-building relationships between FSA and many partners (often with complimentary or matching funds from nonfederal sources). Potential downsides for regional or national programs of this scale are larger bureaucracies, increased orientation toward process as opposed to conservation interventions, and less direct engagement with stakeholders (Prager 2010).

Another example of a public/private/social partnership is the Federal Energy Regulatory Commission Licensing Process. There are three approaches allowed in the process, yet all three bring together the federal government, the private sector energy providers, and NGOs and other groups interested in fish and wildlife conservation, water quality, recreational opportunities, and other beneficial public uses that could be impacted by continued operation of hydroelectric projects. There are opportunities built into the licensing process for all the partners to engage and collaborate to resolve natural resources issues associated with the generation of hydroelectric power, thus increasing capacity to fulfill as many stakeholder interests as possible (Federal Energy Regulatory Commission 2015).

Partnerships Relative to the WGPs

Three of four types of partnerships described above involve government in some way, and as key contributors in the conservation institution due to their administrative role, SWAs can play a pivotal leadership role in fostering and improving partnerships. This leadership role can be realized by adopting and promoting consistent principles of conduct, characterized by positive traits, practices, and behaviors. These characteristics are embodied in the wildlife governance principles detailed in Decker et al. (2016), and several of the WGPs are particularly important to partnerships. Partnerships are a critical avenue to increase capacity for conservation in the foreseeable future.

Effective engagement with stakeholders is either explicitly stated or implied in most of the WGPs. Honest engagement can lead to informal or formal relationships and these relationships may lead to partnerships where risks, rewards, and decision-making power are shared between two or more groups. The degree of sharing depends on the type of partnership and reasons why and how relationships were formed in the first place. Partnerships within and across the spectrum of types (Figure 1) are arrangements, in part, in response to the current needs and trends of society, with the expectation that government agencies will work together and will engage with stakeholders in transparent decision-making and implementation of management interventions. As such, partnerships can be considered an advanced form of stakeholder participation or engagement (Arnstein 1969; Decker and Chase 1997; Lauber et al. 2012).

For SWAs, partnerships represent opportunities to increase support for agency programs and build capacity. However, we believe SWAs who recognize when they lack capacity to fulfill their public trust responsibilities and acknowledge the important roles the private sector or civil society play in collective conservation are more likely to create sustained success in achieving objectives (cf. Stoker 1998). Despite being the administrative role of government to fulfill public trust responsibilities, recognition by SWAs that capacity is lacking allows mechanisms to be crafted to help ensure effective partnerships can fulfill that need, with accountability and transparency measures in place for all sectors involved in the partnership. For example, if the expectation is partners can take on some of the roles of trust managers (as suggested by WGP #9), additional measures (e.g., memoranda of understanding or similar formal agreements) may be required to help ensure public trust responsibilities are not abdicated by SWAs but are fulfilled by the partnership. In addition, SWAs mindful of potential conflicts caused by partnering with particular stakeholder groups at the expense or exclusion of others create an environment more likely to sustain partnerships and public support (Decker et al. 2015).

If SWAs conduct more intentional engagement required to incorporate multiple and diverse perspectives (WGP #2), decisions will be based on a broader diversity of information and the partnerships that emerge from that engagement likely will be less traditional and have the added benefit of helping safeguard against “agency capture” by stakeholder groups. This enhanced engagement has the additional benefit of allowing SWAs to explore and understand diverse partner’s interests more closely (WGP #1), as long as extra efforts are taken to ensure all the interests are considered and not just those of special interest groups. If agencies take actions to align their practices and behaviors with the WGPs, we believe partnerships will be strengthened and more effective. In addition to our belief that SWA alignment with the WGPs will result in better partnerships, we believe that engaging diverse stakeholders in partnerships can help agencies align with the WGPs, in affect a self-reinforcing feedback loop resulting in greater capacity and more effective conservation outcomes.

Complex issues that span ecological, jurisdictional, and ownership boundaries (WGP #10) often cannot be addressed except through partnerships. Whereas public trust responsibilities include “all wildlife for all people," management interventions to protect or enhance wildlife populations or wildlife habitat may only be possible for SWAs on lands they have direct access to. Partnerships seem to be a necessity to address conservation issues on private lands—partnerships that may involve NGOs such as land conservancies and corporations such as Timber Investment Management Organizations that hold millions of acres of property open to public hunting and angling. Again, concerns regarding abdication of public trust responsibilities can be minimized or mitigated through accountability and transparency requirements spelled out in agreements. These often take the form of fiscal accounting standards, reporting requirements, and sometimes-competitive arrangements at the front end of the process if the SWA is providing funding for management efforts.

Conservation issues are complex and management decisions require careful consideration of many types of information. Citizens have a role to play by becoming involved, and citizen science projects (WGP #3) by their nature are partnerships that increase capacity through the collection and sharing of local ecological and social information. Examples include Audubon Christmas Bird Counts, which have yielded some of the longest continuing data sets (more than 100 years in some areas) on species that are often underrepresented in normal SWA survey and inventory efforts, and the Monarch Watch program sponsored by the University of Kansas that has been collecting population data on butterflies since 1992 (Monarch Watch 2016).

Wildlife governance principles 1, 2, 6, 7, 8, and 10 all suggest SWAs develop and use more effective stakeholder engagement techniques. Traditionally, SWAs always have been involved with partnerships, and building on these past experiences is one way to maintain or build capacity for conservation. Yet, few guidelines for sustaining successful partnerships exist, and metrics to evaluate such partnerships are generally lacking. Adopting the practices and traits detailed in the WGPs will help SWAs foster and maintain more effective partnerships and build capacity for conservation.

Partnership Challenges

Partnerships are not a panacea for building capacity, nor are they automatically effective. They require the expenditure of time and resources. To leverage those resources, SWAs mindful of challenges will be in a better position to take intentional actions to change and to put mechanisms in place to craft partnerships that broaden perspectives among all concerns, are transparent, and assure public trust beneficiaries understand why the partnership was formed. Poorly executed partnerships have the potential to reduce SWAs alignment with the WGPs, decreasing transparency and accountability and eroding trust with public trust beneficiaries. Further, partnerships that are not well designed could have the opposite effect than intended and can tax capacity rather than increase it.

Agencies, as a general rule, are slow to change, and adoption of the traits and practices described in the WGPs will require intentional actions on the part of SWAs that will allow change to occur. The WGPs provide a useful guide for change. Are we interacting with diverse groups? Are there accountability measures in place? Are we taking differing views under consideration as we make decisions? If SWAs can answer "yes," it is likely that positive changes are occurring.

Some wildlife professionals may be concerned that reaching out to broader constituencies will leave traditional stakeholders behind. This does not have to be the case. Some of the best examples of partnerships to emulate are with traditional stakeholders (i.e., hunting groups and agricultural interests). Agencies (trustees and trust managers) can play a leadership role to ensure the past positive practices are encouraged when forming new or broader partnerships. If some stakeholders feel threatened by broader approaches, SWAs can again play a leadership role by facilitating discussions and insisting on expression of interests rather than staking out positions and focusing on the similarities of groups' interests rather than the differences. Challenges to partnerships are real, yet SWAs providing a leadership role by taking actions to align with the WGPs will increase the focus on gathering diverse perspectives, understanding and responding to citizen's needs, providing benefits for all beneficiaries, and allowing more involvement by more groups in decision-making.

Conclusions and Additional Information Needs

Partnerships are governance activities that can build or erode agency (trustee and trust manager) capacity to achieve objectives for wildlife conservation. Our expectation is that, in the short term, the breadth and number of partnerships will increase based on current trends in partnering arrangements—expectations that public (beneficiary) participation will intensify and that declines in revenue generated by wildlife agencies will continue. We believe wildlife governance principles will enhance rather than hinder trust administrators' ability to conduct partnerships (Decker, Forstchen, and Hare 2016). Nonetheless, these conclusions are predicated on an assumptions that SWAs will not simply engage more and partner more but will intentionally engage and partner more thoughtfully using the WGPs as a guide for the behaviors and practices necessary to make those efforts effective.

Capacity of trustees and trust managers to achieve conservation objectives can be enhanced through research that focuses on factors influencing effective, sustained partnerships that manifest good governance:

1. Exploration of roles, responsibilities, and expectations by participants in various types of partnerships that occur or could plausibly occur in wildlife conservation. What are the expectations of external stakeholders for participation by SWAs in regards to initiation and governance of partnerships? Conversely, what are the expectations of trustees and trust managers for their role in partnerships? Are there gaps between the internal and external perspectives that could be minimized through communication and education?
2. Development of metrics that help evaluate the effectiveness of various partnership arrangements in wildlife conservation and whether those arrangements help SWAs align with the WGPs and increase capacity. Do these arrangements deliver what the beneficiaries are seeking from partnerships?
3. Do partnerships build legitimacy of SWAs to govern? How can partnerships build legitimacy such that trustees and trust managers can act appropriately on issues, such as disease management or during emergencies (e.g., Kapucu, Augustin, and Gerayev 2009), when time for extensive stakeholder engagement is not readily available?

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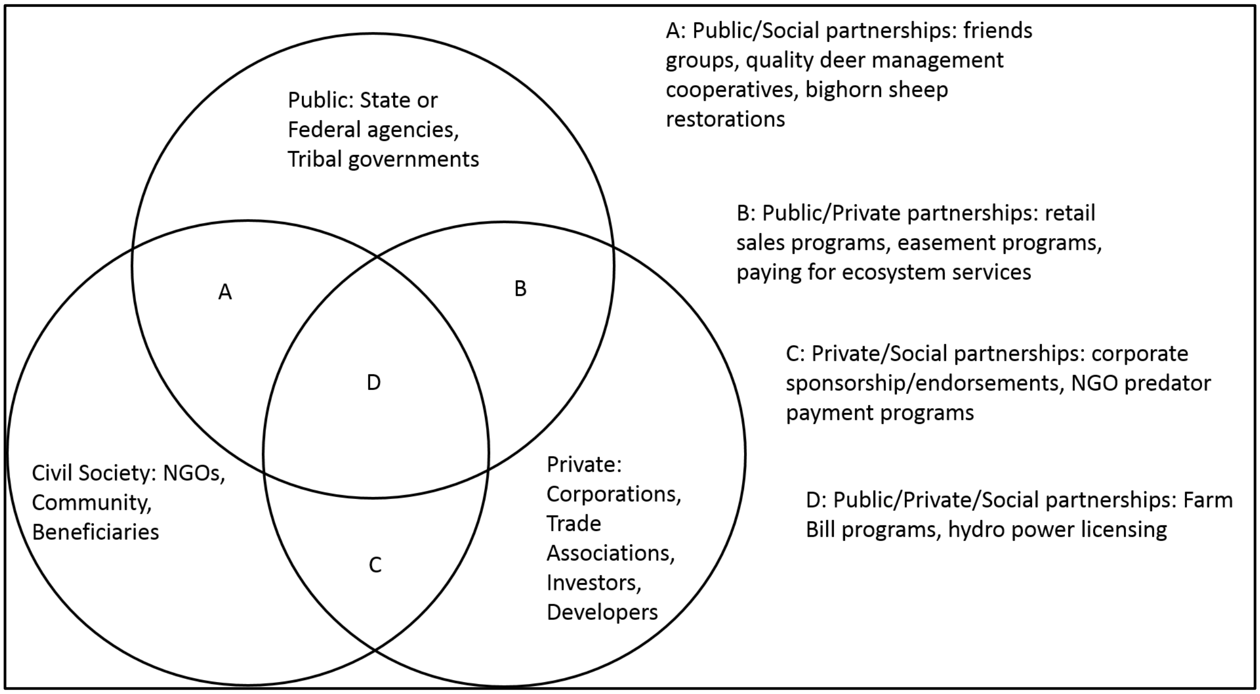
Figure 1. A typology of partnership arrangements within a governance framework (adapted from Delmas and Young 2009), with examples.



A: Public/Social partnerships: friends groups, quality deer management cooperatives, bighorn sheep restorations

B: Public/Private partnerships: retail sales programs, easement programs, paying for ecosystem services

C: Private/Social partnerships: corporate sponsorship/endorsements, NGO predator payment programs

D: Public/Private/Social partnerships: Farm Bill programs, hydro power licensing

Adoption and Diffusion of Wildlife Governance Principles: Challenges and Suggestions for Moving Forward

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Introduction

Jacobson and Decker (2006) suggested the system of fish, wildlife, and habitat conservation in the United States meets the criteria of an institution and labeled it the "conservation institution" (CI) (i.e., the people, processes, and rules as well as the norms, values, and behaviors associated with conservation). Institutions are characterized by stability and "taken-for-granted scripts" or norms that reflect the reality of institutions' organizational actors (Beckert 1999). Organizations within an institution are considered the organizational field, "a community of organizations that partakes of a common meaning system and whose participants interact more frequently and fatefully with one another than with actors outside the field" (Scott 2001). Institutions are founded on three interrelated pillars—regulative, normative, and cultural cognitive (Scott 2001). The regulative pillar comprises formal institutional rules and policies. The normative pillar includes values as expressed by norms. The cultural-cognitive pillar refers to what people know or their social construction of reality, shaped in large part by their cultures.

The CI emerged in the late 1800s, when the social-ecological context was considerably different, and the need for transformation of the CI to address contemporary challenges has been identified and discussed in the literature and at conferences and workshops for more than a decade (Nie 2004; Jacobson and Decker 2006; Decker et al. 2016). In well-established institutions, however, organizations will tend to remain grounded in the past and follow routine patterns of behavior (Dorado 2005). Concerns about the continued legitimacy of the CI have been expressed, particularly related to the influence and sustainability of the dominant funding mechanism for conservation at the state-agency level; biases inherent in governance structures; ability of the CI to meet public trust obligations; and lack of integration of social and ecological considerations into conservation decision-making (Jacobson, Decker, and Carpenter 2007; Gill 1996; Hare et al. in press; Forstchen and Smith 2014; Jacobson and Robertson 2012). It has been stressed that the CI must expand in three areas—goals, boundaries, and activities—or compromise its ability to maintain legitimacy with society and subsequently effectiveness in its conservation endeavors (Jacobson and Decker 2006).

Although the need for reform has generally been acknowledged, the nature of that change and how it should occur has not been widely discussed (Decker, Jacobson, and Forstchen 2010). It has been suggested, though, that transformation of the CI must start at foundation of the CI (Jacobson et al. 2010a). Although related to each of the three institutional pillars, the ten Wildlife Governance Principles (WGPs) proposed by Decker et al. (2016) are most closely related to the normative element (i.e., a manifestation of institutional values). That is, they represent a proposed innovation that suggests what the CI's norms might need to be to help "bring the institution into line with modern expectations for governance of public natural resources" (Decker et al. 2016: 290). As norms reflect our values, the significance of this innovation to inspire transformational change within the CI should not be underemphasized. If the CI adopts these principles or some variation of them, it would represent a clear and robust articulation of institutional norms. Diffusion of these norms throughout the CI could result in expansion of goals, boundaries, and activities resulting in needed transformation of the CI (Decker et al. 2016).

Initiation of the process leading to adoption and diffusion of WGPs into the normative—and subsequently, cultural-cognitive and regulatory—fabric of the CI depends on a variety of factors including receptivity, strategic agency, and ability to activate institutional networks. This paper explores those factors and offers considerations to help facilitate adoption of WGPs as an institutional innovation and ultimately implementation of the practices that support them. It is important to note that the focus of this paper is more about initiating adoption and diffusion processes related to the WGPs as part of the normative foundation of the CI versus considerations of implementation of specific principles themselves (e.g., practicalities/legalities of conserving benefits to future generations). Realistic issues and concerns regarding implementation will emerge and must be incorporated into the dialogue should the principles conceptually move forward within the CI. Saenz-Royo, Garcia-LaZaro, and Moreno (2015) note that innovations become effective only when they are adopted and diffused through the implementation stage within organizations.

Factors Related to Adoption and Diffusion of WGPs

Introduction of innovation, especially that which challenges institutional norms, is often met with resistance, particularly among well-established institutions (Beckert 1999). The WGPs represent such innovation for the CI. Three key internal factors that influence initial efforts to introduce and diffuse innovation within an institution are discussed. These factors are the institution's receptivity to the innovation; the presence of strategic agency within the institution; and the ability of organizational actors to activate diffusion through institutional networks. (Note: external barriers and factors that influence adoption are important in this discussion but not addressed specifically in this paper.)

Receptivity to Innovation

Institutions face strong inertia, especially those institutions in which government bureaucracies are key organizational actors (Battilana, Leca, and Boxenbaum 2009; Wilson 2000). Institutional inertia can be the product of laws, policies, and structural impediments that hinder and even provide disincentives for innovation (Scott 2001). As considerable as these barriers can be, often resistance to change of the normative pillar is the first and most formidable obstacle because it relates to institutional values (Scott 2001). The CI has a well-established culture and has not been particularly receptive to adoption of innovations that challenge the dominant institutional values and norms (Gill 1996; Jacobson and Decker 2006). In order for institutional change to occur, the institution must be receptive to it (Dorado 2005). Receptivity emerges out of common understanding of a benefit associated with a proposed change. Inertia can be overcomeif a "shared sense of urgency" exists among a critical mass within the organizational field (Dorado 2005; Kotter 2008). Westley et al. (2013) describe a "tipping point" for the existence of opportunity for change, when resistance is outweighed by receptivity.

A sense of urgency resulting in a desire for change has been identified and acted upon to address some of the challenges that exist within the CI. For example, realization of the inability of the current funding model for state wildlife agencies to sustain conservation into the future has resulted in dialogue and adoption within the CI of some innovations, such as efforts to secure alternative funding in some states and the Teaming with Wildlife initiative at a national level (Jacobson, Decker, and Carpenter 2007). In their comparison of funding methods for four state wildlife agencies within the CI, Jacobson and Robertson (2012) found that two state agencies that were receptive to broadening their organizational goals and boundaries to be more responsive to diverse public interests had success in securing alternative funding (i.e., percentage of sales tax dedicated to conservation).

