Aquatic Ecosystems Publications

Aquatic Ecosystems Report

2019

An assessment of the potential impacts of climate change on the freshwater habitats of Indiana, U.S.A.

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Recommended Citation

Höök, Tomas; Foley, Carolyn; Collingsworth, Paris; Dorworth, Leslie; Fisher, Brant; Hoverman, Jason Dr.; LaRue, Elizabeth; Pryon, Mark; and Tank, J. L., "An assessment of the potential impacts of climate change on the freshwater habitats of Indiana, U.S.A." (2019). *Aquatic Ecosystems Publications.* Paper 1.
https://docs.lib.purdue.edu/aquaticpub/1

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An assessment of the potential impacts of climate change on freshwater habitats and biota of Indiana, USA

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This article is part of a Special Issue on “The Indiana Climate Change Impacts Assessment” edited by Jeffrey Dukes, Melissa Widhalm, Daniel Vimont, and Linda Prokopy Electronic supplementary material The online version of this article (https://doi.org/10.1007/s10584-019-02502-w) contains supplementary material, which is available to authorized users.

Abstract

Recent climate-driven, physico-chemical changes documented in aquatic systems throughout the world are expected to intensify in the future. Specifically, changes in key environmental attributes of aquatic systems, such as water quantity, clarity, temperatures, ice cover, seasonal flow regimes, external loading, and oxygen content, will undoubtedly have a broad set of direct and indirect ecological consequences. Some anticipated impacts may be similar across different aquatic ecosystems, while others may be system-specific. Here, we review the potential effects of climatic changes for different freshwater habitats within the state of Indiana, USA, a Midwestern state with diverse land and water features. Given this heterogeneity and that the state is among the southernmost states of the US Midwest, evaluation of freshwater habitats of Indiana provides a useful perspective on potential impacts of climate change. In our study, we first review expected or anticipated changes to physico-chemical and habitat conditions in wetlands, lotic systems, small glacial lakes and Lake Michigan. We then highlight anticipated responses of select aquatic biota to these changes. We describe how climatic changes may interact with other anthropogenic stressors affecting freshwater habitats and consider the potential for evolutionary adaptation of freshwater aquatic organisms to mediate any responses. Given anticipated changes, we suggest aquatic ecosystem managers take a precautionary approach broadly applicable in temperate regions to (a) conserve a diversity of aquatic habitats, (b) enhance species diversity and both inter- and intrapopulation genetic variation, and (c) limit stressors which may exacerbate the risk of decline for aquatic biota.

1 Climatic effects on freshwater systems in Indiana

Spanning from roughly the 37° 42′ to the 41° 42′ northern parallels, Indiana, USA, is home to several types of aquatic ecosystems. Many streams and rivers run through the state, ultimately draining to the Ohio and Mississippi Rivers and lakes Erie and Michigan (Fig. 1). Of particular note, the Wabash River watershed drains almost 75% of the state and includes a 661-km undammed, free-flowing section, the longest such stretch in the US east of the Mississippi River. Small, glacially formed lakes abound in the north, while in the south most lentic waterbodies are reservoirs. Wetland ecosystems and small private ponds are found throughout the state. And, the northwest region of the state abuts Lake Michigan, which when combined with hydrologically uniform Lake Huron, constitutes the largest-by-surface-area freshwater lake in world. Given this diversity plus the physical location of Indiana (i.e., one of the southernmost states in the US Midwest), Indiana is an interesting geographic area to consider the potential consequences of climate change on aquatic systems, especially considering that physico-chemical and biotic attributes of aquatic systems here are already affected by climate change.

Over the past century, Indiana has warmed by 0.7 °C and annual rainfall has increased by > 140 mm (Widhalm et al. 2018). This trend is expected to continue in the future, as downscaled climate models consistently forecast warmer air temperatures and an increase in total precipitation across the Midwest and Great Lakes region (e.g., Wuebbles and Hayhoe 2004, Byun and Hamlet 2018, Hamlet et al. in press). Though projections are variable, most predictions over the next century suggest the largest increases in air temperatures in summer and the largest increases in precipitation in winter and spring (Kling et al. 2003, Hayhoe et al. 2010, Byun and Hamlet 2018, Hamlet et al. in press).

Increased air temperatures directly affect aquatic systems by increasing mean water temperatures, e.g., offshore surface water temperatures in Lake Michigan have increased ~ 0.5 °C per decade since 1980 (Collingsworth et al. 2017) with consistent increases in late summer and early fall (Fig. 2a). However, thermal characteristics of aquatic systems are more complex than simple mean temperatures, and characteristics such as diurnal temperature variation, vertical stratification patterns, and extent of ice cover may also respond to climate change.

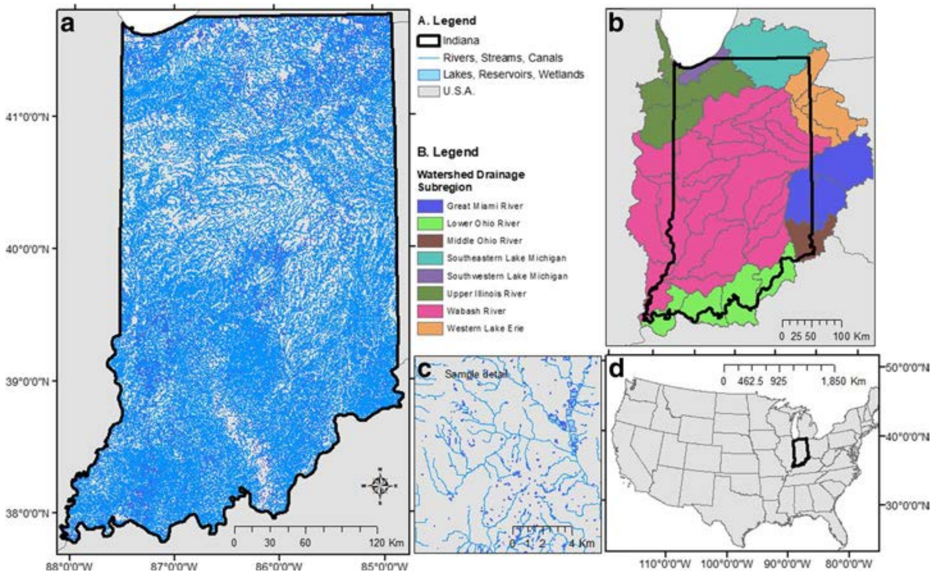

Fig. 1 a Waterways of Indiana that may serve as habitat for aquatic and semi-aquatic organisms. b Eight-digit hydrologic accounting unit watersheds categorized by major drainage region. c Sample detail of waterways depicted in A. d Location of the state of Indiana within the USA

