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Physiological Basis of Climate Change Impacts on North American Inland Fishes

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

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

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

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

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

KEY POINTS

- **Neuroendocrine:** Climate change can result in chronically elevated environmental stressors that challenge the neuroendocrine system of some fishes, elevating metabolic costs and decreasing growth and survival.

- **Cardiorespiratory:** Climate change can expose some fishes to thermal conditions outside of their species- or population-specific optimal thermal range for aerobic scope, but for other species or populations thermal conditions will become more suitable and aerobic scope will increase.

- **Immune:** Climate change may elicit hyperactive or suppressive responses from fish immune systems, both of which may result in compromised immune function; these immunocompromised fish have to cope with a climate-altered environment containing altered disease prevalence, pathogenicity, and novelty.

- **Iono- and osmoregulatory:** Rising salinities associated with climate change will disrupt the hydromineral balance of fishes with narrow salinity tolerances, decreasing their abundance in assemblages, while leaving fishes with broader salinity tolerances less affected.

- **Reproduction:** Deviations from optimal temperatures, salinity, and dissolved oxygen will influence reproductive timing and investment of fishes, thus potentially reducing reproductive output and success.

INTRODUCTION

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

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

Box 1: Terms

Acquired immune response: The immune response that is inducible, temperature dependent, slower, and has more targeted disease specificity.

Aerobic scope: The difference between maximum and standard metabolic rate; defines the opportunity for aerobic activity.

Conservation physiology: "An integrative scientific discipline applying physiological concepts, tools, and knowledge to characterizing biological diversity and its ecological implications; understanding and predicting how organisms, populations, and ecosystems respond to environmental change and stressors; and solving conservation problems across the broad range of taxa (i.e., including microbes, plants, and animals)" Cooke et al. (2013:2).

Critical thermal tolerance (T_{crits}): Organism-specific upper and lower threshold temperatures where aerobic scope is zero and mortality is imminent.

Ectothermic: Organisms whose internal temperature is controlled by the ambient environment (antonym = endothermic).

Endothermic: Organisms whose internal temperature is controlled by metabolism (antonym = ectothermic).

Euryhaline: Aquatic organisms with a broad salinity tolerance of approximately 5 to >40 ppt (antonym = stenohaline).

Eurythermal: Organisms with a broad thermal tolerance (antonym = stenothermal).

Functional thermal tolerance: The organism-specific range of temperatures where specific aerobic activities are possible; varies across aerobic activities (e.g., locomotion, digestion).

Homeostasis: The normal physiological set points in an organism.

Hyperosmotic: The ionic concentration of an aquatic organism's blood serum is greater than the ionic concentration in the ambient aquatic environment (antonym = hypoosmotic).

Hypoosmotic: The ionic concentration of an aquatic organism's blood serum is less than the ionic concentration in the ambient aquatic environment (antonym = hyperosmotic).

Hypoxia: Low dissolved oxygen concentrations in the ambient aquatic environment.

Innate immune response: The immune response that is preexisting, temperature independent, rapid, and has general disease specificity.

Iteroparous: A life history strategy where an organism has multiple reproductive events during its lifetime (antonym = semelparous).

Maximum metabolic rate: The maximum rate of oxygen uptake for an organism.

Optimal temperature (T_{opt}): Organism-specific temperature where aerobic scope is greatest.

Osmolality: The total ionic concentration of an organism's blood serum.

Phenology: The timing of life history events.

Phenotypic plasticity: The ability of a single genotype to produce multiple phenotypes depending on environmental conditions.

Poikilothermic: Organisms whose internal temperature varies greatly through time (antonym = stenothermal).

Semelparous: A life history strategy where an organism has a single reproductive event during its lifetime (antonym = iteroparous).

Standard metabolic rate: The minimum rate of oxygen uptake to maintain life in a nonreproducing, nondigesting organism.