Although change is occurring for a variety of reasons (e.g., attrition, new generations of conservation professionals entering the field), it has been stressed that the rate of change is insufficient in regard to the impact of challenges (e.g., public apathy, habitat degradation and loss) facing fish, wildlife, and habitat (Organ and Fritzell 2000; Jacobson et al. 2010a; Decker et al. 2016). Further, while change is occurring in some organizations (e.g., some state and federal wildlife agencies, nongovernmental organizations [NGOs], tribes), it is not yet occurring systematically and collectively among the organizational field of the CI. It is within the organizational field where both change and/or resistance to change begins. Saenz-Royo, Garcia-LaZaro, and Moreno (2015) stress that that pressure within the organizational field to maintain the status quo is a strong determinant that blocks adoption of innovations within institutions.

There are indicators that the CI is receptive to innovation that will initiate a transformation process. For example, at its 22nd annual conference (2015), the Wildlife Society hosted a symposium to explore the North American Model (NAM) and its relevance to contemporary society. At this session, leaders within the CI (e.g., state agency directors, Wildlife Society Council members) discussed ways in which the NAM—the predominant articulation of values of the CI—might need to adapt to address a changing social-ecological context. Whether or not the receptivity to a broadening of institutional norms exists remains to be seen, but it is certain that strategic agency will need to be exercised among a particular type of change agent(s) within the CI to move it forward.

Strategic Agency

Institutional theorists emphasize the taken-for-granted aspects of institutions resulting in inertia and resistance to change (Scott 2001). The ability of organizations and actors within institutions to make strategic decisions and instigate change, however, is acknowledged among most scholars (Oliver 1991; Beckert 1999; Westley et al. 2013). Strategic agency refers to actors' "planned persuasion of ends…based on a rational assessment of available means and strategic conditions" (Beckert 1999). It is possible, albeit challenging, for introduction of innovation leading to transformational change within well-established institutions. In fact, there have been many examples of strategic agency demonstrated within the CI. Jacobson et al. (2007, 2010b) discuss strategic agency related to state wildlife agencies securing alternative funding for conservation; Aune et al. (2010) offer an example of diverse conservation NGOs finding common ground and working together to achieve shared goals; and Decker, Jacobson, and Forstchen (2010) outline an innovative process undertaken by Florida Fish and Wildlife Conservation Commission to identify a collaborative vision and restructure the agency to become more effective in their conservation efforts.

In his book that coined the term "diffusion of innovations," Rogers (2003) noted that change agents are needed to initiate adoption of new ideas, practices, or objects within a system. In the context of transformation, change agents willing and able to influence adoption of innovations such as a vision for change or holistic WGPs need to be of a particular kind. If seeking to create new or transform existing institutions, those actors—individuals, organizations, or groups of organizations—are considered institutional entrepreneurs (IEs) (DiMaggio 1988; Levy and Scully 2007; Westley et al. 2013). According to Battilana, Leca, and Boxenbaum (2009), IEs can be distinguished from change agents in that they initiate change that: 1) clearly diverges from the established norm of the referent institution and 2) actively participates in facilitating that change. Battilana, Leca, and Boxenbaum (2009) note that only when actors generate and promote new business models can they be considered IEs. Successful IEs tend to engender motivation and creativity to compel actors to question and expand beyond institutional norms. They are artful at convincing other organizational actors about the "desirability and viability of collaborating to jumpstart development of a solution to a problem" (Dorado 2005). Dorado (2005) suggests that institutional change depends on the "will and creativity" of IEs, the most effective being those who have a futuristic versus historic or contemporary orientation. Although IEs tend to include authority figures within organizations as these individuals may be more able to mobilize resources, it is important to stress the need for IEs at different levels and positions and often across organizational boundaries to facilitate successful transformation. Particularly innovative organizations can model innovativeness and in some cases be very effective in initiating transformative change within organizational fields (Hoffman 2001; Hall and Tolbert 2005).

IEs have and will continue to exist within the CI, and some have been very successful in diffusion of innovation leading to reform at the individual organization level (Jacobson et al. 2010b; Decker, Jacobson, and Forstchen 2010). Transformational change of the CI, however, has not occurred. Likely, the sense of urgency has not yet reached the social tipping point leading to broad scale action within the CI (Decker et al. 2016). Decker, Jacobson, and Forstchen (2010) provide an example of a state wildlife agency demonstrating strong transformative leadership (i.e., serving as an IE). The authors stress that change-ready organizations work collectively towards a compelling vision, one that has broad buy-in among all staff within the organization. While some organizations within the CI have established change visions, the CI collectively has not, which will continue to be a barrier to moving forward.

If we entertain the possibility that receptivity and a sense of urgency exists, the timing may be right for IEs to introduce innovation (DiMaggio 1988; Rogers 2003). Levy and Scully (2007) stress that IEs must be particularly strategic in their actions as they work against inertia and strong forces of resistance that exist within the organizational field. Introduction of an innovation (i.e., the WGPs) into the dialogue of the CI might be the strategic action needed to reach the social tipping point, similar to Kotter's (2008) sense of urgency (Westley et al. 2013).

Ability to Activate Institutional Networks

To move an innovation through the process of adoption, diffusion, and implementation, an IE will need to work through existing or new networks, either within or among organizations (Mintrom and Vergari 1998). Dorado (2005) notes that strategic agency is possible by "creating collaborative exchanges" among "institutional referents." This situation is best achieved through building support and momentum, making connections leading to the social tipping point. The most effective IEs tend to be embedded in the referent institution and help facilitate successful innovation adoption and diffusion because of existing relationships and shared cultural understanding (Dunning et. al 2012). Diffusion of innovation relies on contagion resulting from peers within an organization modeling behaviors of early adopters (Rogers 2003). Further, dialogue and social learning, a key component for diffusion of innovation, occur when networks are activated. Innovation that is instigated from authority positions without institutional input and buy-in can result in nondiffusion.

Institutional networks within the CI include agency-specific networks, professional societies (e.g., The Wildlife Society, Society of Conservation Biology), associations (e.g., Association of Fish and Wildlife Agencies), and professional support groups (e.g., Organization of Wildlife Planners). In order to be effective in engaging networks in dialogue about the need for change, starting at the normative foundation will require IEs to have persuasive skills and a clearly articulated vision for the outcome of the change (i.e., how it will benefit the CI). It is important to point out that activating networks within organizations or the organizational field requires a mobilization of resources, whether that be employee capacity to initiate social media campaigns or to convene individuals to engage in dialogue and learning. Dorado (2005) identifies the ability to mobilize resources as one of the key factors dictating an IEs success. Whether or not they act as IEs, buy-in from authority figures within organizations will be critical to generate the resources necessary for the WGPs to diffuse throughout the CI, so securing their support will be an important initial step.

Moving Forward

Westley et al. (2013) note that successful entrepreneurism will depend on the receptivity of the institution to the innovation. It has been suggested that the CI, because of its long-established norms and culture, is unreceptive to innovation leading to change in its foundational pillars. Over the past decade, however, the topic of CI transformation has been brought into the mainstream (e.g., publications, conferences, organizational networks), so it may be close to the social tipping point. If the following question is posed: Why, in more than a decade of discussion, hasn't transformation moved forward in a demonstrable way? The answer may be because a shared vision has not yet emerged regarding what the CI aspires to be. In other words, the organizational field knows the reasons why the CI needs to transform but has not prioritized collectively crafting a vision of what it wants/needs it to transform into. Kotter (2008) and others have stressed that a critical first step in leading change is establishing a vision for it (Westley et al. 2013). The WGPs are an important but not the first step the CI may need to take. The organizational field needs to reassess and reground itself in its values and develop a vision of what it aspires to be. Then collectively assess whether these WGPs are a normative expression of the CI's shared values. The purpose, then, in offering the WGPs is for them to be a catalyst of a much needed transformative dialogue within the CI.

Westley et al. (2013) note that a primary role of IEs is to help the institution establish and shape its vision. For transformation to move forward, it will require IEs to activate existing institutional networks and perhaps even inspire new ones. Organizations with access to many organizations within the organizational field would be effective IEs. Embedded within the CI are organizations that have such access—for example, The Wildlife Society, Wildlife Management Institute, or the Association of Fish & Wildlife Agencies. Any of these or other potential early adopters could serve as IEs and spearhead an effort to initiate dialogue using the WGPs as a springboard. Currently, an ad hoc group comprised of university, NGO, and state agency staff have taken it upon themselves to work with select state agencies to introduce the WGPs and gather feedback and ideas with the purpose of instigating discussion and eventually adoption and implementation of a set of holistic principles that can better position the CI to address contemporary and even future challenges. Kretser et al. (2016) suggests that NGOs and other entities (e.g., industry partners) that are not constrained by bureaucratic rules and policies or may have more fluid resources can be IEs that help lead or otherwise facilitate adoption, diffusion, and implementation of WGPs within the CI. Dorado (2005) notes that in some cases organizational actors on the "fringe" of an organizational field may be better able to identify and introduce innovation than those more entrenched in the existing institutional norms.

Finally, transformation is a process that can be catalyzed if the conditions are right. Adoption and use of the WGPs by the organizational field will be determined in part by how the collective decision process is structured and managed (Saenz-Royo, Garcia-LaZaro, and Moreno 2015). This process involves influence of some over others and can manifest itself either unidirectionally (e.g., via authority figures, opinion leaders) or multidirectionally (e.g., via institutional networks). Resource mobilization will be required at each step through to implementation, so must be part of strategic action undertaken by IEs. Even if the timing is not quite right, according to Dorado (2005), IEs can accumulate resources and otherwise prepare in anticipation of an emerging window of opportunity.

Conclusion

Adoption of holistic WGPs as the normative expression of the values of the CI would be a significant step towards transformation. In order for WGPs to be institutionalized, however, the organizational field must truly believe that the status quo is insufficient to address the threats facing conservation. The introduction of the WGPs provides a challenge and opportunity for the CI and those IEs that recognize the need for transformation but are not sure how to initiate it. WGPs should not be discussed in isolation but in the broader context of institutional values and a vision for change. There are indications that the CI is close to the social tipping point, and IEs seeking to help proactively shape the future of the CI may find that the momentum generated by this innovation can instigate a broader dialogue about transformation. IEs will, creativity, and ability to mobilize resources (i.e., initially human capital and time away from other priorities) are factors that will influence the success of moving forward with the adoption, diffusion, and even implementation of the WGPs. Discussions about transformation of the CI are already occurring in university classrooms, among professional societies, and within some agencies. Perhaps it is time the CI takes the next step collectively to help ensure an outcome in the best interest of conservation. The question we must ask ourselves is: Can we afford to wait?

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Workshop.
A Foundation for Managing Pennsylvania's Fish and Wildlife: Partnerships in the Early 21st Century

Approaches to Address Multiple Invasive Species in Pennsylvania: Successes, Failures, and Challenges

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Introduction

For centuries, humans have moved species from their native ranges, either intentionally or unintentionally, thus representing a source for invasive species (Vitousek et al. 1997; Lovell and Stone 2005; Hulme 2009; Holmes et al. 2009). Not all species moved from their native ranges become invasive, yet in recent decades, the increasing rate of species translocation from their native ranges has contributed to a reduction in regional distinctiveness in species composition and has been recognized as a feature of global environmental change (Lovell and Stone 2005; Vitousek et al. 1997; Mack et al. 2000). In an increasingly global economy and associated commerce, as well as expanding human population and movement, the potential economic and ecological risks associated with movement of invasive species appear to be escalating (Hulme 2009; Pimentel et al. 2000). For example, in Europe, between the year 1800 and 2000, the highest rate of alien plant, invertebrate, and mammal species establishment occurred in the period 1975 to 2000 (Hulme 2009). Invasive species can pose significant risk to human health as well as ecosystem functions and native biodiversity (Vitousek et al. 1997).

As defined in Presidential Executive Order 13112 (1999), an invasive species is considered "an alien species whose introduction does or is likely to cause economic or environmental harm or harm to human health." Here we use the term "nonnative" synonymously with "alien species," which, with respect to a particular ecosystem, is "any species including its seeds, eggs, spores, or other biological material capable of propagating that species, that is not native to that ecosystem" (Executive Order 13112 1999).

Determining the economic cost of invasive species is complex, and in the United States, estimates range widely from millions to billions of dollars annually (Pimentel et al. 2000; Lovell and Stone 2005; Pejchar and Mooney 2009; Holmes et al. 2009). Similarly, in Pennsylvania, determining the comprehensive economic impacts of invasive species is difficult given effects on a broad range of activities, such as commercial trade and agricultural and recreational activities, as well as many habitats (e.g., forests, streams) (PISC 2009). The potential economic implications can be found, for example, in recreational fishing and fishing related activities. Although estimates vary, these activities have been reported to generate more than $531 million for Pennsylvania's economy each year and support an estimated 5,602 jobs (American Sportfishing Association 2015). In Erie County, Pennsylvania, steelhead fishing has been estimated to include $9.5 million in trip-related expenses with $5.71 million in value-added activities. This resource supports an estimated 219 jobs through direct and indirect benefits (Murray and Shields 2004).

Ecologically, nonnative species have been reported as the second greatest threat to native biodiversity, with habitat loss considered the greatest threat, and nonnative freshwater fish introductions are considered an increasing threat to aquatic life, contributing to extinction of species (Wilcove et al. 1998; Cucherousset and Olden 2011). In Pennsylvania, native flora and fauna are already impacted by a broad range of environmental threats, including land-use change, pollution (e.g., municipal, agriculture), energy development activities (e.g., abandoned mine lands, shale gas extraction), and a changing climate (see PGC-PFBC 2015 for overview of threats). Invasive species can further confound environmental threats such as land-use change (Vitousek et al. 1997).

In the 2015 Pennsylvania Wildlife Action Plan, a total of 664 native species were identified as imperiled or declining (PGC-PFBC 2015). For these species, referred to as Species of Greatest Conservation Need (SGCN), taxonomic experts noted environmental threats, including invasive species, contributing to the imperilment of each species. Cumulatively, 34% of the SGCN were reported to be negatively affected by invasive species. For example, dense thickets of multiflora rose (*Rosa multiflora*), autumn olive (*Elaeagnus umbellata*), and tatarian honeysuckle (*Lonicera tatarica)* prevent native shrub and forb establishment and are suspected to be detrimental to nesting native birds, including those listed as SGCN (Luken and Thieret 1996; Hutchinson and Vankat 1997; Miller and Jordan 2011).

At an "ecological and economic crossroads" in the eastern United States, Pennsylvania is especially vulnerable to invasive species because of the many ecoregions intersecting the state and waterways used to transport goods and provide recreational opportunities. Through commercial and recreational activities and other pathways, as well as natural movement, plants and animals may reach the state via the Ohio River, the Great Lakes (Lake Erie), and from the Atlantic coast via the Delaware River (Delaware Bay) and Susquehanna River (Chesapeake Bay) (Figure 1; PISC 2009). Species that become established in local waters from these points of entry may then be transported by numerous pathways and become established beyond natural ecoregional boundaries. Species invasions may also occur along land-based pathways (e.g., Appalachian Mountains) or anthropogenic corridors (e.g., highways, pipeline rights-of-way).

Addressing Invasive Species in Pennsylvania

The diverse array of invasive species in the Commonwealth poses particular challenges for agencies and organizations to prioritize management resources. Of the many components in the Pennsylvania framework addressing invasive species, here we highlight initiatives that encompass biosecurity, outreach, coordination (intrastate and interstate), and habitat management (PISC 2009).

Biosecurity

When human activities serve as a pathway for transmission, providing decontamination and preventative measures are important management actions to reduce the rate of invasive species advancement. The impacts of aquatic invasive species (AIS) can pose significant ecological and economic implications for wild and hatchery-reared fishes and other biota. Thus, as Pennsylvania's aquatic resource management agency, the Pennsylvania Fish and Boat Commission (PFBC) developed biosecurity protocols for field staff and fish production facilities to reduce the potential for transmission of AIS (PFBC 2011). For staff conducting field surveys, this policy includes disinfection protocols for equipment (e.g., boats, motors, nets) and personal gear.

Detailed disinfection procedures are also provided for fish production facilities and stocking procedures. For these facilities, minimizing the potential transmission of AIS is multifaceted and extends beyond the immediate vicinity of the fish production facilities. For example, zebra mussels (*Dreissena polymorpha*) are present in Pennsylvania waters, mainly in western Pennsylvania where PFBC staff operate boats for capturing fish used for spawning (i.e., brood fish). Viral Hemorrhagic Septicemia IVb (VHS) virus has been identified in the Great Lakes basin from where PFBC staff collect and spawn adult steelhead (*Oncorhynchus mykiss*) and more recently, in fall 2013, the New Zealand mudsnail (*Potamopyrgus antipodarum*) was confirmed in Spring Creek, Centre County, near three PFBC fish production facilities (PFBC 2013).