With warming temperatures, across the Great Lakes, the mean extent of ice coverage (December 1 to April 30) declined by 67% from 1973 to 2017, and during the same period, ice cover on Lake Michigan declined by 70% (Wang et al. 2017).

Future changes in water temperatures and other thermal characteristics will vary with system type (i.e., lentic vs. lotic), size, depth, and drainage characteristics (including relative surface runoff vs. groundwater inputs). In the Great Lakes, future surface water temperatures have been projected to increase 2–12 °C (Kling et al. 2003), and by mid-century, Lake Michigan summer surface temperatures may exceed historical averages by 2.4–3 °C (Kao et al. 2015a). Warming air temperatures will likely delay ice formation in the winter and advance ice melt in the spring (Sharma et al. 2019). Ultimately, systems that have historically experienced ice cover during most winters may remain ice-free in the future, with important implications for not only ecosystem processes but also human winter activities (e.g., ice fishing may become less common). Similarly, as water temperatures warm, thermal stratification in sufficiently deep bodies of water (e.g., Lake Michigan, glacial lakes, reservoirs) will likely develop earlier in the spring with turnover later in the fall.

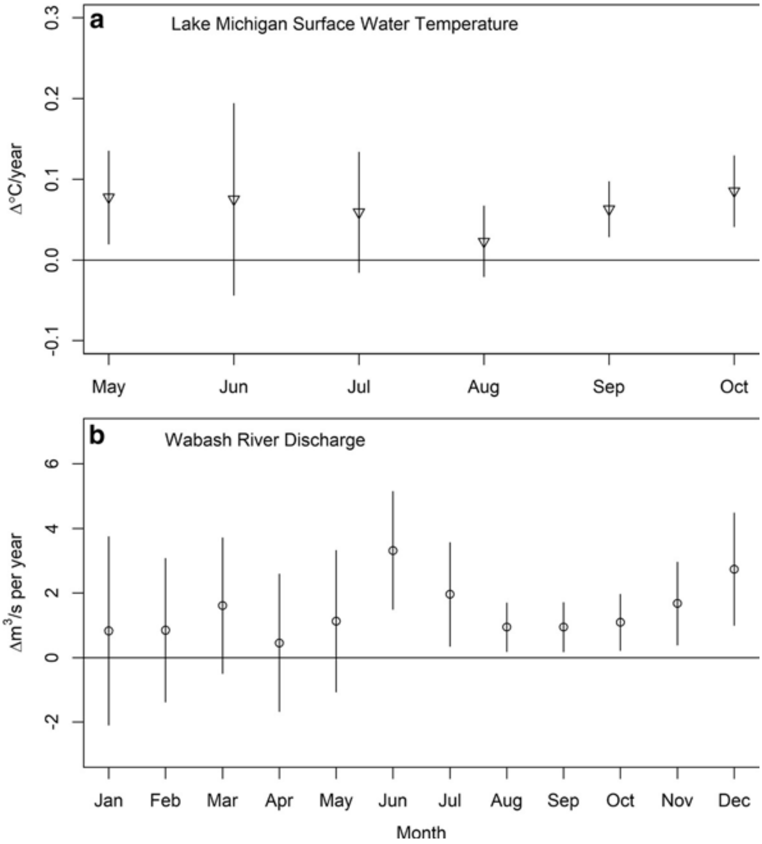

Fig. 2 Example changes in key abiotic variables over time. A. Annual change in monthly mean surface water temperatures of southern Lake Michigan, including all years from 1982 to 2017 (°C/year). Temperature data from NOAA southern Lake Michigan buoy 45007. B. Annual change in monthly mean discharge at the Montezuma USGS gage station on the Wabash River, including all years from 1928 to 2017 (m^3/year). Points represent slopes and error bars represent 95% confidence intervals

The duration and depth of stratification will likely also be affected by wind and storms, which influence the mixing depth of the epilimnion, and solar radiation and water turbidity, which influence depth-specific warming (Stefan et al. 2001). Local and regional predictions for these four variables are scarce. Wind is a particularly important variable for which future predictions are lacking. Unlike large marine systems where water movement is strongly influenced by tidal currents, water currents in Lake Michigan and lakes of northern Indiana are almost entirely wind-driven. In addition to influencing the depth of the thermocline and the timing of onset and breakdown of stratification, prevailing wind directions can alter characteristics of seiches, upwellings, and other features with potential to affect biota. While there is past evidence that prevailing wind direction over the Great Lakes has shifted on a decadal timescale (Waples and Klump 2002), it is unclear how wind intensity and direction in Indiana will change in the future.

There is more information and consensus regarding projected precipitation patterns. Average precipitation may increase slightly, extreme precipitation events may become more frequent, periods of drought may occur more often, and precipitation may shift seasonally. In Indiana, annual precipitation is expected to increase by 6–8% by middle of this century and 5–10 % by the end of the century. Specifically, winter and spring precipitation are expected to increase 16–20% and 13–16%, respectively, by mid-century, while summer and fall precipitation extremes are expected to become more variable, with overall declines in rainfall of 2– 3% (Hamlet et al. in press, Cherkauer et al. This issue). Changes in discharge will vary depending on catchment characteristics and the extent to which flows are regulated. With increases in precipitation over the past century, the Wabash River has shown trends of increasing streamflow (Fig. 2b). In the future, fluvial systems, especially those receiving relatively high surface runoff, will likely become more flashy, small shallow water bodies including small streams and wetlands may experience more frequent periods of drying, and water levels of lakes, reservoirs, and even Lake Michigan may become more variable (Cherkauer et al. This issue).