Stenohaline: Aquatic organisms with a narrow salinity tolerance of approximately 0.0–5.0 ppt (antonym = euryhaline).

Stenothermal: Organisms with a narrow thermal tolerance (antonym = eurythermal).

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

All physiological systems

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

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

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

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

Neuroendocrine

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

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

Cardiorespiratory

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

What are the rates of adaptation for aerobic scope?

Immune

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

Iono- and osmoregulatory

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

Reproduction

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

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

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

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

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

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

Neuroendocrine Responses

The neuroendocrine system functions in maintaining homeostasis (Box 1) in fishes and thus exerts control over all other physiological systems. Stressful environmental conditions can perturb homeostasis, initiating a neuroendocrine response via the hypothalamic–pituitary–interrenal (HPI) axis (see review by Barton 2002). The ultimate outcome of the HPI response is the release of cortisol and other hormones into the bloodstream, which causes a series of secondary physiological changes that promote adaptation and/or recovery to the stressor (Mommsen et al. 1999). The biochemical reaction rates responsible for the HPI response are regulated by temperature, whereby for every 10°C increase, the speed of reactions approximately doubles (i.e., Q_{10} effect). As such, the most profound effect of climate change on neuroendocrine function in fish occurs through an increase of water temperature outside species- or population-specific optimal temperature ranges. Our understanding of how temperature affects neuroendocrine systems is largely derived from studies of salmonids, with a dearth of information from other families. For instance, Chadwick et al. (2015) found that
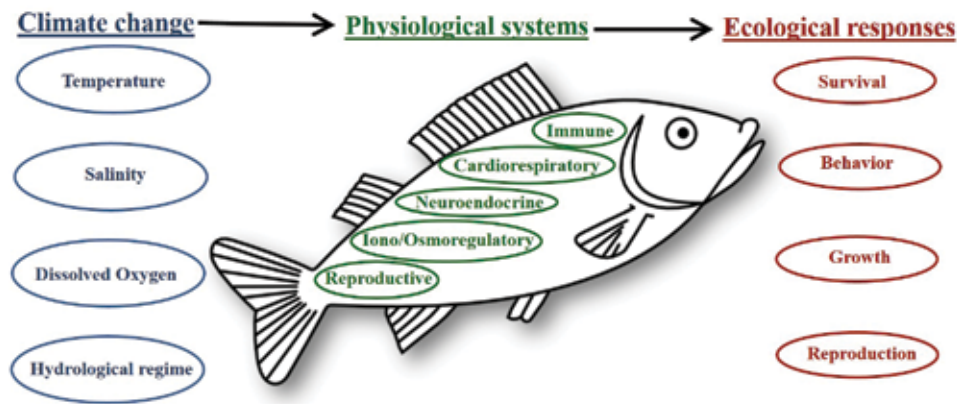
Figure 1. Conceptual model describing the responses of fish physiological systems to climate change. The left column lists abiotic character-istics of freshwater ecosystems that are influenced by climate change, which, in turn, influence five physiological systems within an individual fish. The right column describes how scientists or managers could measure different responses resulting from climate change effects on fish physiology. Fish image is from 4vector.com/free-vector/fish-outline-clip-art-118446.