Biosecurity plans with specific protocols for operations, fish production, and disease monitoring have been developed for PFBC fish production facilities and cooperative nurseries, which produce 4.2 million adult trout annually, one million steelhead smolts, and more than 50 million juvenile fish of other popular sportfish species (PFBC 2011; PFBC 2012; B. McHail, personal communication 2016). Education, awareness and adherence to AIS biosecurity plans for these facilities and the protocols include: limiting visitor and staff access to facilities and buildings, evaluating and treating facility influent water sources (including UV treatment), raceway protection to prevent contact with wildlife, and minimizing egg and fish transfers in and out of facilities. Protocols for fish production include: equipment disinfection, footbaths and disinfection stations for staff and visitors, and disease prevention within the hatchery. For disease monitoring, protocols encompass annual hatchery disease inspections and annual viral testing in brood fish. A chain-of-command approval process for fish or egg transfers into or out of each facility is based on historical disease monitoring results of the source hatchery and receiving hatchery for both intrastate and interstate facilities. These measures are necessary to secure the integrity of these fish production facilities and must be regularly evaluated for effectiveness to ensure the methods address new invasive species that may appear.

Outreach

Prevention is an important early management approach for invasive species, and in Pennsylvania, developing and distributing information in appealing formats for delivery to diverse audiences is crucial to help prevent the spread of invasive species (Lodge et al. 2006). The significance of this outreach is exemplified by anglers desiring to fish for trout in Lake Erie or its tributaries and who must purchase a Lake Erie stamp or combo permit. In 2012, stamps or permits were purchased by anglers in every county, although the largest number of these stamps and permits was sold in western Pennsylvania (Figure 2), thus indicating the likelihood of angling in Lake Erie or its direct tributaries. In 2012, with more than 97,000 anglers potentially accessing waters within Lake Erie, the opportunity for invasive species transmission either from or into the Great Lakes demonstrates the scale and importance for communicating preventative measures to this important user group. For these anglers, prevention messaging has focused on proper disinfection of fishing gear and boats.

In Pennsylvania, enlisting hunters, anglers, boaters, and other outdoor enthusiasts in preventing the spread of AIS has been the focus of the Pennsylvania Sea Grant, PFBC, and other key partners. The task of coping with multiple invasive species and multiple pathways depends upon consistent messaging that encourages anglers, hunters, divers, and other resource users to practice appropriate biosecurity measures. Local organizations (e.g., conservancies, angling clubs, boating organizations) are important recipients of outreach initiatives such as presentations and demonstrations. Venues offering the potential for large numbers of attendees (e.g., sports shows) have also proven useful for distributing crucial preventative messages.

Coordination and Partnerships

Coping with the statewide scope and diversity of invasive species exceeds the capacity of any individual agency or organization and thus requires coordination and collaboration. Partnerships occur at many scales (e.g., locally, statewide), and a comprehensive discussion of all collaborative efforts in Pennsylvania is beyond the scope of this document. However, provided here are cases that exemplify both interstate and intrastate partnerships in Pennsylvania.

Interstate Coordination

A recent focus of the Ohio River Fish Management Team (ORFMT), a consortium of state agencies, is the progressive upstream movement of invasive carp species (i.e., bighead carp *Hypophthalmichthys nobilis* and silver carp *Hypophthalmichthys molitrix*) in the Ohio River drainage. Significant populations of these invasive fishes are established downstream of the McAlpine Locks and Dam near Louisville, Kentucky (river mile 606.8), and adult fish are documented to be expanding their range upstream (ORFMT 2014).

Pennsylvania's participation with the ORFMT contributed to the Ohio River Basin Asian Carp Control Strategy Framework designed to guide efforts related to these invasive species (ORFMT 2014). Emphasis on controlling the spread of these invasive carp species in the Upper Mississippi and Ohio River basins and tributaries was expanded with the Water Resources Reform and Development Act of 2014, Public Law 113-121, and as reported by the U.S. Fish and Wildlife Service (USFWS), this legislation supported activities designed to slow and eventually eliminate the threat posed by these species (United States Cong. 2014; USFWS 2014).

With support and guidance from the USFWS—from 2013 to 2015, in West Virginia, Ohio and Pennsylvania—water samples were collected for eDNA (i.e., environmental DNA) analysis. Environmental DNA assesses the genetic composition of biological material in the water. For the Pennsylvania samples, positive eDNA results for these invasive carp species were collected near Baden, Pennsylvania (river mile 20.6); Montgomery Slough (river mile 31.6); and Little Beaver Creek (river mile 39.5). For this technology, detection of biological material (i.e., DNA) in the water sample is linked to possible occurrence but is not confirmation that a target species is present. Subsequent to collection of the positive eDNA samples, standard fish collection methods (e.g., daytime boat electrofishing, gill netting) did not yield either bighead carp or silver carp. Given the progressive upstream movement of the invasive species in the Ohio River, eDNA and traditional fish sampling will be ongoing.

Intrastate Coordination

Pennsylvania Invasive Species Council (PISC). Within Pennsylvania, coordination of invasive species issues is being addressed at many strategic and tactical levels. At the statewide scale, the Governor's (Pennsylvania) Invasive Species Council (PISC) serves as the coordinating body for state agencies and conservation partners engaged in invasive species topics. Formed under Executive Order 2004-1 and chaired by the Secretary of the Pennsylvania Department of Agriculture, the purpose of the council is to "minimize the harmful ecological, economic and human health impacts of invasive species through the prevention and management of their introduction, expansion and dispersal into, within and from Pennsylvania" (Commonwealth of Pennsylvania 2006; PISC 2016). The council advises the Governor on development and implementation of Pennsylvania's nonnative invasive species management plan and provides guidance on prevention, control of current invasive species, and rapid response to new infestations. The council also facilitates coordination among federal, regional, state, and local initiatives and organizations and has overseen development of the state's invasive species management plan and the Pennsylvania Aquatic Invasive Species Rapid Response Plan (RRP) (PISC 2009, 2014).

Pennsylvania's Aquatic Invasive Species Rapid Response Plan. Pennsylvania's Aquatic Invasive Species Rapid Response Plan (RRP) is an interagency decision-support tool designed to aid regulatory agencies in conducting a coordinated and structured response to new AIS infestations (PISC 2014). Upon receipt of reported AIS, the RRP guides interagency coordination by using a three-tiered approach and outlining implementation procedures for agencies, as well as appropriateness and types of responses (PISC 2014). The RRP is complimentary to the framework developed by the ORFMT response to the invasive carp species in the Ohio River, as well as current response and action plans such as PFBC species-specific action plans.

Tracking invasive species. Supporting intrastate coordination, the Pennsylvania *i*MapInvasives database contains information about invasive species observations and treatment records, including invasive control efforts in the Erie Cooperative Weed Management area. The database currently holds more than 5,000 (aquatic and terrestrial) plant and animal invasive species records in Pennsylvania. As a web-based mapping tool it allows sharing of invasive species distribution and control information among organizations, including land managers, who can map invasive infestations and observe threats in the vicinity of their management area. Where resources are limited, mapping invasive species distributions and knowledge of a species' invasiveness can focus response efforts, thus providing for more efficient and effective implementation responses. Information on new invasive species reported in the database is shared with jurisdictional agencies to enable AIS rapid response.

Habitat Management

American Woodcock Habitat Management and Integrated Invasive Species Management

Species of Greatest Conservation Need, as identified in the 2015-2025 Pennsylvania Wildlife Action Plan, often share a common theme—the habitats on which they rely are rare, declining in quality and availability for their use (PGC-PFBC 2015). To address the suite of species associated with these special habitats, managers often use "umbrella species" that can serve as a model for increasing the quality and quantity of these special habitats. In recent years, much success has been achieved in increasing the creation and management of early seral (i.e., intermediate) forested habitat by managing for American woodcock (*Scolopax minor*).

Throughout the American woodcock's range, habitat loss and degradation are major causes of population decline. Thus, creating and maintaining young forest habitat is important to returning this species and ally populations to past levels. This can be difficult where invasive vegetation is present. Treating invasive vegetation is expensive, yet native woody vegetation growth can greatly increase with proper invasive control. In Pennsylvania, early seral habitat management has responded to the work of the Appalachian Mountains Woodcock Initiative, which has provided funding and a blueprint for habitat creation. Though beneficial, this initiative did not address the role of invasive vegetation nor actions to address it. Research conducted in 2008 to 2010 suggested that invasive vegetation may negatively affect woodcock populations, and management of degraded early seral habitats should address invasive vegetation presence (Miller and Jordan 2011). Similarly, Borgmann and Rodewald (2004) reported that nest success was lower for American robin (*Turdus migratorius*) nests located in invasive shrubs, and these shrubs can reduce the nesting success of forest birds.

Thus, it is reasonable to assume that invasive vegetation must be managed if populations of SGCN, such as American woodcock, are to be returned to previous population levels as outlined in the Pennsylvania Game Commission (PGC) Woodcock Management Plan (PGC 2008). To address this need, the PGC began an aggressive program to reduce invasive vegetative biomass present on state game lands and to replace the invasive vegetation with native vegetation across the Commonwealth. This vegetation management program has been implemented to: 1) reduce/remove above-ground invasive biomass mechanically with forestry machines equipped with mulching attachments; 2) activate the seed bank with a flush of sunlight; 3) treat the resprouting invasive vegetation with wetland-approved herbicides while protecting the native vegetation that is also sprouting; and 4) implement long-term invasive management and control at the stand-level. Using this approach, the PGC has successfully treated invasive vegetation and restored native plant communities on 20,000 acres of state game lands since 2010 (H. E. Miller, personal communication 2016). To monitor species response, PGC volunteers annually conduct ground surveys for singing American woodcock and other birds that benefit from this native plant restoration program.

*Hydrilla (*Hydrilla verticillata*)*

Hydrilla (*Hydrilla verticillata*), a federally listed aquatic noxious weed, was introduced into the southeastern United States in the 1950s as an aquarium plant (Dayan and Netherland 2005). In the interim, it has been released beyond confined aquaria and become established in ponds, lakes, and waterways on the East Coast. With its capacity to adapt to diverse habitats, it has been labeled as "the perfect aquatic weed" (Langeland 1996). Native to Asia, hydrilla has become established in freshwater lakes, ponds, rivers, and streams, outcompeting native vegetation for limited space. Once infested, the weed forms a mat on the surface of the water, leading to reduced oxygen levels and stagnation and, thus, a suitable breeding area for insects and cyanobacteria. The thick areas of vegetation are poor habitat for fish and other aquatic life as these conditions eliminate previously available food sources. Recreational water activities (e.g., swimming, fishing, boating) may become limited or prohibitive by floating mats of vegetation.

First reported in a Pennsylvania water body in 1996, new populations of hydrilla were identified in successive years, although the threat to waters of the Commonwealth were not fully recognized at that time (USGS 2015). In 2010, hydrilla was identified in a well-known and recreationally important reservoir in Crawford County, about 60 miles (96.6 kilometers) southwest of Lake Erie. A portion of this reservoir is in Ohio where the reservoir watershed boundary adjoins the Lake Erie watershed. Boaters and anglers are known to travel between the two water bodies and beyond, as is common in most of the state. In 2015, due to the proximity of hydrilla to the Erie shoreline and the increased risk to recreation in the state, this plant was deemed a threat to Pennsylvania. As of December 2015, the Pennsylvania Department of Agriculture confirmed the presence of hydrilla in 15 lakes and ponds across the Commonwealth (Figure 3).

Early detection and rapid response are essential to the success of controlling an invasive weed such as hydrilla, thus a work group was formed to focus on management and control of this plant in Crawford County and throughout the state. Comprised of federal, state, and local agencies, as well as PISC and one nongovernmental organization, this group will be developing management plans for 2016 and beyond.

Proposed objectives for the prevention and control in the Commonwealth include:

1. Outreach and education to the public, specifically targeting anglers, boaters, and other water recreationists on preventing spread of invasive species.
2. Continued surveying and monitoring throughout the state, focusing on the Great Lakes basin and areas surrounding previously confirmed sites.
3. Initializing rapid response for control of hydrilla in confirmed sites, especially in the Lake Erie watershed and other positive water bodies within the state.

Beyond tracking hydrilla populations, 2016 surveying and monitoring will also include sampling of hydrilla plants for research purposes, including testing for a pathogen found on the plant. Avian vacuolar myelinopathy is a neurological disease caused by a cyanobacterium that grows on the underside of hydrilla leaves. This cyanobacterium, recently named and identified as *Aetokthonos hydrillicola gen.et sp. nov.*, is attributed to the deaths of water birds and bald eagles in southeastern United States. With steady expansion of hydrilla into the northeast, there is concern this expanding distribution may facilitate movement of the cyanobacteria into new regions, especially those with substantial bald eagle populations

(Wilde et al. 2014). Ongoing management efforts are focused on cooperation and participation with researchers to aid in early detection, which could minimize risks to Pennsylvania's wildlife.

Ecologically Sensitive Areas

Similar to the vegetative management approach for American woodcock, one invasive vegetation management effort in Erie County, Pennsylvania, has focused on ecologically sensitive Natural Heritage Areas (NHAs) (Figure 4). These areas support Pennsylvania's threatened or endangered species, as well as plant communities that are considered to be rare or exceptional in the state. To maintain and recover the ecological health of these habitats, in 2015, invasive plant species were managed in the Erie Cooperative Weed Management Area (CWMA). The treatment process included plant surveys in NHAs where invasive species infestations had been previously mapped. Eight sites were treated in 2015, and in coordination with the CWMA, the highest priority infestations were identified for treatment. For example, the Mercyhurst Fen NHA was prioritized for treatment of wetland plant invaders because it is a rare plant community supporting seven plant species designated as Critically Imperiled (state rank S1) or Imperiled (state rank S2) in Pennsylvania. Without implementing control measures for the invasive vegetation, the habitat for the imperiled species may be lost, contributing to the overall degradation of the fen. Treatment of 7.4 acres (3.0 hectares) included foliar herbicide suitable for aquatic environments, and in some cases, plants were cut and herbicide was applied to stumps.

On the globally significant Presque Isle Peninsula, Presque Isle Bay, and Presque Isle Gull Point, NHAs are ecologically sensitive areas. The Presque Isle Peninsula supports more 70 species of concern—greater than any other NHA in Pennsylvania (PNHP 2012). In Presque Isle State Park, the Pennsylvania Department of Conservation and Natural Resources has been actively addressing the threat of invasive vegetation using a combination of physical removal (e.g., cutting) as well as ground and aerial herbicide treatments (H. Best, personal communication 2016).

Challenges

The scope and dynamic status of invasive species is an ongoing significant threat to Pennsylvania's native species and prevention is the priority goal, for there is diminishing likelihood of eradication of invasive species established in open ecological systems (e.g., rivers, forests) (Lodge et al. 2006). Beyond the efforts highlighted in this paper, work is also being directed at other invasive species framework components (e.g., research, early detection and monitoring). Despite this multifaceted approach and collaboration of many agencies and organizations, the scope and dynamic status of the problem exceed the current level of available resources. Of the topics discussed here, we highlight needs to meet these challenges.

Challenges for Outreach Initiatives

Extensive efforts are being implemented to provide invasive species prevention messaging across Pennsylvania. Yet, development of social science studies to assess the effectiveness of these outreach initiatives is constrained by limited funding. Support for these studies could guide more effective messaging to audiences.

Challenges Implementing Biosecurity Protocols

With a rapidly changing species composition, resource managers will be continually challenged to identify effective biosecurity measures that can be safely implemented. When control measures are unknown, research—and its associated costs—will be required.

Challenges Coordinating Invasive Species Issues

Addressing components of an invasive species program is beyond the capacity of any individual agency or organization, and thus, coordination is essential. Through the Pennsylvania Invasive Species Council, the Commonwealth is well situated for this coordination. Developed under the auspices of PISC, the Pennsylvania Aquatic Invasive Species Rapid Response Plan is an important decision-support tool fostering coordination among members (PISC 2014). Given recent completion of this document, an early challenge for the RRP will be its proper implementation.

Challenges of Managing Native Habitats and Invasive Species

The scope of invasive species distribution can range from local to landscape scale, thus posing a crucial challenge for resource managers. Eradication is the desired management action for early occurrences, but for well-established and widespread species, this goal is typically not practical—leaving control as the primary course of action (PISC 2009). For species that have become well established and distributed, identifying priority areas is important. For some invasive plant species, seeds and other reproductive materials may remain viable for many years. Thus, a significant challenge will be consistent, long-term implementation of control measures.

As a crucial tool for developing efficient management strategies, the Pennsylvania *i*MapInvasives database tracks invasive species occurrences and control measures and provides information to natural resource managers. Yet, as with most data tools, long-term funding to keep records current and maintain functionality poses an indirect challenge to invasive species management.

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Figure 1. Major drainage basins and ecological connections providing opportunities for transfer of invasive species.