Nutrient and sediment losses from Midwestern watersheds are strongly tied to precipitation and runoff (Royer et al. 2006; Royer and David 2005). Nutrient runoff is already elevated in many areas of Indiana (e.g., National Research Council 2000; Smith et al. 2008). Given that large amounts of manure and fertilizer are applied to agricultural fields in spring, increased precipitation at this time of year may result in increased loading of phosphorous and nitrogen to aquatic ecosystems. Similarly, an expected decrease in winter snow cover will result in increased exposure of bare soil to rain storms (Jeppesen et al. 2009, Hayhoe et al. 2010). Thus, in the absence of altered land-use management practices, climatic changes are expected to lead to increased runoff of both nutrients, especially in the winter and spring. Such increased nutrient loading would in particular be expected to stimulate intense spring and summer algal blooms, with potential consequences including increased growth of harmful Cyanobacteria, expanded extent and magnitude of hypoxic conditions and changes in community structure of both lower and upper food web components.

2 Effects on aquatic biota

Physical effects of climate change on Indiana waterbodies will affect aquatic communities, populations, and individuals both directly and indirectly in positive and negative manners (e.g., Noyes et al. 2009). Most aquatic species engage in complex biotic interactions, and their populations are internally regulated through both compensatory and depensatory processes.

For example, limited resources may lead to decreased individual survival but increased population-level growth and reproductive success through release of density-dependent controls. By contrast, decreased survival may be exacerbated if individuals encounter mates less frequently or populations experience inbreeding depression. In addition to internal regulation, populations respond to the dynamics of their predators, prey, competitors, and symbionts. Community context will therefore be critical for making predictions of responses of different aquatic species to the physical effects of climate change. Phenological shifts are one of the most commonly reported consequences of climate change (Hall 2014). Because phenology is closely linked to long-term patterns in temperature and precipitation, climate change can alter emergence time, flowering time, growing season, dispersal, and reproduction. In addition, aquatic systems in Indiana are threatened by many other natural and anthropogenic stressors (e.g., invasive species, habitat loss, pollution), and it is important to consider the potential for these to interact with climatic changes and exacerbate or mitigate effects on aquatic ecosystems (Fig. 3).

As examples, climate change may favor the establishment and spread of invasive species (Rahel and Olden 2008) and affect pathogen dynamics. Thermal conditions may shift to within ranges that meet the physiological requirements for an invasive species (Bierwagen et al. 2008). Increased flooding could facilitate movement of invasive species (e.g., bighead and silver carp Hypophthalmichthys nobilis and H. molitrix). After an extreme spring flooding event on the Ohio River, the green tree frog (Hyla cinerea) expanded its geographic range from Kentucky into Indiana (Lodato et al. 2014). Conversely, drying up of riparian areas may create new areas for colonization by invasive plant species such as common/giant reed Phragmites australis (Tougas-Tellier et al. 2015). In addition, warmer temperatures are expected to increase parasite replication rates, which could facilitate transmission to hosts (e.g., Hoverman et al. 2013) and lengthen growing seasons, leading to increased frequency of transmission. Conversely, if warmer temperatures increase the mortality rate of parasites or enhance the immune function of hosts, transmission would be reduced. For

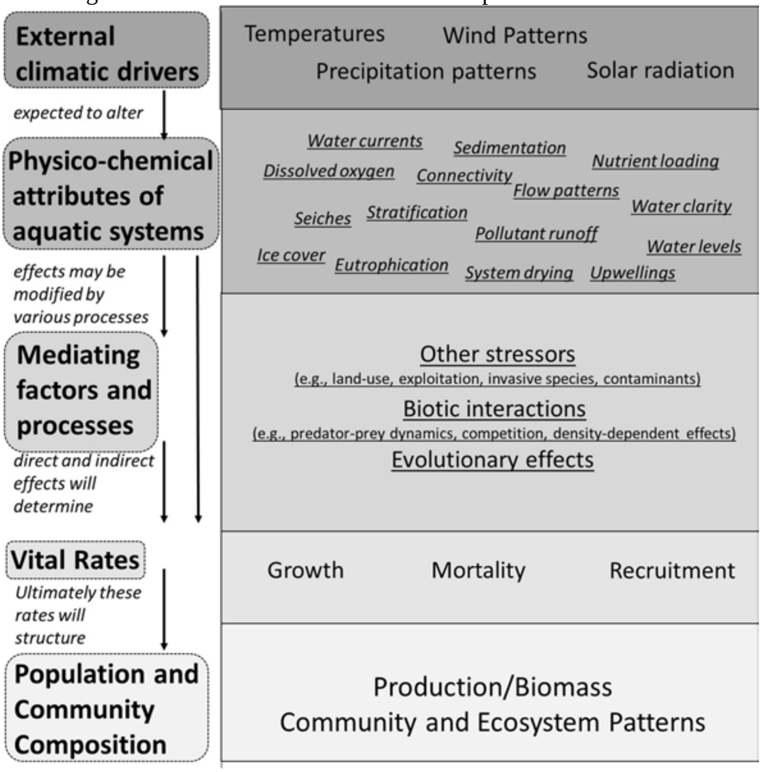

Fig. 3 Conceptual diagram of processes leading to climatic effects on aquatic ecosystems. External climatic driver's will lead to a suite of physico-chemical responses in aquatic systems. These climatic responses will interact with various other anthropogenic stressors and eco-evolutionary processes to affect vital rates of aquatic organisms and thereby structure population dynamics, community composition, and ecosystem patterns

example, severe drought can reduce the severity but not the prevalence of the pathogenic fungus Batrachochytrium dendrobatidis in the Indiana endangered crawfish frog (Lithobates areolatus) (Terrell et al. 2013); thus, climate change-induced drought may benefit infected frog populations.