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

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

Cardiorespiratory Responses

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

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

Climate change results in a complex range of stressors beyond changes in temperature, which can act additively or synergistically to negatively impact cardiorespiratory
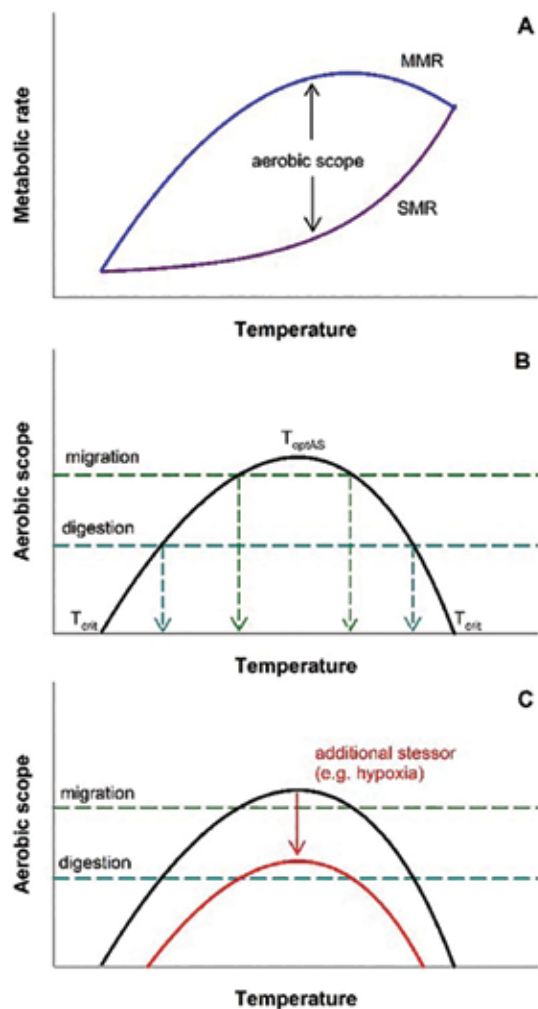
Figure 2. (A) Changes in maximum metabolic rate (MMR; blue) and standard metabolic rate (SMR; purple) with temperature (aerobic scope = MMR − SMR). (B) The aerobic scope curve is indicated in black, with the temperatures corresponding to maximal (T$_{optAS}$) and zero aerobic scope (T$_{crit}$) indicated. Some activities (migration) require more aerobic scope than others (digestion); thus, the temperature range for migration is narrower than that for digestion. (C) The decrease in aerobic scope with the addition of an environmental stressor (e.g., hypoxia); migration is no longer possible with the added stressor.