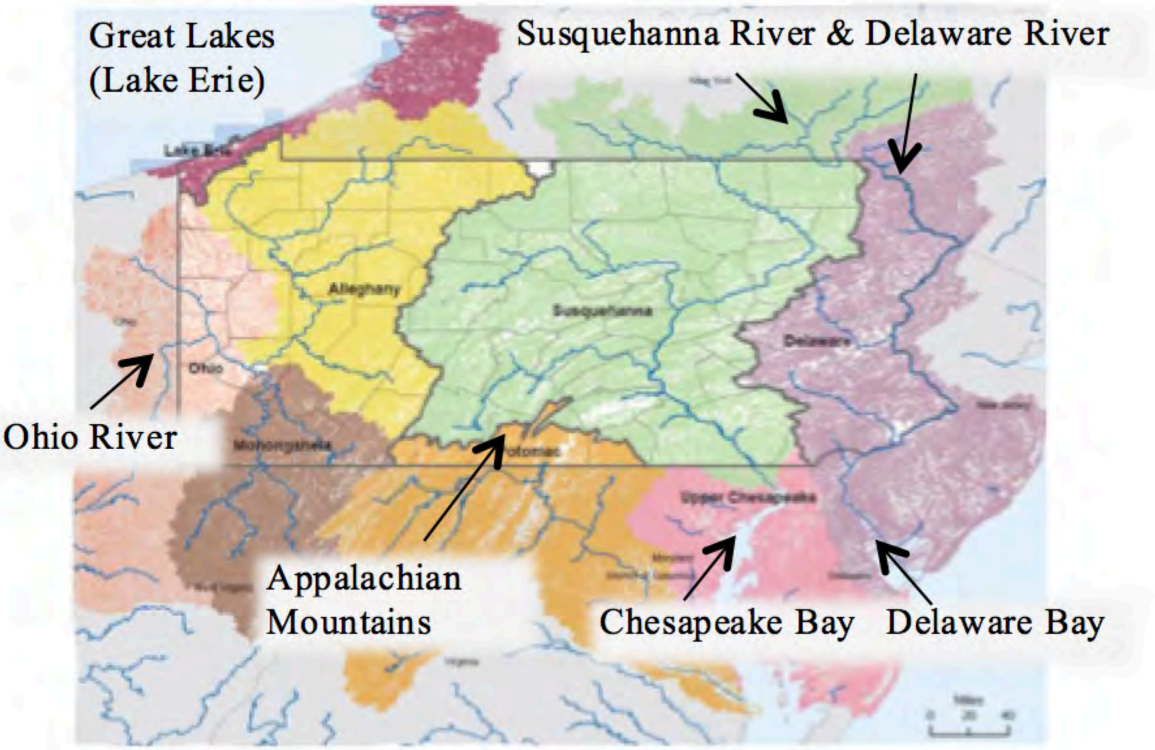


Figure 2. Number of anglers, by county, who purchased stamps or permits to fish in Lake Erie in 2012. Source: PFBC.

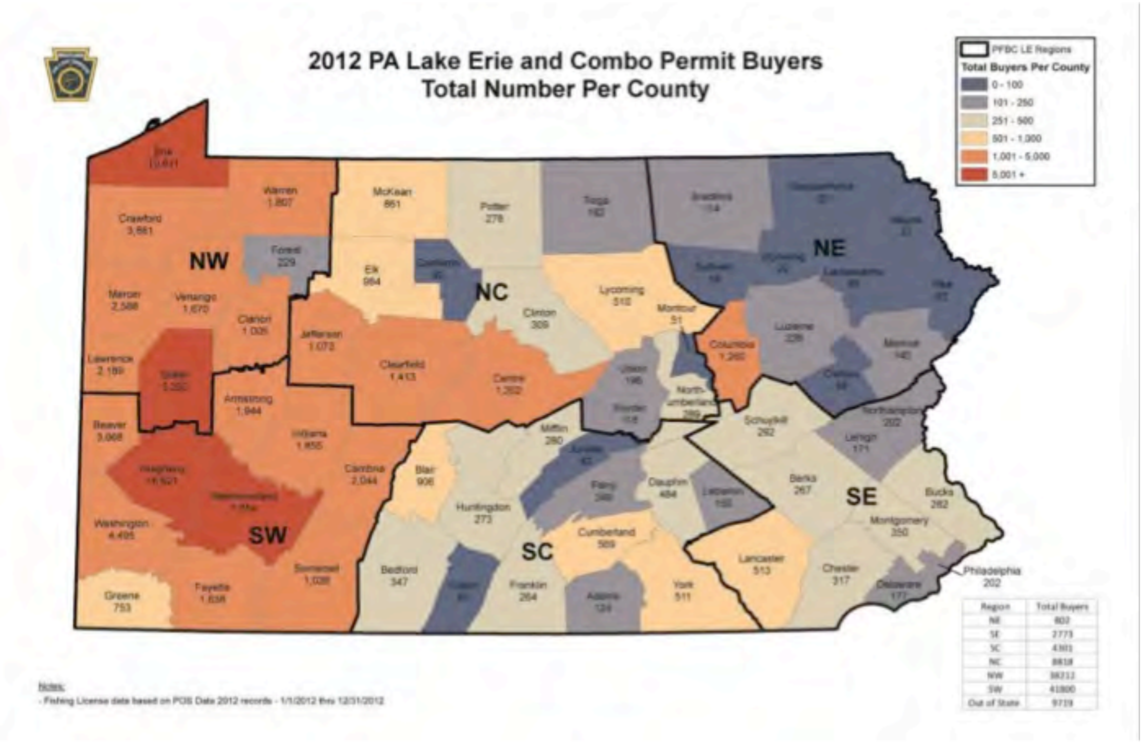


Figure 3. Pennsylvania counties with water bodies reporting hydrilla (H. verticillata) as of March 2016. Source: PA Department of Agriculture.

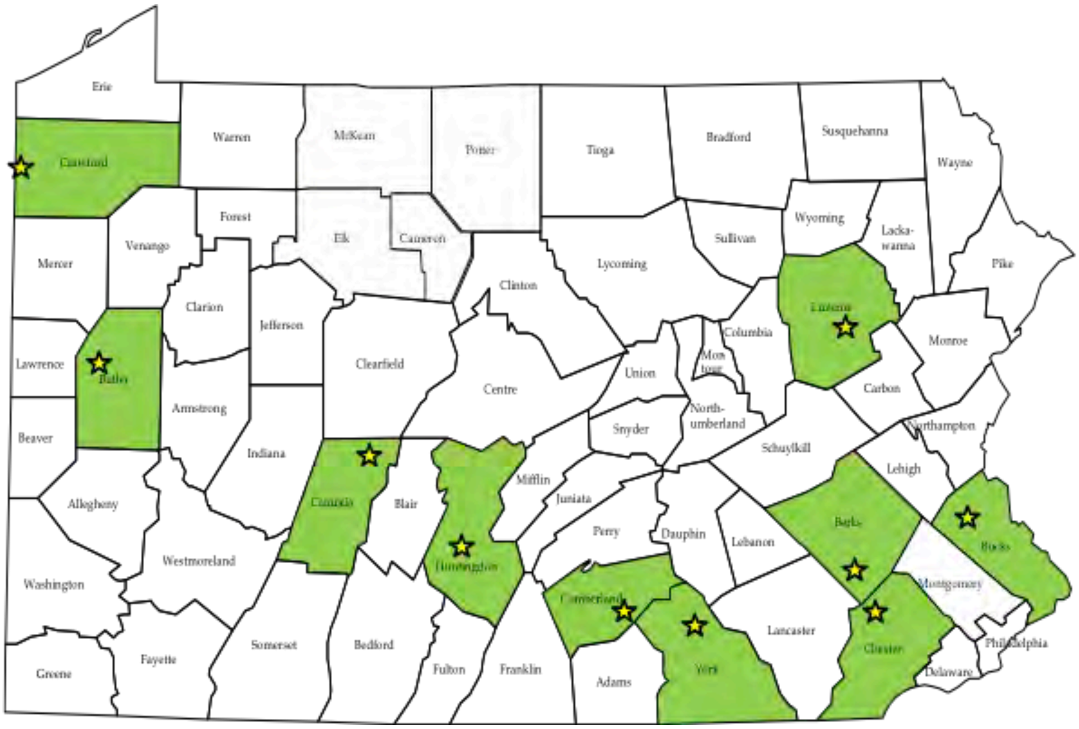
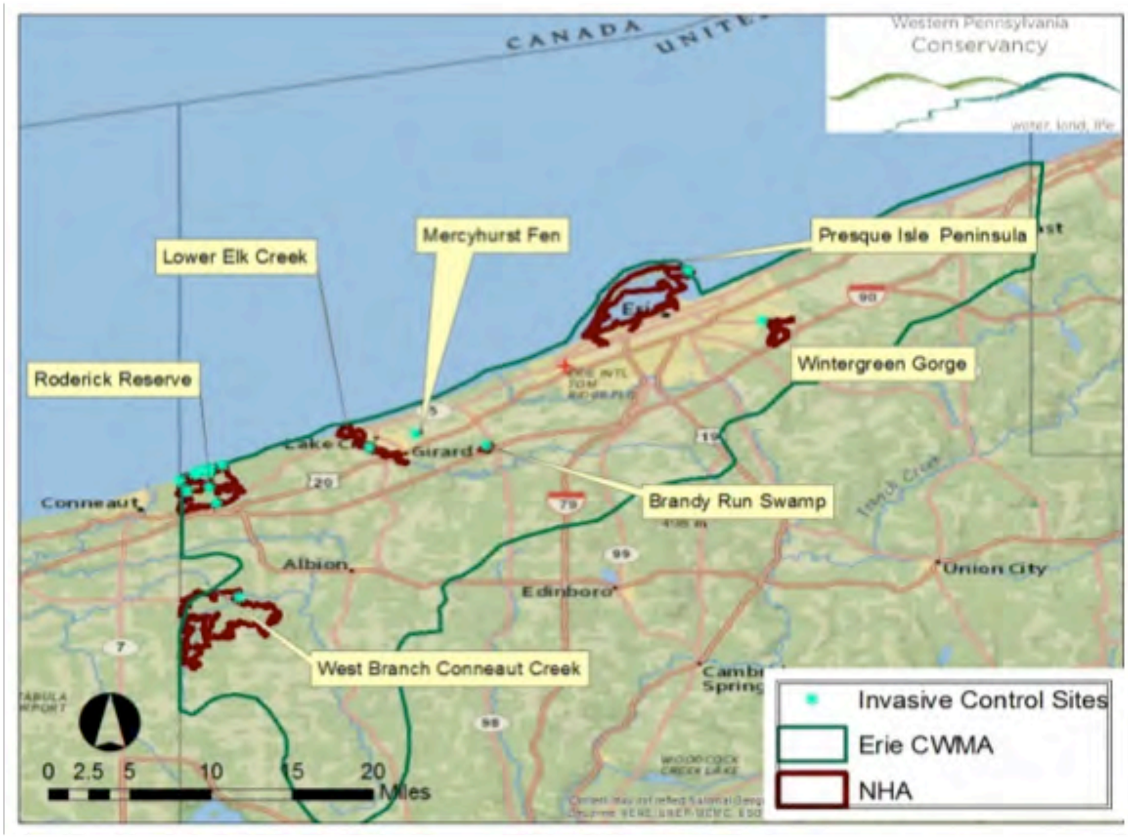


Figure 4. Ecologically important areas within the Erie Cooperative Weed Management Area (CWMA) treated in 2015. Source: Western Pennsylvania Conservancy.



Wildlife Disease—A Threat to the Future of Wildlife Conservation

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Background

Pennsylvania has confirmed two wildlife diseases in mammalian populations that will present significant financial and management challenges. The first is a newly emerged disease impacting multiple species of hibernating bats called white-nose syndrome (WNS). Caused by a psychrophilic fungal pathogen that was introduced to a site in Albany, New York, hibernating species have been documented in Pennsylvania to suffer a 98.8% mortality (Turner et al. 2011). This pathogen was first noted in December 2008 at one site, confirmed at multiple sites across four separate counties by February 2009, and was considered to have contaminated all hibernation sites statewide by the Pennsylvania Game Commission by 2012.

The second disease of focus here is chronic wasting disease (CWD). This cervid disease is caused by transmission of a malformed protein (prion) from one individual to another or from the environment to susceptible cervids and is always fatal. It has been transported and become established in captive and wild cervid herds at various locations across North America during the past several decades. CWD was first confirmed in Pennsylvania at a cervid farm in Adams County, Pennsylvania, in 2011, and was subsequently found in two other cervid farm herds in Pennsylvania. CWD was first found in wild white-tailed deer in south central Pennsylvania in 2012. The number of wild deer testing positive for CWD now stands at 20.

Emergence of CWD has coincided with emergence of a captive cervid industry in North America, which has been implicated in the spread of the disease to Canada (Kahn et al. 2004). It has also coincided with increase in feeding and baiting of deer.

Prions are not typical disease vectors as they are not living organisms. Prions can persist in the environment for at least 15 years and are very resistant to destruction. Lack of any effective treatment and limited ability to live test animals for CWD severely limit disease control even within captive cervid herds.

For these reasons, high-risk parts import bans, feeding/baiting bans, control of captive cervid movement, and destruction of infected captive herds are the only disease prevention measures currently available. Once CWD is introduced into wild cervid herds, population reduction via hunter harvest and targeted removal within infected areas are currently the only measures available to control disease prevalence levels.

These control measures require the cooperation of hunters, landowners, industry, and government. They affect people personally and have been controversial where applied. Political decisions driven by public sentiment determine law and resource availability. Thus, politics is a major factor determining whether or not disease control measures will be implemented to control CWD. Hence, the knowledge of the science of the disease, the politics within infected regions, and the choice of effective control measures all must come together in order to implement an effective disease control program.

Innovative Management Approach

White-Nose Syndrome

An emerging disease first discovered by state biologists in New York during winter surveys in 2007, the white-nose syndrome pathogen and subsequent mortality were discovered in Pennsylvania in 2008. At this time, the pathogen was not known and the first management decision was to make sure surveys did not assist the spread of this disease. Monitoring for the presence of disease focused on entrance-only surveys at known hibernacula. As the pathogen became identified and decontamination protocols were established, mortality estimates were produced with surveys at sites with multiple survey records, with overall site mortalities ranging from 90 to 100% (Turner et al. 2011). Models from these results being obtained in Pennsylvania and adjacent states suggested the very high mortality of little browns could lead to possible extinction in seven to 30 years (Frick et al. 2010). Research became an immediate focus along with collaborations with other state agencies and universities. We soon knew that the disease caused massive infections in the wings, that infection caused bats to arouse more frequently and burn through energy stores too quickly, and that dehydration and an imbalance of electrolytes was occurring (Meteyer et al. 2009; Reeder et al. 2012; Warnecke et al. 2012; Cryan et al 2013).

The collaborations established with Pennsylvania Game Commission led to many of these significant discoveries, but as this disease became established, a new focus on innovative approaches to protect and manage the survivors was born. As survivors were monitored, the Pennsylvania Game Commission led a group that pioneered the development of a screening tool using UV light (Turner et al. 2014). This tool allows us to confirm infection in a nonlethal way and follow survivors—quantifying levels of infection, measuring efficacy of treatments, or comparing individuals across many variables such as site, roost location, species, etc.

Monitoring roost location conditions, which began in 2014 in Pennsylvania, has indicated that multiple species of bats are now being found in areas colder than previously noted in past surveys, and new sites previously avoided due to higher airflow and colder temperatures are increasing in species diversity and abundance. To this end, actions taken by the Pennsylvania Game Commission have been to use multiple techniques to eliminate disturbance to bats to reduce this additive impact to energy reserves. We have also altered openings to trap cold air, increase airflow, or reduce temperatures as needed in an effort to impair fungal growth and increase bat survival.

Other innovative techniques more recently initiated involve treatments that target the roost structures as opposed to the bats. Additionally, we are seeking to find viruses associated with the fungus in an attempt to see if any of these could be used as a biocontrol in a process similar to what was used with Chestnut blight in Europe.

Chronic Wasting Disease

An emerging disease first identified as a clinical disease in 1967 among captive mule deer at a Colorado Division of Wildlife Research Facility in Fort Collins, Colorado, chronic wasting disease was first classified as a transmissible spongiform encephalopathy (TSE) in 1978 (Williams and Young 1980). CWD is a contagious and fatal disease with no cure or treatment that has continued to spread slowly within endemic areas and to “leap” long distances to new parts of North America. These “leaps” seem to be associated with anthropogenic activities. Recognizing that the science related to prion diseases remains in infancy and that politics control the ability to apply control measures, an innovative and integrated approach involving extension of the science and focusing of “political will” is necessary if a CWD pandemic is to be avoided. Manjerovic et al. (2014) concluded that localized culling might be the most effective control strategy for maintaining low CWD prevalence levels in deer without compromising hunter harvest opportunities. To gain public acceptance of disease control measures, it will be necessary to engage the public in the process of disease control such that landowners, hunters, cervid farmers, the general public, and governmental agencies see benefits and jointly take ownership of control programs. Efforts to control the spread of CWD have been hampered by political issues as much as by incomplete science. The Pennsylvania Game Commission has recognized these problems and is now turning its attention to these issues, engaging the various interested parties in an attempt to address the CWD control problem in Pennsylvania. This must involve a "ground game" where the public is personally engaged as well as a steady flow of information.

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A Change in Abundance of Smallmouth Bass at a Popular Recreational Fishery Leads to Policy-Level Action on Multiple Scales

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Introduction

Black bass *Micropterus* spp., including smallmouth bass (*Micropterus dolomieu*), are the most sought-after group of freshwater fish in the United States and the second most popular species group in terms of days spent fishing in Pennsylvania behind only trout (U.S. Department of Interior et al. 2011; Harris 2015; Long et al. 2015). As such, management of these species has been an important focus of resources agencies throughout North America.

In Pennsylvania, the smallmouth bass is native to the Ohio drainage but was introduced to the Delaware River, Schuylkill River, and Susquehanna River in "about1869" or 1870 by industrious groups of anglers and was abundant within three years of introduction (Milner 1874; Bean 1892; Meehan 1893). Since that time, smallmouth bass have been managed as naturally reproducing populations using recreational fishing regulations that have sought to limit angler-induced loss through a variety of seasonal harvest periods governed by various minimum length limits over time.

The Susquehanna River and its large, warm-water tributaries provide a popular and economically valuable recreational smallmouth bass fishery. A comprehensive creel survey including the middle and lower Susquehanna River (103 mi [165 km]) and lower Juniata River (32 mi [52 km]) found that, between May and October 2007, anglers made an estimated 66,871±4,814 trips and expended an estimated 286,144±20,585 hours targeting smallmouth bass. Estimated smallmouth bass catch rates during this survey were 0.6481±0.0241 fish/angler-hour while harvest rates were 0.0090±0.0014 fish/angler-hour (Smucker et al. 2010). In 2007, the recreational black bass fishery of the middle and lower Susquehanna River and the lower Juniata River had an estimated annual economic contribution of $1,975,842 and an annual economic impact of $864,161 (Shields 2010).