Given the potentially complex mediating effects of biotic interactions and multiple stressors, it is difficult to anticipate how aquatic organisms will respond to future environmental conditions by simply considering current ecological tolerances (i.e., niche breadth). Such predictions may be more difficult still given the potential for evolution to mediate responses. Adaptation to climatic and hydrologic changes could help avoid a reduction in fitness and extinction; however, standing genetic variation must be sufficient to allow for such responses (Merila and Hendry 2014). For example, a plant population of Cakile edentula var. lacustris in Indiana Dunes National Lakeshore evolved drought tolerance in response to drier beach conditions (Dudley 1996). These populations may therefore persist in the face of future drought events. While increased dispersal ability can also evolve in response to shifting habitat suitability (Weiss-Lehman et al. 2017), a particular challenge for many aquatic organisms is that they are severely limited in ability to disperse among systems.

It is beyond the scope of this review to consider all potential effects of climate change on biota in Indiana's aquatic ecosystems. As described above, very precise predictions for specific population- and community-level responses are unrealistic given the potential for intra- and inter-specific interactions, evolutionary processes, and additional external stressors to mediate such responses. Instead, we provide qualitative perspective of likely responses, organized by aquatic ecosystem type and major taxa, noting where responses are anticipated to be similar across systems and taxonomic groups.

3 Habitat effects

In a temperate environment like Indiana, direct impacts of warmer temperatures on aquatic systems may come in several forms. Physiological rates of most aquatic species are directly responsive to water temperature. Warmer temperatures and shorter ice cover will lead to a longer growing season, with subsequent increases in primary productivity and microbial activity. Algal blooms will likely be more intense, with greater potential for growth of harmful Cyanobacteria (e.g., Paerl et al. 2016). Warm water temperatures may also cause greater release of nutrients (e.g., phosphorus) and contaminants (e.g., mercury) from sediments, further exacerbating effects of nutrient and contaminant runoff (Cherkauer et al. This issue).

Increased temperatures combined with shifts in precipitation will likely alter variability of hydroperiods, including increased frequency and magnitude of dry conditions (e.g., drought; Mishra et al. 2010). Alterations to the flow regime of lotic habitats and the hydroperiod of lentic habitats may substantially change freshwater ecosystems (Dawson et al. 2003; Brooks 2009; Junk et al. 2012). An immediate result of dry conditions is loss of freshwater habitats, e.g., a loss of floodplain habitat around lakes and along rivers due to less frequent inundation with water.

3.1 Wetlands

Wetlands are significant reservoirs for biodiversity and provide ecosystem services including flood control, groundwater replenishment, water purification, and shoreline stabilization. As noted in Cherkauer et al. (this issue), changing drought conditions in Indiana may lead to increased use of groundwater resources from a variety of sectors. Natural and constructed wetlands may help mitigate negative impacts related to climate change and water use. However, human activities have greatly reduced the extent of natural wetland habitat across the globe. In Indiana, an estimated 86% of wetland area has been removed (IN DNR 1989) to establish agricultural lands, control vector-borne diseases, or expand urban centers. Climate change will likely exacerbate natural wetland habitat losses. Moreover, an increased frequency of both droughts and intense precipitation events will increase wetland variability.

Wetlands exist along a physical gradient from ephemeral to permanently covered by standing water (Wellborn et al. 1996). With warmer temperatures and flashier precipitation, it is likely that many ephemeral ponds in Indiana will be lost. Simultaneously, the hydroperiod of semi-permanent wetlands may become more ephemeral. Because only a subset of species is capable of reproducing in ephemeral wetlands (Wellborn et al. 1996; Brooks 2009), overall diversity would decrease.

In addition to loss of freshwater habitat, changes to flow regimes and inundation periods affect community composition and relative abundance of plant species. In particular, drier soils favor terrestrial plant species over wetland adapted species. Increased encroachment of terrestrial vegetation within wetland systems can alter the water holding capacity of soils and reduce the likelihood of water retention during precipitation events. Thus, the frequency and magnitude of dry conditions can accelerate the conversion of wetlands into terrestrial systems (Brooks 2009).

3.2 Lotic systems

Given that temperature affects primary production, decomposition, and litter processing (Durance and Ormerod 2007), with warmer temperatures, there will likely be an upstream shift in both the biotic and abiotic characteristics of river systems along the river continuum. Greater precipitation could lead to continued increase in stream discharge (Fig. 2b) and contribute to deposition of fine sediments, bank erosion, and channel widening. Altered hydrology, e.g., that seen in the Wabash River watershed (Pyron and Neumann 2008), can lead to ecological responses such as loss of sensitive species, algal scour, disruption of fish life cycles, and altered energy flow (Poff et al. 2006). Similarly, increased sedimentation will likely negatively impact growth of submerged plant communities that serve as habitat for fish and macroinvertebrates (Jeppesen et al. 2009).

Riparian corridors form a diverse and complex interface between streams and terrestrial ecosystems (Naiman et al. 1993). As their width varies with stream size, geomorphological setting, and hydrologic regime, they are likely extremely susceptible to climate change (Capon et al. 2013). Increased surface and air temperatures plus altered precipitation patterns are expected to shift reproductive phenology and distributions of plants (Meyer et al. 1999). While riparian species may be more resilient to increased flooding than upland species (Seavy et al. 2009), if bank erosion increases with extreme flow events, riparian ecosystems may be negatively impacted. In addition, increased sedimentation affects downstream riparian ecosystems (Palmer et al. 2009).

Climatic changes and anthropogenically mediated processes that alter stream dynamics may also impact riparian assemblages, which can further modify in-stream dynamics. For example, riparian vegetation of prairie streams will change with modification of wildfire regimes and grazing, ultimately altering ecosystem properties of streams (Riley and Dodds 2012). Riparian vegetation contributes allochthonous inputs, including woody debris, to streams which influence stream ecosystem properties and hydraulics (Harmon et al. 1986). Large woody debris can modify local sediment dynamics or cause flooding via debris dams. Stream organisms utilize woody debris as habitat, while breakdown of woody debris by fungus and bacteria contributes energy and nutrients to aquatic systems.