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

Immune Responses

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

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

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

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

Iono- and Osmoregulatory Responses

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

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

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

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

Reproductive Responses

The development of fish reproductive systems is controlled by the temperature-dependent reaction rates of the neuroendocrine hypothalamic–pituitary–gonadal axis (Pankhurst and Munday 2011; Miranda et al. 2013) and thus temperature influences all aspects of fish reproduction. Given the thermal control of fish reproductive systems, alterations in temperature under a changing climate have implications for individual reproductive success. Previous work on the complex interaction between reproductive physiology and temperature-dependent processes suggests four critical areas to consider in a changing climate: (1) cues to commence gamete development and progression, (2) energy allocation for gamete investment, (3) fertilization, and (4) larval hatching and survival (Pankhurst and Munday 2011). First, photothermal cues stimulate the onset of gamete development in both spring and fall spawning fish; the spawning seasons occur within a photoperiod window, but commencement of spawning is controlled by species-specific water temperature thresholds (Bradshaw and Holzapfel 2007). Changing water temperatures proximally altered the onset, progression, and conclusion of reproductive maturation stages in Striped Bass *Morone saxatilis* (Clark et al. 2005). Second, allocation of energy to gametes is controlled by aerobic scope, which, if decreased by climate change as described above, could lead to trade-offs that result in reduced reproductive investment. In Atlantic Salmon, elevated temperature during gametogenesis hindered gonadal steroid synthesis, vitellogenin production, and estrogen receptor dynamics, thus reducing female gonadal investment and gamete viability (reviewed by Pankhurst and King 2010). Third, temperature influences fertilization success, with recent studies outside of North America demonstrating that warmer than optimal temperatures can reduce the percentage of eggs that are externally fertilized by European Whitefish *Coregonus lavaretus* (Cingi et al.
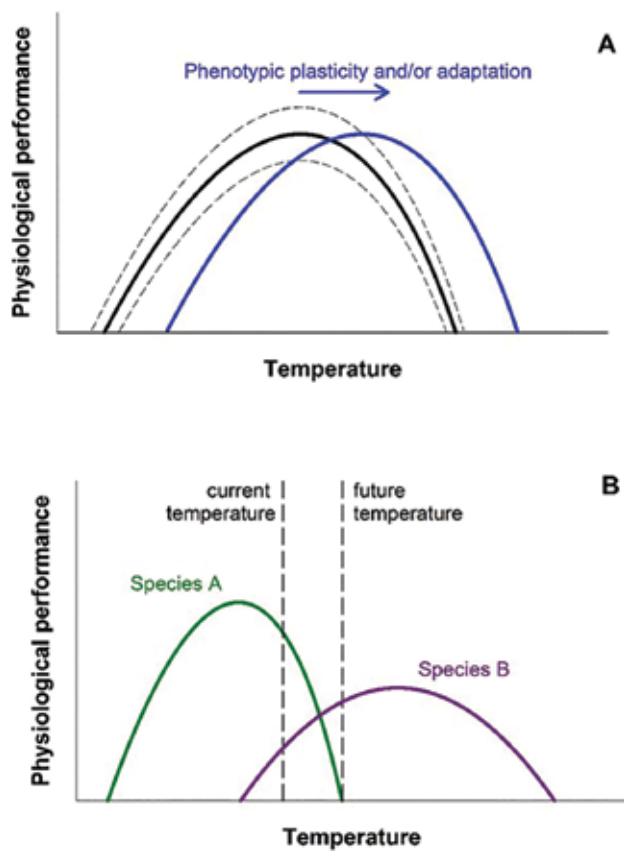
Figure 3. (A) Mean physiological performance (black line) and associated estimate of individual variability (dashed lines) for a hypothetical fish population. The population may be able to respond to elevated temperatures through phenotypic plasticity and/or evolutionary adaptation to right-shift their reaction norm and increase their functional thermal tolerance. (B) Under current climate conditions, species A encounters near-optimal temperatures, whereas species B is operating at the limits of its functional thermal tolerance. Under a warming future scenario, physiological performance (e.g., aerobic scope) collapses to zero for species A, leading to extirpation, whereas species B may thrive under the new conditions.

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

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

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

Intra- and Interspecific Variation in Climate Response

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

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

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

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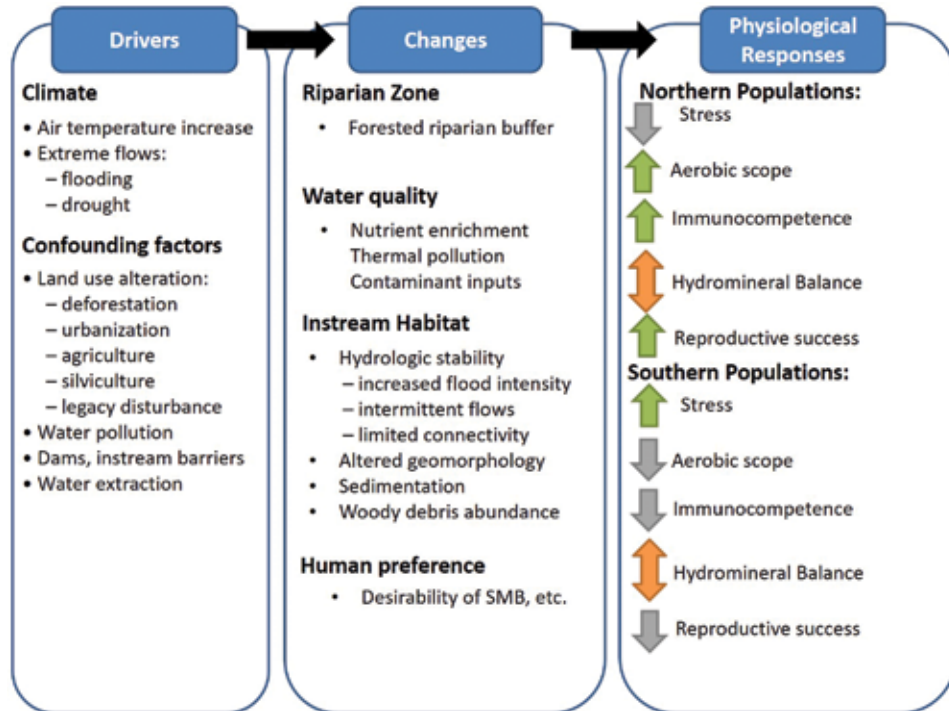
because of extrinsic differences arising from geography, as well as from intrinsic differences resulting from age and sex (Seebacher et al. 2012; Stitt et al. 2014). The extrinsic effects of climate change on fish physiology varies according to a population's position within the species' overall range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