Study Area

The Susquehanna River originates at Otsego Lake in Cooperstown, New York, and flows 444 mi (715 km) south to the Chesapeake Bay at Havre de Grace, Maryland (Figure 1). The basin drains 27,500 mi^2 (71,224 km^2), including parts of New York, Maryland, and Pennsylvania (Brown et al. 2005). Included in this are a number of large, warm-water tributaries that also support smallmouth bass populations such as the Chemung River, West Branch Susquehanna River, and Juniata River. Generally, it is a wide (exceeding 1 mi [1.61 km] in some locations), shallow river with moderate to low gradient (Pazzaglia and Gardner 1993). Throughout this paper we will be referring to three primary large-river reaches in the Susquehanna River watershed: the middle Susquehanna River from Sunbury, Pennsylvania, to York Haven, Pennsylvania; the lower Susquehanna River from York Haven, Pennsylvania, to Holtwood, Pennsylvania; and the lower Juniata River from Port Royal, Pennsylvania, to the confluence of the Susquehanna River (Figure 1).

Onset of Disease

Beginning in 2005, disease outbreaks among young-of-year (YOY) smallmouth bass have occurred annually with varying degrees of severity at the West Branch Susquehanna River, Susquehanna River, and Juniata River. Fish were characteristically observed swimming weakly near the surface with noticeable white lesions, sores, eroded fins, and some were found dead. While disease has a large impact on YOY smallmouth bass, it appears to have little if any effect on other species. Pathological analysis has indicated that bacterial infections by *Flavobacterium columnare* (columnaris), *Aeromonas allosaccarophila*, *A. hydrophila*, *A. popoffii*, *A. veronii-sobria* biovar, *A. veronii-veronii biovar*, and *Pseudomonas aeruginosa* are responsible for disease and mortality (Chapin et al. 2009; Chapin and Crawford 2012; Starliper et al. 2014; Smith et al. 2015). All are opportunistic bacteria so the mechanism of infection is similar despite species differences.

Pathological analysis has identified other pathogens present as well. Analyzed smallmouth bass had substantial myxozoan and trematode parasite infections. Among these was *Myxobolus inornatus*, which was originally isolated and described from YOY largemouth bass (*Micropterus salmoides*) in a Montana hatchery and adult smallmouth bass from Lake Erie, but was previously unknown from YOY smallmouth bass (Fish 1939; Dechitar and Nepszy 1988; Muzzal and Whelan 2011; Walsh et al. 2012). These infections may have resulted from disease but could also contribute to its presence by causing stress. Largemouth bass virus (LMBv) has also been detected in smallmouth bass from the Susquehanna River system. Smallmouth bass, like many other species, are known carriers of LMBv but are not believed to be directly affected by the virus (Grizzle et al. 2003). It is unknown if carriers of the virus experience additional stress that may weaken the immune system.

Analysis of adult smallmouth bass from the West Branch Susquehanna River (2009), Susquehanna River (2008–2010), and Juniata River (2010) identified very high rates of intersex: a condition in which female egg precursor cells are found in the testes of males (Blazer et al. 2014). Although this condition is natural among gonochorist fish like smallmouth bass, the proportion of the fish affected and the severity of the cases documented in the Susquehanna River Basin are not considered typical (Blazer et al. 2014). While intersex is not directly related to YOY smallmouth bass mortality, many of the compounds that cause these effects could contribute to immune suppression in YOY smallmouth bass.

Stressful water quality conditions in near-shore habitat used by YOY smallmouth bass potentially contribute to immune suppression, making them more susceptible to bacterial infection. Water quality investigations conducted by the United States Geological Survey (USGS) Pennsylvania Water Science Center in 2008 documented stressful water quality conditions in critical near-shore habitats (Chaplin et al. 2009). They determined that minimum daily dissolved oxygen concentrations (DO) were significantly lower at near-shore locations when compared to adjacent main-channel locations. Water temperature of the Susquehanna and Juniata rivers were also typically higher and more varied when compared to Allegheny River or Delaware River locations (Chaplin and Crawford 2012). Both factors are stressful to some fish species.

In addition to conventional water quality parameters, recent studies have documented substantial impacts of endocrine disrupting compounds (EDC) and emerging contaminants (EC) in the Susquehanna River Basin (Reif et al. 2012; Blazer et al. 2014). These compounds are attributable to a number of sources—including pharmaceuticals, fertilizers, and household cleaning products—and can have major effects on aquatic environments. The severity of these impacts is only now starting to be understood. These contaminants can cause various physiological imbalances in fish, such as intersex, and other aquatic organisms and have the potential to alter many aspects of the aquatic ecosystem. EDCs and ECs can cause undue stress to fish and other organisms and predispose them to diseases—similar to what has been observed in smallmouth bass.

Changes in Smallmouth Bass Population Characteristics

Effects of disease, in conjunction with the typical variables that drive population characteristics, can manifest into population-level issues. This is especially true when they affect survival and recruitment (Smith et al. 2015). Reproduction and recruitment of smallmouth bass to river fisheries is highly variable across Pennsylvania rivers and other rivers across the country (Lorantas et al. 2012; Pflieger 1975; Paragamian 1984; Slipke et al. 1998; Buynak and Mitchell 2002; Swenson et al. 2002; Smith et al. 2005). The severity of these impacts is further magnified when the occurrence is prolonged and affects several consecutive cohorts, as is the case in portions of the Susquehanna drainage. Despite variability in reproduction and recruitment, regression residual technique analysis demonstrated that large year classes exposed to disease exhibited survival that was below average relative to those not exposed both within and outside the incident area and time (Lorantas et al. 2012). Periodic boat electrofishing relative abundance estimates (catch per unit effort, CPUE, fish/h) of adult smallmouth bass have demonstrated a significant decrease in relative abundance between pre-2005 and post-2005 periods (Smith et al. 2015; Figure 2). Further, the length distribution—used, in this instance, as a surrogate measure of age—of smallmouth bass is different as a result of changes in recruitment at this reach. Smith et al. (2015) found that proportional stock density had significantly increased from a median of 33% during pre-2005 surveys to 62% during post-2005 surveys, suggesting that the contribution of stock-size and larger fish to the population had increased to a point where there was potential for functional problems. This change is attributable to difference in the contribution of smaller, presumably younger fish to the population since 2005.

In addition to fisheries managers, anglers who frequently fished the middle Susquehanna River also noted the changes in adult smallmouth bass abundance and population characteristics and observations of diseased YOY smallmouth bass. Acknowledgement of these changes and observations led to calls from anglers and the public at large for sweeping policy changes to address the problem. Thus, managers recognized the opportunity for both a short-term remedy—that included maintenance or enhancement of existing smallmouth bass abundance—and a long-term remedy that included addressing circumstances contributing to disease and mortality manifestation in YOY smallmouth bass. We will discuss specific policy-level actions that were initiated in response to those calls.

Fishing Regulation Changes

As a result of changes in abundance of adult smallmouth bass, there was increased interest in altering existing recreational fishing regulations in an effort to stem the continued decline as well as bolster abundance. The setting of harvest policies and rules in managing exploited sport fish populations such as smallmouth bass are often carried out using guidance from computer or mathematical models in Pennsylvania. This is especially true when population vital rates are leading to appreciable declines in population number. Circumstances beyond angling likely contribute substantively to observed recruitment and density reductions of smallmouth bass in this instance. Given that fishing-related exploitation was not the principal cause of the changes in abundance, application of more restrictive harvest regulations would be focused on preserving extant populations until recruitment improved. Objectives of these efforts were to eliminate harvest, reduce latent catch-and-release mortality associated with weigh-in tournaments, and reduce catch-and-release mortality of adult bass during the spawning period (Lorantas et al. 2012).

Existing fishing regulations within these subject reaches were part of the Big Bass Program, which included a harvest season with a 15-inch minimum length limit from mid-June through September with a six-fish-daily creel limit; a catch-and-release season from mid-April to mid-June where no organized fishing tournaments were allowed; and a trophy harvest season with an 18-inch minimum length limit and two-fish-daily creel limit from October through the following mid-April. Model simulations would compare a series of outputs derived from three proposed fishing regulation options to existing Big Bass Program simulated outputs. Regulation alternatives compared to existing regulations included year-round, catch-and-release fishing with no black bass harvest and no weigh-in fishing tournaments; year-round, catch-and-release fishing with no black bass harvest and a closed season prohibiting targeting black bass during a mid-April to mid-June nesting and parental care period; and year-round, catch-and-release fishing with no black bass harvest and a closed season prohibiting targeting black bass during a 1 May to mid-June nesting and parental care period.

Model simulations coarsely described hypothesized changes in smallmouth bass density in the subject reaches using a modification of the single cohort dynamic pool model, developed by Clark (1983) (Beverton and Holt 1957; Gulland 1969). Specifically, the model was developed and parameterized so that output detailed equilibrium number of smallmouth bass within a cohort by age. A novel formulation of the classic dynamic pool model, Clark's (1983) model included a measure of catch-and-release mortality and a measure of instantaneous catch rate, as well as other parameters typical of age-structured models:

$$C=f(R, G, M, F, H, Q)$$

Where equilibirum catch (C) is a function of recruitment (R), growth (G), instantaneous natural mortality (M), instantaneous fishing mortality (F), instantaneous catch-and-release mortality (H), and instantaneous catch rate (Q). In this analysis, our hypothesized outcomes were largely a function of the accuracy and precision of parameter estimates, some of which we could only coarsely estimate. Model simulations that were applied incorporated vital statistics—growth (in length and weight), mortality, maturity, and specific recruitment measures—derived from smallmouth bass inhabiting the middle and lower Susquehanna River and lower Juniata River. Additional parameters, descriptive of fishery instantaneous capture rates, were derived from an angler catch-and-harvest survey for these reaches and the scientific literature, including literature pertaining to related species (Smucker et al. 2010; Lorantas et al. 2012).

Simulations were designed to guide decision makers in judging merits of alternative fishing regulations but were not intended to precisely predict outcomes. Those alternatives compared the simulated equilibrium number of smallmouth bass ≥ age 4 (mean TL 12.7 inches [322mm]) and ≥ age 6 (mean TL 15.1 inches [384mm]) under various regulatory alternatives to simulated equilibrium numbers of smallmouth bass described by Big Bass Program regulations. Simulations used two different catch rate (Q) scenarios—a high catch rate and modest catch rate—for generating outputs. Similarly, model runs incorporated parameters indicative of very low and modest harvest levels for use in guiding decision-making based on anecdotal input that fishing mortality was low and also provided the most conservative estimates of simulated change so as to not set unrealistic expectations for any regulation option.

For simulations where parameter estimates were secured and deemed reasonably descriptive of smallmouth bass populations on these river reaches, increased harvest restrictions lead to modest increases in smallmouth bass ≥ age 4 and ≥ age 6 where no spawner-recruit relation was assumed (constant average annual recruitment). Simulated change, without factoring changes in recruitment, ranged from 13 to 38% for smallmouth bass ≥ age 4, depending upon the rule applied (Table 1). Simulated change, without changes in recruitment, ranged from 24 to 62% for smallmouth bass ≥ age 6, depending upon the rule applied (Table 1). The greatest increases in equilibrium smallmouth bass abundance relative to Big Bass Program regulations occurred for regulation options that included a closed season during the nesting and parental care periods. The estimated increase in equilibrium smallmouth bass abundance for the year-round catch-and-release rule with a closed spawning season from mid-April to mid-June was hypothesized to be at least 20% for age-4-and-older fish and at least 35% for age-6-and-older fish. Similarly, the estimated increase in equilibrium smallmouth bass abundance for the year-round catch-and-release rule with a closed spawning season from 1 May to mid-June was hypothesized to be at least 20% for age-4-and-older fish and at least 34% for age-6-and-older fish. In the current analysis, as harvest rules became more restrictive, greater numbers of mature smallmouth bass were preserved and potential for greater recruitment resulted, as measured by the spawning potential ratio (SPR) in most scenarios (Goodyear 1993). For all scenarios, SPR was greatest when a closed season was applied from mid-April or May to mid-June. Although unable to concisely account for mechanisms influencing annual change in reproduction and recruitment, recent lower abundance measures of YOY were used in computing equilibrium abundance per recruit in all model runs. Some rule changes examined, as well as known and unknown anthropogenic or climactic influences, have potential to affect annual reproduction and recruitment, which have potential to substantively influence hypothesized outcomes. The hypothesized model results identify outcomes under prevailing average conditions through use of parameter estimates that conservatively describe smallmouth bass population dynamics within river reaches under consideration.

Recommendations for regulations moving forward called for institution of year-round catch-and-release fishing for black bass species with no organized, weigh-in tournaments and a closed season during 1 May through mid-June period. The recommendation for beginning the closure period on 1 May instead of mid-April was the result of a number of factors. A review of scientific literature and water temperature data from the subject reaches suggested that the smallmouth bass nesting period in this area, although annually variable, typically began in early May and would be protected by this start date. Second, model results suggested that there would have been little if any estimated benefit by extending the closed season the additional two-week period during a popular time for anglers targeting smallmouth bass. Third, opinions in consultation with avid recreational anglers and guides—and those received during open public comment periods—were more supportive of the regulation that had a closure beginning 1 May. The regulation was proposed in September 2011 and was adopted and implemented prior to the 2012 fishing season.

Causal Analysis

During the course of investigations into the factors contributing to disease outbreaks among young-of-year smallmouth bass, several variables were identified that may be contributing to their cause; however, no definitive causative agent could be identified. Previously mentioned studies by Chaplin et al. (2009) and Chaplin and Crawford (2012) identified water quality-related factors that could be contributing to outbreaks. After repeated calls for action from the public, legislators, and agency officials, large-scale data collection was initiated by several organizations. In 2014, the Pennsylvania Department of Environmental Protection (PADEP) and the Pennsylvania Fish and Boat Commission (PFBC) initiated an effort to synthesize the large body of potentially relevant publications, data, and analyses. Consequently, PADEP and PFBC requested assistance from the United States Environmental Protection Agency (USEPA) in identifying the causes of the smallmouth bass declines at the Susquehanna River. USEPA recommended and offered to facilitate their stressor identification process—Causal Analysis/Diagnosis Decision Information System (CADDIS)—to defensibly identify factors contributing to the smallmouth bass decline (Norton et al. 2009). CADDIS was developed to identify the cause(s) of an environmental problem by determining which of a set of alternative candidate causes is best supported by the body of evidence. The CADDIS process was chosen because it provides transparency and reduces bias without restricting the types of evidence used. It provides a framework for engaging experts and brings different sources of data together in order to identify one or more likely causes of an environmental problem (Norton et al. 2009; Suter et al. 2010; Norton et al. 2014). This process assisted in developing appropriate programmatic strategies that will eventually result in an improved fishery.

In cooperation with the PFBC, PADEP, and USEPA, a group of interdisciplinary scientists were identified from various state, interstate, federal, and academic organizations to vet hypotheses on factors contributing to the decline. Other participants included representatives from the Susquehanna River Basin Commission (SRBC), USGS, United States Fish & Wildlife Service, and Susquehanna River Heartland Coalition for Environmental Studies. This group conducted three workshops over the course of a year to make a preliminary determination of the focal issue (the case); determine possible factors contributing to that issue (candidate causes); and pool, analyze, and review available data and literature to determine which suspected candidate cause(s) is contributing to the problem.

The group defined the case as a decrease in abundance of smallmouth bass resulting from poor recruitment of juvenile smallmouth bass into the population. The temporal frame of the effect was established as 2005 to the present, since 2005 was the initial year that the decline was documented.

However, some longer-term trend data were reviewed in order to elucidate the relationship between several candidate causes and the effect. The geographic range or study area was identified as the middle Susquehanna River and the lower Juniata River. These reaches were selected because they had the most pronounced decrease in smallmouth bass abundance. For comparative analysis, similar stream reaches were selected with stable and sufficiently robust smallmouth bass populations without documented instances of smallmouth bass population decline. These included the upper Allegheny River; lower, nontidal Delaware River; upper Juniata River; upper Susquehanna River; lower West Branch Susquehanna River; Pine Creek (Lycoming County, Pennsylvania.); and Loyalsock Creek (Lycoming County, Pennsylvania). Available data and anecdotal evidence suggested that smallmouth bass populations have not declined in abundance or experienced changes in length and age structure within these reaches, despite observations of disease occurring in some or all of these reaches during the study period.

After case definition, participants fielded and vetted a number of potential candidate causes and modes of action (causal pathways) that could lead to the observed reduction in smallmouth bass abundance. The candidate causes identified represented in-stream stressors that could be directly responsible for mortality or could induce stress, increasing susceptibility to disease. The causal pathways described provided the interim steps by which human activities, sources, and in-stream ecological processes result in a candidate cause. For example, increased nutrient loads are part of a multiple-step causal pathway that can produce stressors that harm fish. Increased nutrient loading (nitrogen and phosphorus) associated with certain land-use patterns and storm-water runoff can increase algal growth (Dodds and Whiles 2002; Smith et al. 2015). The algae photosynthesize and respire, increasing the range of daily variation of pH and dissolved oxygen concentrations, which is widely accepted as harmful to fish species (Wiebe 1931; Alabaster and Lloyd 1980; Schäperclaus 1991).

Fourteen potential candidate causes were initially accepted by participants for the decline in smallmouth bass abundance (Table 2). As the analytical process continued and familiarity with the data improved, several of the candidate causes were subdivided to address multiple mechanisms that were not originally considered. More than 50 separate analyses were conducted to assess various aspects and mechanisms of each of the list of candidate causes and to gauge their relevance in contributing to declines in smallmouth bass recruitment. The evidence and analyses were evaluated by comparing data—both spatially and temporally; comparing with available scientific literature; and determining whether the mechanism is occurring and is feasible. Each analysis was evaluated and its relevance weighted using data available at the time. Each candidate cause was categorized based on its contribution to decline in recruitment of smallmouth bass as either likely, unlikely, or uncertain (Table 2).