3.3 Inland glacial lakes

The majority of Indiana’s lentic water bodies are presently classified as eutrophic due to natural processes plus culturally elevated nutrient loading, but climate change will likely exacerbate these conditions. Eutrophication, the process of a system becoming more productive, can lead to more intense algal blooms and increased turbidity in lentic systems, ultimately contributing to hypoxic conditions and reorganization of both producer and consumer communities (Paerl and

Huisman 2009). Eutrophic conditions may favor certain primary producers, including Cyanobacteria. Some of these are inedible by consumers and toxic, and several nuisance and toxic Cyanobacteria are already present and monitored in Indiana. Changes in available prey and altered physico-chemical conditions (i.e., decreased water clarity and oxygen) can favor consumers tolerant of these changing environmental conditions and able to exploit novel prey. One of the more impactful consequences of eutrophication may be the development of bottom water hypoxia (typically defined as less than 2–3 mg O_2/L, but see Hrycik et al. 2017) or anoxia (0 mg O_2/L_{water}). Large algal blooms stimulated by nutrient loading eventually die and settle to the bottom of aquatic systems, where they decompose. This process requires high respiration by bacteria and other decomposers; thus, large algal blooms in the top of the water column may cause high consumption of oxygen down below. When stratification is present in a waterbody, there is minimal mixing between the epi- and hypolimnion, and depleted oxygen in the hypolimnion may not be replenished from the epilimnion. Essentially, all natural glacial lakes in Indiana which are deep enough to stratify experience hypolimnetic hypoxia or anoxia, with strong potential for negative impacts on organisms residing in this benthic zone.

The climate change-induced combination of increased nutrient loading, higher water temperatures (plus resulting decreased solubility of oxygen), and earlier onset and later breakup of stratification are expected to contribute to increased magnitude and duration of hypoxic conditions in Indiana's lakes. In turn, this may contribute to further loss of suitable habitat for aquatic organisms and changes to community structure.

While permanent lakes are more buffered against reductions in water level than wetlands, future variable precipitation and evaporation dynamics could contribute to more alterations of lake levels. This could affect organisms' access to important nearshore habitat features, e.g., coastal wetlands, and thereby limit species persistence.

3.4 Lake Michigan

With altered thermal conditions, lake levels, and loading patterns of nutrients and sediments, habitat conditions in Lake Michigan will be affected by climate change in a manner similar to other aquatic systems in Indiana. In general, warming in coastal regions of Lake Michigan will likely result in altered habitat and community composition of plants, macroinvertebrates, and fish (e.g., Dudley 1996). However, due to its large size and depth, thermal habitat in Lake Michigan will not change uniformly, with nearshore zones reaching higher temperatures in summer than deep offshore waters.

In the Lake Michigan basin, Robertson et al. (2016) modeled 24 different climate change scenarios and predicted that an average increase in precipitation of 5%, coupled with a 2.6 °C average predicted increase in air temperature, would reduce annual tributary flow to the lake by 1.8% over the next century. While projections of total annual changes in phosphorous loading to Lake Michigan were inconsistent, there was general consensus predicting increased phosphorus loading in the spring and decreased loading in the summer (Robertson et al. 2016). While phosphorous loading was a serious concern for Lake Michigan in the past, more recent nutrient reduction efforts plus the filtering effects of invasive dreissenid mussels are causing oligotrophication. Decreased primary production has likely contributed to decreased secondary production and declines in several piscivorous fishes and the economically valuable fisheries that depend on such species. Whether future climatic conditions contribute towards reversing or exacerbating oligotrophication in Lake Michigan may have important implications for the suitability of habitat, the type of fish species which may thrive in the lake, and the potential yield and economic value of the lake's fisheries.

4 Taxonomic responses

Water temperature has strong effects on the physiology and vital rates of most aquatic biota and is often a signal for emergence or migration at appropriate times (e.g., Voelz et al. 1994). Changes in the amount and flow of water can affect the overall quantity of aquatic habitat, dispersal ability within and across systems and phenology of emergence, migration, and reproduction. Thus, altered thermal characteristics, flow regimes, and hydroperiods are expected to affect a broad suite of aquatic biota.

4.1 Non-mussel invertebrates

In general, invertebrate communities are expected to respond to changes in water temperatures, flow regime, and hydroperiods. In a temperate climate area, headwater stream macroinvertebrate assemblage composition changed and density decreased as stream temperatures increased over a 25-year period (Durance and Ormerod 2007). Similar results were demonstrated experimentally in headwater stream manipulations (Hogg and Williams 1996). Invertebrate species specialized to intermittent flow regimes are negatively influenced by more frequent dry periods (Brooks 2009). While many invertebrates are adapted to the short hydroperiods of vernal wetlands, droughts can substantially reduce the length of time that these water bodies hold water and, consequently, prevent successful animal emergence before the wetland dries up. Moreover, extended periods of drought can reduce the availability of wetland habitats for these species on the landscape. While some semi-aquatic organisms may be able to disperse overland, the lack of suitable habitats may ultimately lead to population declines.

4.2 Mussels

Freshwater mussels (Unionidae) are the most endangered group of Indiana’s aquatic organisms, with nearly half of the almost 80 native species either extirpated or listed as endangered (both federally and in-state) or of special concern. The reasons for their decline include overharvest during the peak of the button and cultured pearl industries, negative effects of point and non-point source pollution, loss or alteration of critical habitats, and impacts of nonnative species. Freshwater mussels, because of their limited mobility, patchy distribution, and complex reproductive strategies, could be especially vulnerable to some of the predicted impacts of climate change on local environments.