under elevated temperatures. Lastly, Dittmar et al. (2014) found that Threespine Stickleback collected from a warmer pond had a higher optimum temperature for immune function compared to individuals collected from a cooler stream. Although rare, studies such as these that provide information concerning 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., this issue). For instance, understanding fish physiology can help define remediation strategies that could make habitats physiologically suitable in a changing climate (Cooke and Suski 2008). Furthermore, physiological information can be used to identify appropriate source populations to be used in managed translocations (Olden et al. 2011) and select suitable habitats for receiving translocated populations or species (Dunham et al. 2011), although this management strategy remains controversial and could result in unintended negative consequences (Ricciardi and Simberloff 2009). Physiological understanding can also

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

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

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

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

The functional thermal tolerance has been determined for seven populations of Sockeye Salmon *Oncorhynchus nerka* in the Fraser River watershed in British Columbia, Canada (Lee et al. 2003; Eliason et al. 2011, 2013). Managers from the Pacific Salmon Commission and Fisheries and Oceans Canada closely monitor river temperatures during the summer and fall months as adult salmon are migrating upstream to their spawning grounds. If temperatures are forecasted to exceed the optimal thermal tolerance of the population, they adjust their escapement predictions and alter commercial and recreational fishing opportunities.
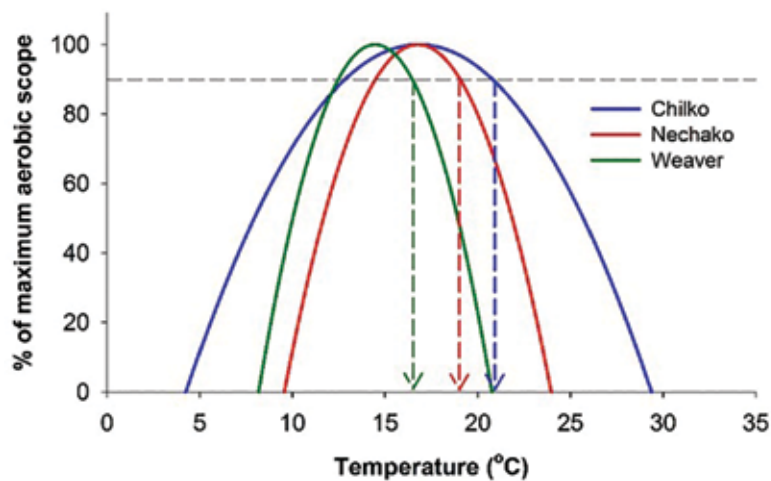
Percentage of maximum aerobic scope (i.e., the functional thermal tolerance) is shown for Chilko, Nechako, and Weaver Sockeye Salmon populations. The dashed line indicates the amount of aerobic scope that is likely required for successful upriver migration. Temperatures exceeding 20.7°C, 19.0°C, and 16.4°C (for Chilko, Nechako, and Weaver populations, respectively) could prevent successful upriver migration. Data are from Eliason et al. (2011). See Eliason et al. (2011) for a map of population spawning locations.

CONCLUSION

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

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

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