The CADDIS process narrowed the scope of concerns that may be affecting smallmouth bass populations in the Susquehanna and Juniata rivers. Based on all available evidence, eight candidate causes were not supported by the data analysis and were considered "unlikely" for directly causing the decline of smallmouth bass recruitment. As such, the amount of resources devoted to continue with data collection and analysis of these aspects will be reduced by partner agencies and organizations except where it is critical to their respective missions.

The evidence for eight additional candidate causes was judged to be "uncertain." Candidate causes within this category generally had insufficient data to make a confident decision on placement in another category, the type and quality of available data was not adequate for assessing specific components of the cause, or a new aspect of that cause that was not originally considered came to light as part of the analysis. Many of the causes that fall under this category are a result of subdivisions of existing candidate causes that occurred as participants became more familiar with the available data. Others within this category had ongoing or planned studies for which data was not available at the time of analysis, but mechanisms seemed plausible. Studies devoted to aspects of these candidate causes are either ongoing or considered high-priority to determine the role they are playing in declines in smallmouth bass abundance.

The group considered two candidate causes as "likely" factors in contributing to declines in smallmouth bass abundance: 1) herbicides and endocrine disrupting compounds and 2) pathogens and parasites. In both instances, however, they are not believed to be directly responsible, rather operating in conjunction with other factors or indirectly contributing to the decline in recruitment. In the case of herbicides and EDC, the mode of action considered is immune suppression of young-of-year smallmouth bass, making them more susceptible to parasites and pathogens present in the system. Available data for herbicides and other select EDC demonstrated that their concentrations within affected reaches were higher than unaffected or comparison reaches supporting their association with the decline. Additionally, adult smallmouth bass within affected reaches had higher rates of reproductive endocrine disruption than unaffected or comparison reaches, suggesting that young fish were being exposed to EDC at biologically meaningful concentrations (Blazer et al. 2014). Other recent studies looking at pathogens among fish both within and outside of the Susquehanna drainage have demonstrated that they likely play an important role in declines in smallmouth bass recruitment. Simple linear regression analysis demonstrated that there was a very strong relationship between prevalence of disease—or the proportion of fish with signs of clinical disease during young-of-year smallmouth bass surveys—and CPUE of age-1 smallmouth bass the following year in adult smallmouth bass surveys. Additionally, pathological analysis of young-of-year smallmouth bass demonstrated more frequent and severe infections by the parasite *Myxobolus inornatus* at affected reaches than at other reaches (Smith et al. 2014). Similarly, detections of the viral pathogen LMBv were also higher in samples with fish displaying clinical signs of disease compared to populations with apparently healthy fish (Smith et al. 2015). Even though there is strong associative evidence for several pathogens, they are not believed to be causing overt mortality but are, however, working as opportunists taking advantage of compromised immune systems in affected fish. Ongoing and future studies will try to confirm immunosuppression in the affected populations and elucidate the modes of immune suppression of herbicides and select EDC as well as the role select parasites and pathogens play in mortality events and the subsequent effects on recruitment.

Policy Action Resulting From Causal Analysis

In addition to clarifying causal agents associated with declines in smallmouth bass abundance, the CADDIS process also identified a number of programmatic opportunities and policy changes that could be addressed. Most universal among these was that the results and recommendations of the CADDIS process identified and prioritized required study elements for agency and institutional research (Shull and Pulket 2015). Prior to this, agencies and researchers would typically focus on aspects related to their respective expertise and mission or on aspects where grant funding may be available. The CADDIS outcome provided a number of recommended study elements that partner agencies and organizations can cite to leverage both internal and external funding to complete. This information also allows cooperators to justify allocating programmatic resources to capture data to fulfill these recommendations. Also, this framework provides cooperators a means to track progress on meeting the CADDIS recommended needs over time.

Another important programmatic outcome of CADDIS was the identified need to develop monitoring and assessment methodologies specific to large river systems. One common, recurring theme during this investigation was the limitation on the type and quality of data available from large river systems to conduct in-depth analyses and assessments. Existing assessment techniques and methodologies, while effective in smaller systems, were not adequate to detect changes in large systems. As a result, cooperating agencies have now identified these shortcomings and are working collaboratively to develop large-river specific assessment methodologies to complement the extensive and well-developed methodologies already in place for smaller systems. Although it will take time to refine, development is currently underway with hopes of institution in the near future. Similarly, the CADDIS process identified the need to institute new technology and techniques to expand data collection opportunities to address new, previously under-measured or unmeasured parameters. The increase in the importance of EC, including herbicides, and EDC in the health and recruitment issues of smallmouth bass led to the expansion of data collection in these areas. This included the institution of more extensive analytical suites focusing on these parameters, application of passive sampler technology to better characterize contaminants in the system, and more focused collections targeting important seasonal and hydrologic conditions to better understand contaminant dynamics in these complex systems.

The importance of EC and EDC in the CADDIS process also identified the need for appropriate water quality criteria to track and identify conditions to protect aquatic systems. Existing water quality criteria for many of these compounds do not exist. For those that do have established criteria, the concentrations are often protective of human health (e.g., drinking water standard for atrazine) and not necessarily protective of aquatic life where meaningful concentrations may be orders of magnitude lower. PADEP is currently conducting a literature review and comparing other criteria from other jurisdictions to develop criteria for parameters such as atrazine, metalochlor, and glyphosate to be protective of aquatic organisms. These criteria would be set at biologically meaningful concentrations and be protective of sensitive life stages of select organisms. Development of these criteria is in early stages and the timeframe for inclusion in existing criteria is indefinite.

Another sweeping change that was in part supported by the information gathered by CADDIS is the Chesapeake Bay Program "reboot" being instituted by PADEP and Pennsylvania Department of Conservation and Natural Resources. This effort entails a considerable realignment of agency resources in an effort to meet demands set forth in the Chesapeake Bay Agreement. This large effort will be focused on reducing nonpoint contributions (i.e., agriculture and urban storm water) of nutrient and sediment to the Chesapeake Bay. Many of the sources of pollutants identified during the CADDIS process are believed to originate from upland, nonpoint source pollution in tributary systems. Corrective measures identified in this plan will likely benefit water quality in the Susquehanna River system, including many of the parameters of concern identified during the CADDIS process.

The onset of disease in young-of-year smallmouth bass and the decline in smallmouth bass abundance has resulted in an unprecedented opportunity for collaborative research and interagency cooperation. New relationships among agencies have developed and broadened the collective knowledge pool among cooperating agencies. Additionally, responses to these findings have led to policy-level action—both independently and collaboratively—among agencies. These collective efforts will hopefully result in increased recruitment of smallmouth bass and an increase in abundance of this recreationally important and locally economically important species.

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Figure 1. Study reach within the Susquehanna River drainage. Subject reaches include the middle Susquehanna River (Sunbury to York Haven, Pennsylvania), lower Susquehanna River (York Haven to Holtwood, Pennsylvania), and the lower Juniata River (Port Royal, Pennsylvania, to the confluence of the Susquehanna River).

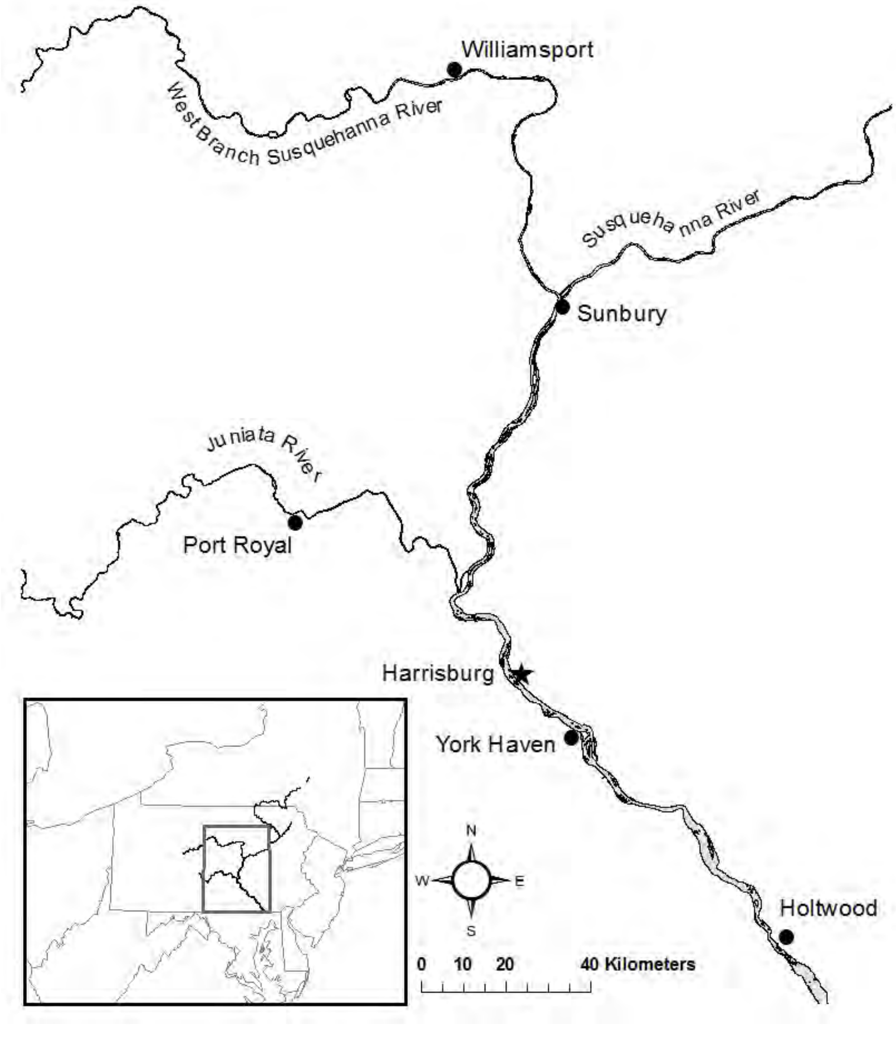


Figure 2. Boat electrofishing catch per unit effort (CPUE; fish/h) of adult smallmouth bass (age 1 and older) at the Susquehanna River between Sunbury and York Haven, Pennsylvania: 1990–2012.

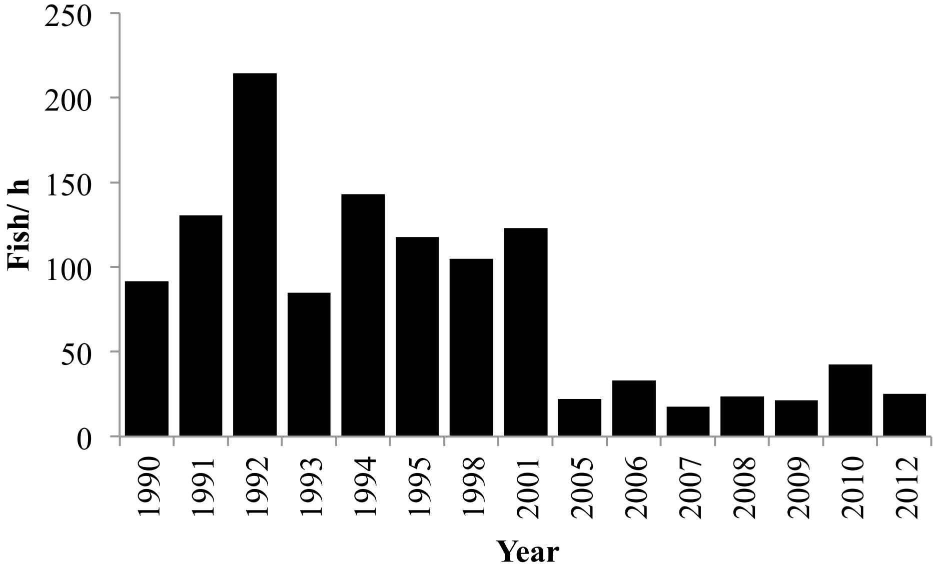
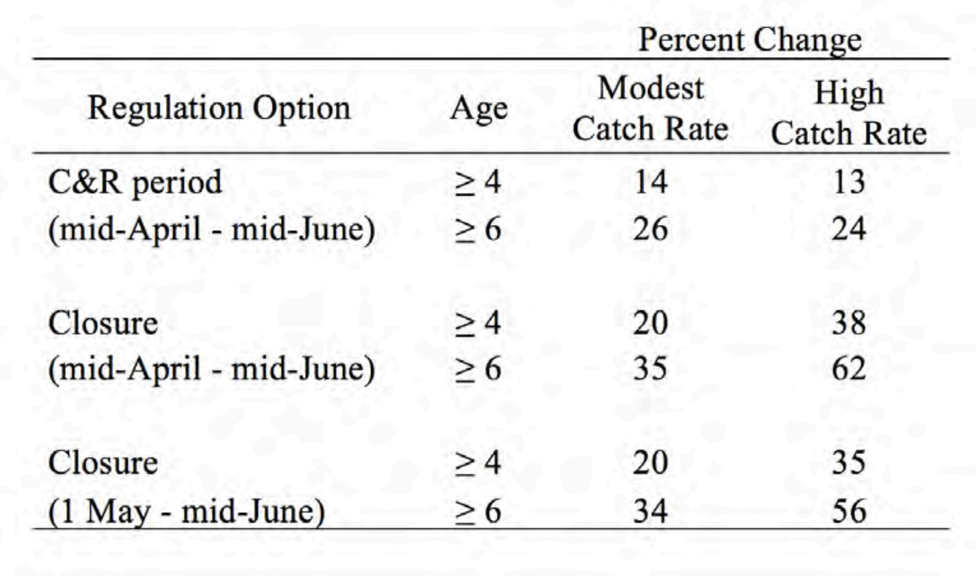


Table 1. Percent change of model-simulated equilibrium abundance values of ≥ age 4 and ≥ age 6 smallmouth bass of three proposed fishing regulations compared to existing Big Bass Program regulations. Each option includes year-round catch-and-release (C&R) regulation with difference among options being treatment of the nesting and parental care period.



		Percent Change	
Regulation Option	Age	Modest Catch Rate	High Catch Rate
C&R period	≥ 4	14	13
(mid-April - mid-June)	≥ 6	26	24
Closure	≥ 4	20	38
(mid-April - mid-June)	≥ 6	35	62
Closure	≥ 4	20	35
(1 May - mid-June)	≥ 6	34	56

Table 2. List of candidate causes and their classification from the CADDIS process.

Candidate Cause
Likely
EDC and herbicides[1]
Pathogens and parasites with other stressors[2]
Unlikely
High flows
Intraspecific competition
YOY food quality: fatty acids
Temperature – direct mortality
pH
Dissolved oxygen – direct mortality
Ammonia (NH_3)
Toxic chemicals: pesticides/PCBs/metals
Uncertain
Interspecific competition
YOY food quality: thiaminase
Egg quality
YOY habitat quality
Temperature – increased disease
Dissolved oxygen – increased disease
Algal and bacterial toxins
Pathogens and parasites alone[2]

[1] The evidence available for herbicides was limited and future monitoring is planned to obtain more data.

[2] The workshop participants concluded that pathogens and parasites were likely interacting with other candidate causes in order to produce the disease. It is uncertain whether they would be capable of doing so alone.

Workshop.
Barriers and Bridges in Connecting Natural Resource Science and Management

Barriers and Bridges in Reconnecting Natural Resources Science and Management: Summary of a Workshop

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Introduction

Fish and wildlife conservation has been characterized by distinct and strong links between science and management since formal establishment as a profession with the formation of the American Fisheries Society (AFS; 1871), the National Association of Game and Fish Wardens and Commissioners (now the Association of Fish & Wildlife Agencies or AFWA; 1902), the Wildlife Management Institute (WMI; 1911), and The Wildlife Society (TWS; 1937). Indeed, the stated mission of The Wildlife Society is "to inspire, empower, and enable wildlife professionals to sustain wildlife populations and habitats through science-based management and conservation" (The Wildlife Society 2016). Scientific results are important to inform management, and conversely, management actions and needs can direct and guide scientific effort (Figure 1). Adaptive management works similarly, with science and management working together to address natural resource questions and issues. In adaptive management, managers, scientists, and stakeholders develop alternatives to address problems; outcomes of alternatives based on the current state of knowledge are predicted; an alternative is selected and implemented; the impacts of the management action are monitored and assessed; and future management actions are adjusted (Williams and Brown 2014).

Recent concern about an increasing disconnect between natural resource science and management led to a workshop with the dual objectives of addressing roots of the fission within fish and wildlife institutions and providing insights into how to transform this fission into a conservation fusion. The workshop was organized and hosted jointly by TWS, AFS, AFWA, the USGS Cooperative Research Units (CRU), and WMI. Discussion of this disconnection is not new—DeMaso (2012) described the history of this phenomenon in the wildlife profession dating back nearly 100 years. His chapter was the first in an entire book volume dedicated to the subject that arose from a symposium held at the annual meeting of TWS in 2008 (Sands et al. 2012a). Nevertheless, continued attention on addressing and improving the relationship between science and management in the natural resources is a wise investment of time and effort by practicing fish and wildlife professionals.