Adult freshwater mussel movement is very limited; thus, they are vulnerable to local changes in water levels. As water levels decrease, freshwater mussels may burrow vertically down into the substrate in an attempt to track the decreasing water table or move horizontally across the substrate searching for water. Neither choice is ideal. Freshwater mussels typically cannot bury themselves to sufficient depth to remain submerged, and long, meandering trails left in the substrate as mussels search laterally for water suggest little-to-no sense of direction. Either way, mussels often end up stranded on dry ground, and drought resulting from climate change could potentially cause massive die-offs, especially in areas that historically did not become dry (Golladay et al. 2004).

Most lotic freshwater mussel species in Indiana tend to cluster in “beds” in areas of stable, non-shifting, non-embedded, substrate (typically, a mixture of sand, gravel, and cobble). Increased flashiness of stream systems due to climate change could potentially scour and destroy these critical reaches along with the mussels they contain (Hastie et al. 2003). Freshwater mussels dislodged during these events may be deposited in areas of undesirable habitat, potentially negatively affecting the overall freshwater mussel community.

During reproduction, most species of freshwater mussels rely on specific fishes as hosts for their parasitic larvae (glochidia), where the release of glochidia coincides with the congregation/migration of host fishes. If fish spawning and migration patterns change in response to altered spring discharge patterns and water temperatures, the critical interaction between mussels and host fish could be disrupted. Higher maximum water temperatures during the summer could also exceed the thermal limits for the survival of mussel sperm, glochidia, juveniles, or adults, or host fish, further disrupting reproductive activity of mussels (Pandolfo et al. 2010; Ganser et al. 2013). Any additional stressors to the limited reproduction of already vulnerable mussel populations would have severely detrimental effects to the longterm sustainability of these species in Indiana.

4.3 Fishes

Increased water temperature affects growth of fishes through physiological and indirect ecosystem effects (Fry 1971; Stenseth et al. 2002). Eaton and Scheller (1996) suggested that streams in the central Midwest will experience some of the greatest warming in the continental USA, leading to substantial reduction of suitable habitat for fishes. Mohseni et al. (2003) repeated their analysis with improved water-air temperature relationships and found that habitat ranges for warm water fishes (i.e., the majority of Indiana fishes) will generally increase or not change. However, 15 species of Indiana fishes that are classified as cool water fishes will experience significant habitat loss with climate change (Mohseni et al. 2003), and the few native cold-water fish in Indiana inland systems are expected to decline. Where possible (e.g., in stratified lakes), these fishes will likely disperse into deeper, cooler water (Magnuson et al. 1979; Hall 2014), but this action may come at a cost (e.g., exposure to hypoxia). Climate warming may positively affect vital rates for some temperate ectotherms, while negatively affecting growth, survival and reproduction of others. Even within a species, thermal effects may be inconsistent, as highlighted by two recent studies evaluating effects of winter thermal conditions on offspring quality of different stocks of yellow perch (Farmer et al. 2015; Feiner et al. 2016a). Ultimately, increased water temperatures will likely lead to changes in fish population and community composition, with communities consisting of a larger proportion of species and genotypes tolerant of warmer conditions.

Bioenergetics studies of Lake Michigan have examined the effects of climate change on thermal habitat for various fishes such as cold-water salmonines (e.g., lake trout Salvelinus namaycush) and lake whitefish Coregonus clupeaformis, cool-water yellow perch Perca flavescens, and warm-water largemouth bass Micropterus salmoides (Hill and Magnuson 1990; Brandt et al. 2002; Kao et al. 2015a, b), all of which occupy the coastal waters of Lake Michigan at different times of the year. Projections suggest that, at the lake-scale, the sum volume of suitable thermal habitat for fish growth may increase as offshore, deep regions of the lake warm. However, suitable habitat for the most desirable cold and cool water salmonids and percids is expected to decrease in the nearshore, relatively shallow Indiana waters of Lake Michigan while habitat for warm water fishes may increase (Ficke et al. 2007).

Changes in warming rates and discharge patterns may affect spawning behavior of several fishes. The direction and magnitude of specific shifts in spawning behavior will likely vary among species, due to variation in life history strategies, physiology, and dependence on climate-driven environmental cues (Collingsworth et al. 2017). While few studies have directly estimated the projected effects of climate change on reproductive phenology of fish populations, there is evidence that climate-induced warming can alter the timing of spawning for some species. For example, Lyons et al. (2015) documented earlier spawning by Lake Michigan yellow perch in response to earlier spring onset and provided evidence that Lake Michigan lake trout have spawned later during the fall during the past several decades. Höök et al. (2001) demonstrated that in northern Lake Huron, the phenology of emergence of several species of larval fishes shifted between 2 years with contrasting thermal conditions. Given that recruitment of bloater Coregonus hoyi, rainbow smelt Osmerus mordax, yellow perch, and alewife Alosa pseudoharengus are all related to prevailing climate conditions (Honsey et al. 2016a; Bunnell et al. 2017), changes in thermal habitat conditions will likely affect the reproductive success of many fish populations in the Great Lakes and other systems.

Altered flow regimes will also differentially affect fishes and contribute to changes in species distributions and composition of local assemblages. The loss of stream habitat due to reduced flow can affect dispersal patterns of fishes, including decreased access of breeding migrations to preferred habitats. Phenological changes in timing of flows can disrupt cues that fish use for spawning and migration. For some populations, this could lead to more frequent mismatches between reproduction or migration events and ideal habitat conditions. Moreover, habitat changes related to novel flow regimes may have influences beyond hydrologic effects. For example, four large flood events in the Wabash River in the last 25 years likely altered substrate habitats (Pyron et al. 2010), and changes to substrate, along with hydrology, led to different fish assemblages (Pyron et al. 2011; Pritchett and Pyron 2012).