The workshop was framed by John Organ, chief of the CRU system, with regard to how scientific information is used in decision-making and issues that need to be considered in discussing the barriers and bridges to better the fusion of science and management. He pointed out that science is used most effectively when stakeholders have common goals, where it can be used rationally and logically to assess decision alternatives. Conversely, science is used more selectively and emotionally to justify decisions when stakeholders have opposing views or goals. He concluded his introduction by posing three questions for the speakers, panel participants, and the audience:

1) What factors drive land-grant universities away from agency-focused actionable science?
2) Why is science funding so difficult for management agencies to prioritize and secure?
3) What role can professional scientific societies have in strengthening institutional ties?

The program was divided into three main sections: first, validating the problem and pinpointing the challenges; second, evaluating the process of science and management decisions through case studies; and third, analyzing workable versus nonworkable solutions.

Validating the Problem and Pinpointing the Challenges

The professional institution of fish and wildlife conservation can be divided into four major components: government agencies, academic institutions, private sector, and professional societies. The majority of the workshop focused on the former two sectors of the profession, with experts from universities and governmental agencies contributing to the discussion. The professional societies provide key links between agencies and academia, yet annual meetings of AFS and TWS have become academic-heavy, whereas the meetings of AFWA and the North American Wildlife and Natural Resources Annual Conference are management and policy-driven. This segregation has contributed to the growing disconnect between science and management.

The university perspective on the drift of faculty research from agency-based science to directly inform management (question 1) was discussed by workshop participants, particularly Steve McMullin (Virginia Tech University), John Hayes (Colorado State University), and Chad Bishop (University of Montana). Many faculty are dedicated to making an impact on societal problems and asking applied questions focused on important management issues. However, university faculty scientists are increasingly entrepreneurial, driven by the existing reward structure and resource availability of academia. These rewards (e.g., tenure, salary raises, internal funding) stem from publishing in high-impact journals, procuring competitive grants (e.g., National Science Foundation) with high overhead return, and training graduate students. Certainly, much of this work can be done through collaboration with state and federal agencies, but increasingly, faculty are trained as graduate students or postdoctoral associates without a direct link to agency-based science. One result is that new faculty members are hired who are not familiar with resource agency missions. Also, some faculty members have the sense that agency work will not obtain the same rewards. Chad Bishop, who transitioned from a 17-year career with a state wildlife agency to being the director of a wildlife biology academic program, noticed this disconnect immediately after becoming a university administrator. He characterized it as university faculty prioritizing prestige via grants and publications, whereas agencies prioritize sociopolitically relevant outcomes. Increasing the overlap of these priorities would be a worthy goal.

Several other reasons may be leading to the putative drift of university scientists from agency-based research. For example, the slow pace of academic research relative to increasingly time-sensitive agency issues causes temporal disconnection. The lack of an organizational structure to address the complex natural resource questions of today with a coordinated science-management response has hindered linkages, although calls for increased collaborations, partnerships, and interdisciplinary work are addressing this barrier. Funding is not always targeted to the most important questions for applied resource management, which can squander research capacity. Finally, a lack of understanding of management needs by university researchers coupled with a complementary lack of understanding by managers of faculty research rewards and motivations are other barriers.

The disconnect between science and management is paradoxical given the necessary interaction between these two areas. A panel discussion format—composed of Dave Chanda, current president of AFWA and director of the New Jersey Division of Fish & Wildlife; Nick Wiley, executive director of the Florida Fish and Wildlife Conservation Commission (FWC); and Virgil Moore, director of Idaho Department of Fish and Game—examined question 2 by detailing how agency managers recognize the need for reliable scientific knowledge but often do not have the resources necessary to obtain that knowledge. Science provides the best knowledge on habitats, threats to fish and wildlife species, and potential outcomes of conservation and management actions. It also allows agencies to make informed decisions. On the other side, resource scientists in academia have a very practical need to work with the state and federal agencies, because these agencies have the legal management responsibility and authority relative to fish, wildlife, and plants. Much of the funding that is available to study these taxa in the U. S. comes from or through the states, through programs such as the State Wildlife Grant, and these agencies also have the regulatory authority to grant research permits for work involving wildlife species and work on state lands. Academic scientists benefit from working closely with fish and wildlife agency biologists to ensure their research aligns with and helps to achieve agency goals related to management of species and habitat resources.

Chanda also discussed state-specific needs and in-house scientific capacity. Recent surveys conducted by AFWA have documented a reduction in the scientific capacity of state fish and wildlife agencies, although capacity varies widely—e.g., from none to as many as 600 scientists in the Fish and Wildlife Research Institute of the FWC. There is a growing need to meet the key science needs of states, such as access to online journals, addressing emerging issues or new threats to managed species, and monitoring species responses to management actions. For states without much research capacity, the importance of external scientific partners such as the CRU, federal labs and research groups, academic institutions, and the private sector is substantial.

Bridging the Gap between Science and Management

Workshop participants provided many ideas on how to restore and strengthen the connection between science and management. Wiley challenged the notion of a widespread or growing disconnect in Florida's case, where there is deliberate, strategic, and robust scientific collaboration between the wildlife management authorities and the academic community. He suggested investment in forums, workshops, and working groups to maintain connections and collaborations—and added that strong leadership and buy-in from both sides of the science-management fence are essential. Hayes concluded that individual scientists and managers are responding to time demands, job expectations, opportunities, and reward structure of their particular institution (hence, the complementary lack of understanding mentioned above). He thought that grass-roots collaborations between individual scientists and managers can affect incremental change but posited that broad institutional solutions are required to produce a transformational change.

Ideas for institutional change were provided by Hayes and expanded upon by other workshop participants. Co-location of researchers and managers was suggested; this strategy could include funding by agencies to develop joint or embedded appointments of scientist or faculty positions at universities. Examples of this latter arrangement exist at land-grant universities, including Michigan State University and University of Florida. Another link would be targeted strategic funding for actionable research. Undoubtedly, the funds recommended by the AFWA Blue Ribbon Panel would be a huge bridge in linking science needs of agencies (associated with state wildlife action plans) with the research capacity of universities, federal labs and research groups, CRUs, and the private sector. National and regional coordination of these efforts through sharing a vision of key issues is a third potential strategy. The adaptive management approach of sourcing research questions from stakeholders, managers, and scientists could produce these shared visions. Fourth, greater use of organizations at the boundary of research and management—perhaps best characterized by the CRU system—would help bridge the science-management gap at a broad scale. This idea justifies the importance of filling vacancies in the CRU system to increase its capacity. Moore concluded the panel discussion with a challenge to administrators to provide the leadership necessary to make these changes and drive connections.

Questions from the audience following the panel discussion addressed other aspects of bridging the science-management gap. For example, the undergraduate curriculum in wildlife biology and management has been perceived as drifting from natural resource agency needs. Reductions in credit-hour requirements from 128 to 132 down to 120 for a Bachelor of Science degree in the field—with a concomitant loss of some field-based training—contribute to this change. It was suggested that managers provide input on curricula, where appropriate. Improving the communication of science to the public from both the research and management areas also was mentioned, with agencies and university scientists communicating together through multiple social media platforms to inform the public during the research process.

Case Studies: Evaluating the Process of Science and Management Decisions

Investment in partnerships among the four major components of the professional fish and wildlife institution, as well as private stakeholders, has produced a number of successful outcomes in natural resource conservation. Paul Souza, assistant director for Science Applications of the U.S. Fish & Wildlife Service, opened the workshop session on case studies by showcasing a number of successful conservation partnerships. For example, the sage-steppe ecosystem in the intermountain region of the western United States has been the site of multiple efforts involving state, federal, private, and academic partners in linking planning, science, and habitat conservation to improve conditions for the wildlife resources of the area, which include the greater sage-grouse (*Centrocercus urophasianus*; "Conservation Issue: Sage-Steppe"). Other multipartner efforts highlighted include sustaining the Connecticut River watershed, developing drought-resilient landscapes in the Central Valley of California, and designing future landscapes of the southeastern United States. Prelisting conservation policy, which is designed to protect species and associated ecosystems from further decline, has been the impetus for science-based collaborations of agencies, private landowners, and nongovernmental organizations that spared species such as sage-grouse and New England cottontail (*Sylvilagus transitionalis*) from requiring protection under the Endangered Species Act ("Conservation Issue: Pre-Listing Conservation"). This policy incorporates the adaptive management cycle by facilitating cooperation among partners to identify science needs and by developing monitoring programs to measure the species and habitat outcomes of implemented conservation practices.

Two successful, large-scale science-management partnerships were detailed by Fred Johnson, of the U.S. Geological Survey, and David Haukos, of the Kansas Cooperative Fish and Wildlife Research Unit. Johnson discussed harvest management of mallards (*Anas platyrhynchos*) in the context of adaptive management. This successful program, in place since 1995, includes a federal-state working group of stakeholders who set objectives and specify alternative management options. Researchers are included to build models and design monitoring protocols to compare predicted and observed changes in population size. Annual iterations of management decisions, monitoring, and assessments complete the process. Johnson identified barriers to the use of adaptive management, including reluctance of managers to share decision-making and reluctance of researchers to engage with stakeholders. Lack of follow-through in terms of monitoring and failure to keep communication lines open were also described as barriers. However, Johnson also suggested that the bridge to an improved science-management interface is the creation of a nurturing institutional environment with strong leadership, a shared understanding of problems, and an acknowledgment that cultural change will not be instantaneous.

Development of a range-wide conservation plan for the lesser prairie chicken (*Tympanuchus pallidicinctus*) required a coordinated, cooperative effort at multiple scales. Haukos described this effort, which was organized by the Western Association of Fish & Wildlife Agencies and included a team composed of researchers, managers, and regulators. Public inquiry and stakeholder input were also included in the process. The results were a dynamic range-wide conservation plan and a comprehensive book on ecology and conservation of the species. Haukos discussed keys to success, with open and frequent communication among all groups at the top of the list. He also focused on how success depended on the ability of each group (scientists, managers, regulators, private stakeholders) to recognize the needs, limitations, and considerations of the other groups.

Kiley Dancy of the Mid-Atlantic Fishery Management Council discussed how changes in federal law (namely, the Magnuson-Stevenson Act) have raised the role of science in marine fisheries management. Federal law created a framework of eight regional fisheries management councils and accompanying Science and Statistics Committees. These councils include a broad diversity of resource uses and are managed under the National Marine Fisheries Service. Science has effectively been hardwired into the management system, helping prevent over-exploitation of the resource.

Synthesis: Analyzing What Works and What Does Not

Themes described, lessons learned, and key challenges identified during the workshop were synthesized by Wendi Weber, northeast regional director of the U.S. Fish & Wildlife Service. One challenge was addressing the need for collaboration and communication among all relevant parties to address shared objectives, which is a component of the adaptive management process. Several participants repeated this need—and overcoming it is necessary to address complex emerging issues in natural resource science. A second challenge was to ensure shared expectations between scientists and managers. Understanding the motivations, constraints, and capacity of each other is important to bridge the disconnection. Haukos noted that for partnerships to be fully effective, all parties need to understand the requirements and expectations of participants in the partnership. Dancy discussed this challenge and reported that integrating fisheries science with federal policy changes has been slowed due to a mismatch between the expectations of managers and the robustness of available science. She noted the importance of communicating the present state of science to stakeholders, especially given inherent scientific uncertainty and ecosystem complexity. Third, the need for an organizational structure to systematically solve problems was identified. Case studies presented during the workshop provided examples of successful organizations that functioned effectively to address large-scale concerns.

Audience input provided two important considerations at this stage of the workshop. Increased study of the human dimensions of fish and wildlife conservation was encouraged. The relevance of social science in decision-making is obvious, because people, not science, make decisions. Therefore, better collaboration between natural and social scientists could contribute to building bridges between science and management. Also, the balance between communicating science and advocating policy was highlighted. Science informs policy, but researchers need to understand that several factors, including economics, public interest, and legislation, also affect natural resource decisions. Communicating science effectively but objectively—without stepping over the line of advocacy—thus, becomes necessary for science to play as large a role as possible.

The workshop concluded with final comments from the executive directors of The Wildlife Society and the American Fisheries Society—Ken Williams and Doug Austen, respectively. They served to address question 3 posed by Organ at the onset of the workshop—namely, what role can professional scientific societies have in strengthening institutional ties? Williams stated that this workshop identified challenges in more effectively connecting science with management/conservation policy and explored promising approaches to integrating knowledge discovery with management application. However, he concluded that much remains to be done. The professional societies have started down the path to reinforce a shared vision of science and management by establishing the first-ever Memorandum of Understanding (MOU) among AFS, TWS, CRU, and USFWS that will facilitate partnership among the societies and key federal research and management agencies. The theme of the annual TWS meeting in 2016 was "Expanding the Partnership," and the meeting featured plenary sessions and symposia that focus on partnerships and themes germane to both scientists and managers. Austen added that the first joint AFS-TWS conference in 2019, which will be the largest meeting of fish and wildlife biologists in history, will maintain the momentum on building science-management bridges. Indeed, the theme of that joint conference is planned to be the integration of science discovery and conservation of fish and wildlife systems. The bidirectional linkage between science and management (Figure 1) is crucial to success in fish and wildlife conservation. Keeping the focus on this linkage will require renewed commitment on behalf of managers and researchers in collaboration with private and public stakeholders (Sands et al. 2012b).

Acknowledgments

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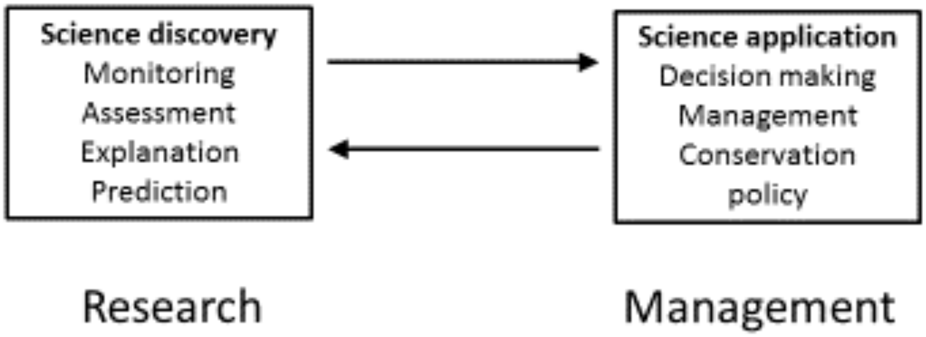
Figure 1. Bidirectional linkages between science and management, in which science influences management by providing information to inform decisions and management reinforces science with actions that facilitate investigation



Registered Attendance

Alaska

Karen Clark, Bruce Dale, Mitch Ellis, Christopher Estes, John Frost, Chris Garner, Geoffrey Haskett, Joel Helm, Cynthia Jacobson, Kim Jochum, Brent Koenen, Gary Larsen, Elizabeth Neipert, Wayne Owen, Mark Sledge, Justin Smith

Alberta

David Ingstrup

Arizona

Josh Avey, Chris Cantrell, Loren Chase, Ron Christofferson, Douglas Cummings, Jim deVos, James Driscoll, Al Eiden, Janet Johnson, Kent Komadina, Scott Lavin, Jim Odenkirk, Esther Rubin, San Stiver, Kellie Tharp, Bill Van Pelt, Larry Voyles

Arkansas

Ricky Chastain, Donald McKenzie, Jennifer Sheehan, Justin Stroman

California

Nina Anderson, Matthew Barr, Michael Barron, Bill Berry, Timothy Bowden, Kirsten Christopherson, Erica Cunningham, Rhys Evans, Paige Farrell, Nancy Ferguson, Claudia Gambaro, Geoff Geupel, Jason Gibbons, Misty Hailstone, Suzanne Hall, Mark Hennelly, Nora Hotch, Dustin Janeke, Aaron Killgore, Dawn Lawson, Robert Lovich, Michelle Maley, Jeanne Mayer, Amy Millan, Kimberly O'Connor, Jean Pan, Robert Powell, Doug Powers, Thomas Rademacher, Bob Schallmann, Greg Schroer, Roland Sosa, Lisa Talcott, Gwen Vergara, Jennifer Wilkening, Todd Wills, Lauren Wilson, Angela Wirsching, Christy Wolf

Colorado

Christine Bern, Bob Broscheid, Robert Brozka, Liz Caldwell, Mark Chase, Larry Clark, Coralie Cobb, John Cornely, Patrick Crist, Tom DeLiberto, Reid DeWalt, Deborah Donner, Patricia Dorsey, James Dubovsky, MattDunfee, Brian Ferebee, Jim Gammonley, Samantha Gibbs, Pete Gober, John Hayes, Chris Herron, Matt Hogan, Rick Kahn, John McKay, Craig McLaughlin, Michael Miller, Ken Morgan, Dale Nolte, Becky Ralston, Terry Riley, Eve Schauer, Natalie Sexton, Melissa Simpson, Stephanie Smith-Froese, Casey Stemler, Gene Stout, Jason Suckow, Gary Thorson, Nick Van Lanen, Jeffrey M. Ver Steeg, Patrick Walsh, Noreen Walsh, Thomas Warren, Mary Kay Watry, Kenneth Wilson, Mike Wrigley

Connecticut

William Hyatt, Rick Jacobson

Delaware

Thomas Creaven, Rob Hossler

District of Columbia

Patricia Allen, Abby Arnold, Leah Baker, Carol Bambery, Jim Beck, Michael Begier, Hannibal Bolton, Steven Bosak, Wilhelmina Bratton, Caroline Brouwer, Douglas Burdin, Greg Butcher, Dan Cecchini, Jeremy Clare, Tammy Conkle, Lindsay Cox, Stephen Darby, Adrian Dascalu, Devin DeMario, Margaret Everson, Shasta Ferranto, Jerome Ford, Whit Fosburgh, John Frampton, Tom Franklin, Julia Galliher, Jeff Gardner, Parks Gilbert, Nancy Gloman, Estelle Green, Deborah Hahn, Megan Haidet, Robert Harper, Joe Hautzenroder, William Higgins, David Hu, Heather Huddle, Mark Humpert, Michael Hutchins, Andrew James, Gary Kania, John Kanter, Patty Klein, Steve Kline, Greg Knadle, Sara Leonard, Matthew Lewis, Brian Logan, John Lord, Carl Lucero, James Lyons, Colleen Madrid, Cynthia Martinez, Jonathan Mawdsley, Tom Mayes, Nikki Moore, Kellis Moss, Priya Nanjappa, Romel Nicholas, Peggy Olwell, Davia Palmeri, Diane Pancoska, Jeff Patchen, Paige Pearson, Frank Quamen, Brent Ralston, Ron Regan, Jacqueline Rice, Lindsey Riibe, Angela Rivas Nelson, Emma Roach, Ryan Roberts, John Rothlisberger, Judith Scarl, Jen Mock Schaeffer, Greg Schildwachter, Andrew Schmidt, Eric Schwaab, Katharine Seguin, Anna Seidman, Dan Shively, Grant Sizemore, Stephen Small, Bruce Stein, Michelle Tacconelli, Monica Tomosy, Kim Tripp, Robert Trujillo, Geoffrey Walsh, Bryant White, Ariel Wiegard, Paul Wilkins, William Woody, Travis Wray, Thomas Wray, Nicole Zimmerman, Dorothy Zolandz

Florida

Paul Catlett, Matthew Corby, Keitha Dattilo-Bain, Steve Dial, Thomas Eason, Diane Eggeman, Ann Forstchen, Joshua Friers, Eric Hellgren, James Higgins, Renee Howell, Jered Jackson, Chris Johansen, Fred Johnson, George Kenny, Lorraine Ketzler, Jared Kwitowski, Mabel O'Quinn, Cathy Phillips, William Powers, Jeremy Preston, Daniel Slone, Rob Southwick, Bill Tate, Taylor Tidwell, Tammy Whittington, Nick Wiley, Michael Willard

Georgia

Jon Ambrose, Laurel Barnhill, John Biagi, John Bowers, Justin Chafin, Steve Chapman, Rebecca Crader, Cindy Dohner, John Fischer, Mark Floyd, Dan Forster, Gregory Lee, Jessica McGuire, Leo Miranda, Kurt Moseley, Brian Murphy, Mike Piccirilli, Mark Ruder, David Scott, Ron Smith, Micah Thorning, Tony Tooke, Bill Uihlein, Robert Warren, Emily Jo Williams, Marshall Williams

Guam

Mark Bonsavage, Anne Brooke, Stephen Mosher, Nicole Olmsted, Thomas Spriggs

Hawaii

Lance Bookless, Meredith Fagan, Tom Gieder, Creighton Hogan, Ian Lundgren, Loyal Mehrhoff, John Nelson, John Polhemus, Kristen Rex, Rebecca Smith

Idaho

Charlie Baun, Jim Fredericks, Jeff Gould, Jeff Knetter, Virgil Moore, Colleen Moulton, Sal Palazzolo, Rex Sallabanks, Ed Schriever, Deb VonDeBur

Illinois

Mark Alessi, Bernice McArdle, Scott Meister, Gary Potts, Wayne Rosenthal

Indiana

Matt Harlow, Zachary Lowe, Mitch Marcus, Jessica Mikels-Carrasco, Falyn Owens, Mark Reiter, Brian Schoenung, Phil Seng, David Windsor, Amanda Wuestefeld

Iowa

Kim Bogenschutz, Todd Bogenschutz, Dale Garner, Joe Larscheid, Kelley Myers, Megan Wisecup

Kansas

Valerie Arkell, Jake George, Michael Houts, Doug Nygren, Jim Pitman, Tina Seemayer, Keith Sexson, Matt Smith, Shawn Stratton, Christopher Tymeson, James Whitney

Kentucky

John Brunjes, Richard Fischer, Ricky French, Jonathan Gassett, Christopher Hettinger, Karen Waldrop, David Wicker, Ashley Wint

Louisiana

Buddy Baker, Bill Bartush, David Breithaupt, Nicole Caldwell, Kevin Chapman, Scott Durham, Mark Gates, John Jackson III, Scott Knaus

Maine

Timothy Bickford, James Connolly, Chris DeSorbo, Derek Hengstenberg, Linda Rivard, Henning Stabins, David Yates

Manitoba

Rick Baydack, Pat Kehoe

Maryland

Douglas Austen, Lowell Adams, Lowell Baier, Michelle Brown, Douglas Burkett, Melanie Frisch, Bess Gillelan, Lynda Hartzell, Bill Harvey, Stephen Kendrot, Donald MacLauchlan, Jeannette Matkowski, Christopher Meaney, Helene Merkel, Caroline Murphy, Keith Norris, Dionne Orr, Paul Padding, Taylor Pool, Kyle Rambo, Alesia Read, Tim Richardson, Christopher Segal, Steve Sekscienski, Jackie Smith, Eileen Sobeck, Angela Somma, Jim Swift, Gary Taylor, Linda Weir, Ken Williams, Mark Wimer, Chris Wright

Massachusetts

Jean Brennan, Jack Buckley, Thomas Decker, Keith Nislow, Paul Phifer, Colleen Sculley, Scott Sheehan, Wendi Weber

Michigan

David Brakhage, Sonja Christensen, Marc Gaden, Doug Gorby, Philip Huber, Dan Kennedy, Keith Kintigh, Patrick Lederle, Russ Mason, William Moritz, Mike Parker, Kristin Phillips, William Porter, Mike Ravesi, Sharon Schafer, Steve Sjogren, Morrie Stevens, Gildo Tori, Gary Whelan

Minnesota

Ed Boggess, Pat Conzemius, Tom Cooper, Steve Cordts, Tom Duffus, John Erb, Neal Feeken, Douglas Grann, Jim Hodgson, Matt Holland, James Kelley, Tom Melius, Pat Rivers, Paul Telander, Charlie Wooley

Mississippi

Eric Britzke, Cynthia Edwards, Tim Hiller, Jerry Holden, Andrew Kouba, Frank Lockhart, Tom Moorman, Ed Penny

Missouri

Keith Donaldson, Mike Hubbard, Brad Jacobs, Craig Paukert, Lisa Potter, Scott Radford, Robert Ziehmer

Montana

Steve Belinda, Chad Bishop, Jodi Bush, Christine Dawe, Jon Haufler, Lorin Hicks, Kevin Hurley, Ken McDonald, Elin Pierce, Melissa Reynolds-Hogland, Dave Schmid, Chris Smith, Kevin Vine, John Vore, Joel Webster

Nebraska

Dan Bigbee, Charles Chamberlin, Karie Decker, Jim Douglas, Keith W. Harmon, Martin Hogan, Steve Riley, Scott Taylor, Eric Zach

Nevada

Tom Allen, Michael Clifford, Ted Koch, Edward Koch, Ken Mayer, Nadine Searles, Deborah Sitarek, Jon Sjöberg, Robert Turner, Brian Wakeling, Tony Wasley

New Brunswick

Josée Lanctôt

New Hampshire

Brian Dresser, Steven Fuller, Arin Mills, Stephen Najjar, Glenn Normandeau, Ian Trefry, Judy Stokes Weber, Steve Weber

New Jersey

Dave Chanda, Richard Crossley, John Joyce, Paulette Nelson, Mark Stevenson, Jonathan Van De Venter

New Mexico

Steve Hattenbach, Junior Kerns, Francis Kilkenny, Stewart Liley, Karl Malcolm, Alexandra Sandoval, Matthias Sayer, Benjamin Tuggle

New York

Sarah Aucoin, Gordon Batcheller, Daniel Decker, Catherine Doyle-Capitman, Jacqui Frair, Darragh Hare, Pete Jensen, Christopher Killough, Heidi Kretser, Rebecca Kusa, Betsy Mortensen, Maia Murphy, Christopher Pray, Terra Rentz, Patricia Riexinger, Ken Rosenberg, Sofia Sainz, Eric Sanderson, Brad Schaeffer, Leonard J. Vallender, Andy Weik

Newfoundland and Labrador

John Blake, Shane Mahoney

North Carolina

Kyle Briggs, Charles Brown, David Cobb, Bill Creighton, Jessica Guilianelli, John Isenhour, Mark Jones, Robert Montgomery, Gordon Myers, Maria Palamar, Braden Ramage, Alan Schultz, Sara Schweitzer, Craig Ten Brink, David Whitehouse

North Dakota

Steve Adair, Casey Anderson, Jesse Beckers, John Devney, Amanda Goldstein, Marshall Johnson, Kevin Kading, Patrick Lantis, Craig Larson, Greg Link, Aaron Pearse, Randy Renner, Terry Steinwand, Michael Szymanski, Keith Trego, Johann Walker, Rick Warhurst, Jeb Williams

Nova Scotia

Mike O’Brien

Ohio

John Beall, Stephen Blatt, Jeff Burris, Carolyn Caldwell, Kate Haley Parsons, Jeff Herrick, Evan Heusinkveld, Luke Houghton, Jim Inglis, Gabriel Karns, David Kohler, Luke Miller, Jennifer Norris, Ray Petering, Nick Pinizzotto, Pat Ruble, Robert Sexton, Susan Vance

Oklahoma

Craig Endicott, Richard Hatcher, Rob LeForce, Keith Owens

Ontario

Ian Barnett, Len Hunt

Oregon

Michael Adams, John D. Alexander, Ron Anglin, Bradley Bales, Janine Belleque, Ken Berg, Barb Bresson, Colin Gillin, Kathy Hollar, Jeff Mach, Jim Martin, Holly Michael, Mark Penninger, Terry Rabot, Brandon Reishus

Pennsylvania

Rocco Ali, John Arway, Mark Banker, Keith Beamer, Bob Boyd, Dan Brauning, Mark Buccowich, Bryan Burhans, Tammy Colt, Diana Day, Jarrod Derr, Ken Duren, John Eichinger, Megan Gambone, Jim Greer, Ian Gregg, Thomas Grohol, Joseph Hovis, Maxine Johnson, Liz Johnson, Benjamin Jones, Daniel Klem, Steve Kralik, Jeffrey Krause, Wayne Laroche, Jennifer Layman, Richard Lorson, Bernie Matscavage, David McNaughton, Wayne Melnick, Randy Metzger, Carol Miller, Kari Morehouse, Tyler Neimond, Ben Page, Thomas Page, Rebecca Picone, Mike Pruss, Michael Robertson, Mark Sausser, Dan Savercool, Jeffrey Schmid, Laurie Shepler, Andrew Shiels, Toren Shirk, Geoff Smith, Rick Southers, Deb Stump, Pete Sussenbach, Samara Trusso, Greg Turner, Steve Williams, Megan Zadecky

Quebec

Silke Neve

Rhode Island

Shannon Kam, Cathy Sparks, Sam Whitin

Saskatchewan

Dave Kostersky, Dean Smith

South Carolina

Layne Anderson, Robert Boyles, Breck Carmichael, Emily Cope, Billy Dukes, Kurt Dyroff, Tracy Grazia, Bryan Hall, Mandy Harling, John Holloway, Becky Humphries, Craig LeSchack, Lynn Quattro, Chris Stone, Gary Taylor, Amy Tegeler, Alvaro Urrutia, Scott Vance

South Dakota

Jim Faulstich, Scott Hed, Kelly Hepler, Ann M. Juette, Tom Kirschenmann, Tony Leif, John Lott, Scott Simpson, Jeff Vonk

Tennessee

Shannon Allen, Gray Anderson, Mike Butler, Ed Carter, Mark Gudlin, Dale Hall, Dale Humburg, Chris Hunter, Amy Turner, Scott Yaich

Texas

Jeremy Adams, Perry Barboza, Mylea Bayless, Joe Betar, Suzanne Bilbrey, Kathy Boydston, Clay Brewer, Kirby Brown, Linda Brown, Tim Buchanan, Timothy Cooper, Kate Crosthwaite, Cat Cude, Justin Dreibelbis, Jackelyn Ferrer Perez, Selma Glasscock, Leslie Hartsell, David Hewitt, Steve Jester, Julie Jeter, Jarrad Kosa, Chuck Kowaleski, Kevin Kraai, Mathew Kramm, Ken Kurzawski, Ross Melinchuk, Alberto Moreno, Dave Morrison, Vanessa Musgrave, Kevin Porteck, Jay Roberson, William Ryan, Dolores Savignano, Jason See, John Silovsky, Wayne Strebe, Richard Trevino, Matt Wagner, Julie Wicker, David Yeates, Larry Zimmerman

Utah

Bill Bates, Marty Bushman, Drew Cushing, Mike Fowlks, Ashley Green, Dale Jones, Robert Knight, C. Russell Lawrence, Lori McCullough, Terry Messmer, Julie Moretti, Greg Sheehan, Braden Sheppard

Vermont

Pete Dufault, Scot Williamson

Virginia

James Adams, Jennifer Allen, Taylor Austin, Steve Barton, Terry Bashore, Jessica Bassi, Michelle Bates, Angelia Binder, Brian Bishop, Paul Block, Roxanne Bogart, Peter Boice, Brad Bortner, Albert Bourgeois, Virginia Burkett, Tom Busiahn, James Caldwell, Joseph Campo, Emmett Carawan, Edwin Christopher, Gary Costanzo, Bob Curry, Steve Czapka, Alison Dalsimer, Naomi Edelson, Mark Edwards, Todd Fearer, Bob Ford, David Gordon, Lewis Gorman III, Healy Hamilton, Camille Harris, Elsa Haubold, Julie Henning, David Hoskins, Glenn Hughes, Brian Hyder, David James, Becky Keller, Mona Khalil, Mary Klein, Mike Leahy, Rachel Levin, Abigail Lynch, Laura MacLean, Brandon Martin, Donald Marx, Thaddeus McDonald, Lawrence McGrogan, Steve McMullin, David Miko, Bryan Moore, Sarah Mott, Bonnie Myers, Collin O'Mara, Thomas Olexa, John Organ, David Pashley, Christopher Petersen, Elizabeth Powell, Kenneth Richkus, John Rohm, Madeleine Rubenstein, Jay Rubinoff, James Sample, Paul Souza, Melanie Sturm, Christopher Topik, David Walker, Meegan Wallace, Blake Waller, Bobby Wells, David Whitehurst, John T. Wilson, Joshua Winchell, Michael Wright, John Yowell

Washington

Harriet Allen, Dennis Buckingham, Jim Chu, Bob Everitt, Eric Gardner, Mike Kuttel Jr., Jennifer Quan, Ryan Risenmay, Jill Rolland, Lori Salzer, Todd Sanders, Rick Spaulding, Katherine Strickler, Rowena Valencia-Gica, Alan Wolslegel

West Virginia

Clifford Brown, John Edwards, Bettina Fiery, Gary Foster, Tiffany Fritts, Chris OBara, Jay Slack

Wisconsin

Kathleen Atkinson, Christina Carlson, Dan Dessecker, Chandra Harvey, Justine Hasz, Tom Hauge, Steve Kuennen, Nathan Roberts, Jonathan Sleeman, Kurt Thiede, Christine Thomas, Ollie Torgerson, LeAnn White, Quinn Williams, Mark Witecha

Wyoming

John Kennedy, Larry Kruckenberg, Bob Lanka, Renny MacKay, Dirk Miller, Brian Nesvik, Scott Smith, Scott Talbott, Cassie Wells, David Willms

Other

Ed Arnett, Bryan Arroyo, Dan Ashe, Paul Baicich, Lowell Baier, Lianne Ball, Lowell Ballard, Michelle Bates, Mary Belknap, Tom Bidrowski, Kristie Blevins, Bill Brassard, Ryan Bronson, Darrell Byers, Bob Byrne, Linda Cardena, Ben Carter, David Case, Randy Clark, William Clay, Jeff Cooper, Jeff Crane, Joe Daigneau, Rogelio Doratt, Robert Dreher, Kayte Dunfee, Eric Ellis, Jennifer Oelke Farley, Carol

Faulstich, Mark Fiely, Danielle Flynn, Cathy Franklin, Dave Gagner, Geoff Giller, Michael Gogal, Jeff Gronauer, Steve Guertin, Michael Hall, Mark Hatfield, Blake Henning, Daniel Holbrook, Matt Hough, Becky Humphries, Stephanie Hussey, Jim Ingalis, Chris Ingram, Doug Inkley, Lisa Irby, Dawn Johnson, Thomas Jones, Elizabeth Karasmeighan, Brent Keith, Chiaki Kimura, Mitch King, Cameron Kovach, Roene Kruckenberg, Jim Kurth, Mark Lambrecht, Michelle Larson, Elaine Leslie, Katherine Lyons, Joseph Madison, Gina Main, Chester McConell, Martin Mendoza, Vicky Michaels, Eric Miller, Weldon Miller, Becky Moore, Miles Moretti, Sara Mueller, Caroline Murphy, Cortney Mycroft, Howard Nass, David Nomsen, Keith Norris, Mike Nussman, Robin O'Malley, Jody Olson, Samantha Pedder, Joel Pederson, Frank Peterson, John Powell, Teresa Radcliffe, Susan Recce, Kelly Reed, David Reinhold, Leah Ricke, Jason Ritzert, Katelyn Roberston, Theodore Roosevelt IV, Marcia Rosenthal, Steve Sanetti, Paul Schmidt, Tony Schoonen, Sonja Schriever, Gina Shultz, Karlie Slayer, Shannon Smith, Vicki Smith, Justin Spring, Wendy Sugimura, Tom Tenerovicz, Lee Ann Thomas, John Thompson, Tom Toman, Julie Tripp, Karen Tyrell, Howard Vincent, Geoff Walsh, Paul Wenninger, Beth Williams, Fay Winters