Future precipitation patterns will likely alter nutrient loading to Indiana's aquatic systems, potentially causing greater prevalence of eutrophic conditions, including more frequent nuisance algal blooms, reduced water clarity, and low oxygen concentrations. Changes in producer and consumer communities in response to eutrophication have been observed in freshwater systems throughout the Midwestern USA (e.g., Ivan et al. 2014). In fact, fish assemblages in Indiana's glacial lakes appear to be responsive to eutrophic conditions (Feiner et al. 2016b). Some species may be particularly affected by synergistic effects of multiple stressors including those related to climate change, e.g., cold-water stenotherms may precipitously decline in lakes with new thermal and hypoxic regimes (e.g., Arend et al. 2011; Honsey et al. 2016b). Cisco (Coregonus artedi), a native cold-water species in Indiana, was present in approximately 50 lakes in the state at the beginning of the twentieth century but only 6 lakes during the most recent state-wide survey (in 2012, Honsey et al. 2016b). During the summer, cisco cannot survive in warm epilimnetic waters and thus move to the cooler hypolimnion. However, if the hypolimnion is hypoxic, fish can become squeezed between a hot epilimnion and a hypolimnion with insufficient oxygen. Such processes have evidently contributed to extirpations of cisco populations in the past, and with increased water temperatures and more severe hypoxia in the future, similar processes may lead to further population extirpations of these and other cool- and cold-water species.

4.4 Other vertebrates

While many amphibians are adapted to the short hydroperiods of vernal wetlands, drought can substantially reduce the length of time that these water bodies hold water and, consequently, prevent successful animal emergence before the wetland dries up. Moreover, extended periods of drought can reduce the total availability of wetland habitats for these species in the landscape. Phenological shifts are potential consequence of climate change (Hall 2014), and calling and breeding phenology in amphibians have advanced up to 3 weeks with climate warming compared to historical averages (Beebee 1995; Gibbs and Breisch 2001). Such shifts in phenology could lead to a mismatch with wetland habitat availability. Most ephemeral wetlands are dependent on seasonal (i.e., spring) precipitation for filling, while the duration of inundation will depend on seasonal (i.e., summer) drying. Temperature-mediated shifts in species phenology may or may not match altered temporal hydrology of wetlands. This potential mismatch could affect energy expenditure and mortality rates of wetland-dependent species.

Water provides a key dispersal vector for many aquatic organisms, including amphibians (Nathan et al. 2008), and changes in hydrology due to climate change will likely influence dispersal rates and directions. Drought increases fragmentation between breeding ponds and wetlands used by amphibian meta-populations, reducing dispersal among suitable habitat (Walls et al. 2013). In Indiana, dispersal-limited aquatic species may have a particularly difficult time in successfully shifting their range to follow suitable habitat since aquatic ecosystems are naturally more fragmented than terrestrial counterparts.

Waterfowl, on the other hand, have the capability to disperse long distances compared to most other aquatic organisms and may be able to expand their range. Nonetheless, the National Audubon Society (2013) predicted that several waterfowl in Indiana will lose a large portion of their summer or winter range, including but not limited to the horned grebe Podiceps auritus, ring-necked duck Aythya collaris, hooded merganser Lophodytes cucullatus, and bufflehead Bucephala albeola. As climate warms in the Midwest, species are expected to need to shift their ranges northwards at a rate of approximately 1 km/year if they are to remain in the same temperature regime (Loarie et al. 2009). Again, increased dispersal can evolve in response to shifting habitat (Weiss-Lehman et al. 2017) and water fowl may in particular benefit from such evolutionary responses.

5. Implications of climate change for long-term management of Indiana's aquatic ecosystems

The examples highlighted above are by no means the exclusive pathways by which climatic changes may affect the composition and dynamics of Indiana's aquatic ecosystems, and we again emphasize the high degree of uncertainty associated with current predictions of responses of these ecosystems to climate change. Nonetheless, we believe there are concrete approaches to managing Indiana's aquatic ecosystems in the face of these potential changes. In particular, we advocate for (1) management actions which promote diversity across various scales of organization, from individuals to populations, communities, and ecosystems; (2) continued research to improve our ability to anticipate how climatic changes will affect physical conditions in Indiana's aquatic systems, including how such changes interact with other anthropogenic stressors to affect aquatic organisms, populations, and communities; and (3) adoption of a precautionary principle when enacting management plans, erring on the side of conserving systems and populations that appear to be at risk of decline as a result of climate change even if there is high level of uncertainty in this risk.

5.1 Promote diversity

Relatively diverse systems may have an increased capacity to respond to disturbances, including impacts of climate change (e.g., Elmqvist et al. 2003; Bernhardt and Leslie 2013; O'Leary et al. 2017). Thus, diversity should be maintained or enhanced within and across aquatic systems, and diversity should be enriched across levels of biological organization, including individuals, populations, and communities. Various studies have highlighted the potential for increased community diversity, food web complexity, and interactions to enhance resistance and resiliency to environmental stressors, as increased diversity should expand the breadth of environmental conditions under, which some component of the system will be able to thrive. For example, multiple species may play similar functional roles within a food web: if one manages for functional diversity (or response diversity; Elmqvist et al. 2003), declines in an individual species as a result of climate change impacts can be buffered by other functionally similar species to maintain overall food web function.

An approach for enhancing diversity within aquatic communities and populations involves promoting habitat connectivity and diversity. Increased connectivity among systems and habitats can allow for new recruits to support locally affected populations and community and promote local recovery rates (e.g., Thrush et al. 2013). Species performance varies across habitat conditions, e.g., in glacial lakes in Indiana, young largemouth bass consume different prey across different habitats (Middaugh et al. 2013) which may translate to differential growth and survival. Access to diverse, complex habitats enhances food web connections for largemouth bass, thus increasing their likelihood of persistence in the face of change. Similarly, distinct habitats may respond differently to climatic changes, and habitats which are currently less suitable for a particular species may become more suitable in the future. For example, fall thermal conditions in a habitat may be presently too cold for a species due to high groundwater inputs and shade. In the future, the same habitat may be near thermally optimal as elevated atmospheric temperatures counteract the historically too cold groundwater and shade cooling effects. Importantly, habitat management should not simply target increased habitat diversity but in many systems should specifically target habitat restoration and improvement. For example, negative impacts of climate change on smallmouth bass in the Kankakee River in northwestern Indiana may be mitigated by restoration of local habitat features (Peterson and Kwak 1999).

In order to ensure maximum ability for aquatic organisms in Indiana to respond to projected climatic changes, it may be critical to promote intra-specific diversity within and across populations. The adaptive potential of a species to climate change is determined by the composition and diversity of genetically based traits within a population that are adaptive under a changing climatic or hydrologic regime (Falconer and Mackay 1996). Ideally, information on functional genetic diversity would be used to predict whether a species will evolve under climate change. However, the genetic diversity of functional traits adaptive under climate change is unknown for most species in Indiana. In the absence of such knowledge, neutral genetic markers can potentially be used to identify populations that have an overall low genetic diversity (Pauls et al. 2013). Phenotypic and genotypic diversity may be maintained by (a) managing for a variety of habitat conditions, favoring different genotypes and promoting phenotypic plasticity and (b) maintaining natural connectivity within populations.

Genetic considerations that will be key for proactive management include fish stocking programs, aquatic restoration, and conservation of existing genetic diversity. Climate change could reduce population sizes and genetic variation as a species' range shifts (Pauls et al. 2013). Managers may consider collecting individuals for use in future stocking efforts now, before such variation is reduced. It will be appropriate to account for future climatic conditions at a specific location when choosing genetic sources for fish stocking and wetland restorations (Havens et al. 2015). An effective strategy for restorations might be to use native species that are projected to occur in Indiana in the next century, but from genetic sources that occur in the southern portions of the species' range and are therefore potentially more resistant to climaterelated impacts (Havens et al. 2015). At the same time, it is not manifest that southern populations will contain the most appropriate genetic variation to respond to climatic changes. Broad conservation of inter- and intra-population genetic diversity is critically important, and maintaining diverse aquatic habitat across systems should help limit loss of genetic material by preserving multiple populations of species at large effective sizes.

5.2 Improve understanding

An improved ability to anticipate specific climatic effects on aquatic systems in Indiana, including the cost-effectiveness of management actions available to counter potential negative effects, would clearly assist with management decisions. There remains a need for continued development and improvement of region- and state-specific climatic projections and resulting physico-chemical conditions in specific aquatic systems. Of note, we suggest that improved projections of future wind patterns are critical for anticipating effects in lacustrine systems. There is high uncertainty regarding future wind patterns but, as alluded to in this review, such patterns can have a strong influence on various characteristics of aquatic systems.

In addition to improving understanding of future physical conditions in aquatic systems, we advocate for studies to continue developing predictions of how specific populations and communities are expected to respond. Essentially, there is a need to advance understanding and predictive certainty of all steps in the cause-and-effect pathways, including interactive influences of other stressors, effects on vital rates, and ultimate effects on populations and communities. For example, consider Indiana's cisco, arguably the fish species in the state most directly threatened by climate change. If cisco population extirpation rate continues as it has over the past 60 years, the species will be extinct in the state between the middle and end of the twenty-first century. However, this trajectory will almost certainly be affected by various unknowns. Will epilimnetic warming in Indiana's glacial lakes accelerate in the future? How will future climatic conditions and land-use interact to structure thermal-oxygen patterns? Will hypolimnetic hypoxia become more severe? Have remaining Indiana cisco populations evolved to tolerate warmer temperatures and lower oxygen conditions? What is the capacity for such evolution in the future? Finally, what are the management options to counteract these effects? Can stocking counteract population declines? How cost-effective would hypolimnetic oxygenation be as a habitat improvement tool?

Improved predictions of how biota in specific aquatic systems may respond to climate change would clearly benefit the management of such biota. Moreover, for some systems in Indiana, elucidation of climatic effects on biota could provide important insights for other systems. Glacial lakes in northern Indiana constitute the southern extent of a distribution of glacially formed lakes through the upper Midwest of the USA and southern Canada. As such, they are expected to reach potentially critical thermal conditions earlier than more northern lakes and their biotic responses may be a harbinger of responses in more northern lakes. Similarly, Indiana contains the most southern and warmest region of Lake Michigan's main basin, and responses in this region may foretell responses in northern areas of the lake (or even into Lake Huron). Further, Indiana contains a relatively high diversity of several aquatic taxa, including fishes and freshwater mussels. Community responses of these taxa may provide insights as to how diverse communities may respond in other regions.

5.3 The precautionary principle

The precautionary principle has been broadly advocated for in natural resource conservation (e.g., Lauck et al. 1998; Hilborn et al. 2001). Even in the absence of climate change, fishery management is rife with uncertainty due to fish stocks' sensitivity to highly variable physical conditions, multiple non-linear biotic, and abiotic interactions which can magnify population dynamics and difficulty in assessing current and past status of fish stocks. Insufficiently accounting for this uncertainty and aggressive harvesting has contributed to declines and extirpation of fish stocks throughout the world. A more precautionary approach would hopefully contribute to limiting such deleterious effects. For brevity, the concept can be summarized by the Wingspread Statement on the Precautionary Principle (1998), "When an activity raises threats of harm to human health or the environment, precautionary measures should be taken even if some cause and effect relationships are not fully established scientifically." We suggest that this principle should also guide management of Indiana's aquatic ecosystems in the face of climate change. It is highly likely that aquatic ecosystems in Indiana and the biota which inhabit these systems will change dramatically in response to climate change. While some systems and species seem to be at greater risk to climate change than others, precisely pinpointing exactly how specific ecosystems, communities, and populations will respond is inappropriate. However, assuming there will be no change to these systems may be even more inappropriate and risky. Thus, we suggest aquatic ecosystem managers take a precautionary approach to (a) conserve and restore a diversity of aquatic systems and habitats, (b) actively work to maintain and enhance species diversity and both inter- and intra-population genetic variations, and (c) limit activities and stressors which may exacerbate the risk of decline for aquatic biota.

Acknowledgments This paper is a contribution to the Indiana Climate Change Impacts Assessment (INCCIA).

Author attribution All authors contributed to overall report structure, drafted individual sections, and edited the entire manuscript. Höök and Foley assembled individual author contributions and organized the manuscript. Funding information The INCCIA is organized and financially supported by the Purdue Climate Change Research Center.

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