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Commentary

A perspective on needed research, modeling, and management approaches that can enhance Great Lakes fisheries management under changing ecosystem conditions

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ABSTRACT

The Great Lakes Fishery Commission sponsored a 2-day workshop that sought to enhance the ability of Great Lakes agencies to understand, predict, and ideally manage fisheries production in the face of changes in natural and anthropogenic forcings (e.g., climate, invasive species, and nutrients). The workshop brought together 18 marine and freshwater researchers with collective expertise in aquatic ecology, physical oceanography, limnology, climate modeling, and ecosystem modeling, and two individuals with fisheries management expertise. We report on the outcome of a writing exercise undertaken as part of this workshop that challenged each participant to identify three needs, which if addressed, could most improve the ability of Great Lakes agencies to manage their fisheries in the face of ecosystem change. Participant responses fell into two categories. The first identified gaps in ecological understanding, including how physical and biological processes can regulate early life growth and survival, how life-history strategies vary across species and within populations, and how anthropogenic stressors (e.g., nutrient runoff, climate change) can interact to influence fish populations. The second category pointed to the need for improved approaches to research (e.g., meta-analytic, comparative, spatial translation) and management (e.g., mechanistic management models, consideration of multi-stock management), and also identified the need for improved predictive models of the physical environment and associated ecosystem monitoring programs. While some progress has been made toward addressing these needs, we believe that a continued focus will be necessary to enable optimal fisheries management responses to forthcoming ecosystem change.

Introduction

Human-induced rapid environmental change (HIREC; Sih et al., 2011), which has been driven by habitat destruction (Pimm and Raven, 2000), non-native species introductions (Carlton, 2003; Holeck et al., 2004), overexploitation and selective harvest (Pauly et al., 1998;

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Worm et al., 2009), altered nutrient inputs (eutrophication and oligotrophication; Stockner et al., 2000; Smith et al., 1999), and climate change (Walther et al., 2002; Parmesan and Yohe, 2003; Hayhoe et al., 2010; IPCC, 2013), has modified the physical, chemical and biological properties of aquatic ecosystems across the planet (Vitousek et al., 1997; Halpern et al., 2008). In some cases, HIREC has led to a whole-scale change in the state of an ecosystem (i.e., a regime shift; Scheffer et al., 2001; McGowen et al., 2003; Scheffer and Carpenter, 2003) that has altered the dynamics of its fish populations (Anderson and Piatt, 1999; Hare and Mantua, 2000; Reid et al., 2001; Beaugrand, 2004). In other cases, HIREC has had a more specific impact on fish population demographics by altering the probability of recruitment through early life stages (e.g., Mueter et al., 2011; Brochier et al., 2013). Examples such as these point to the need to consider the state and dynamics of the broader ecosystem when attempting to understand and forecast fisheries production, not just local-scale processes operating in the aquatic realm.

While much has been learned about how humans can drive change in aquatic ecosystems during the past half century, our ability to predict fisheries production under different ecosystem states is still lacking, particularly in large freshwater ecosystems such as the Laurentian Great Lakes (hereafter Great Lakes; Ludsin et al., 2014; Mulvaney et al., 2014). This gap in knowledge is important because large-scale changes in ecosystem conditions have become evident in each of the Great Lakes (e.g., Hecky et al., 2004; Allan et al., 2013; Bunnell et al., 2014), as they have in other large lakes of the world (e.g., East African Rift Lakes: O'Reilly et al., 2003; Hecky et al., 2010). For example, water warming trends during recent decades have been documented in many of the Great Lakes, including its smallest (Erie: Jones et al., 2006) and largest (Superior: Austin and Colman, 2007) members, with the rate of water temperature increase in Lake Superior being twice that of air temperature (Austin and Colman, 2007). Similarly, precipitation patterns have changed, with the frequency of multi-day storm events increasing during winter and spring (Kunkel et al., 1999; Hayhoe et al., 2010) and with the expectation that this trend will continue (Kling et al., 2003; IPCC, 2013; Kunkel et al., 2013; Michalak et al., 2013).

In addition to climate change, humans have altered the trophic status of many of the Great Lakes through multiple pathways (Ludsin et al., 2001; Makarewicz and Bertram, 2001; Bunnell et al., 2014; Scavia et al., 2014; Turschak et al., 2014). For example, long-term data from several of the upper lakes (Lake Michigan and Lake Huron in particular) point to these systems becoming more oligotrophic and regulated by bottom–up forcing in recent decades, owing to the combined effects of nutrient abatement programs, changes in planktivorous fish (e.g., alewife *Alosa pseudoharengus*) abundance, and the invasion of invertebrate grazers on phytoplankton (i.e., *Dreissena* mussels) and zooplankton (e.g., *Bythotrephes longimanus*) (Bunnell et al., 2011, 2014; Vanderploeg et al., 2012). By contrast, a re-eutrophication of Lake Erie has been occurring during the past decade, seemingly owing to increased precipitation during winter through spring and changing farming practices, both of which have increased inputs of dissolved (bioavailable) phosphorus to the lake (Kane et al., 2014, 2015; Scavia et al., 2014).

To enhance the ability of Great Lakes agencies to understand, predict, and ideally manage variation in fisheries production in large aquatic ecosystems such as the Great Lakes, the Great Lakes Fishery Commission (GLFC), a bi-national agency that coordinates fisheries research and cooperative fisheries management within the basin, sponsored a multi-day workshop that focused on how human-driven changes in climate and nutrient inputs might alter fish populations and the fisheries that they support. This workshop sought to enhance our understanding of how ecosystem state change resulting from these forms of HIREC (i.e., climate change and trophic status change) would independently and interactively influence key physical and biological factors important to the fish recruitment process. This information gap has been previously identified as a research priority by the GLFC (http://www.glfc.org/research/FRra.php) and also has relevance to other large aquatic ecosystems, both freshwater and marine (see Ludsin et al., 2014). Herein, we report on some key findings from this workshop.

Workshop topic and approach

The workshop—entitled "*Physical–biological coupling as a driver of fish recruitment under changing ecosystem states*"—was held in Huron, Ohio during 12–14 August 2013. It was attended primarily by North American marine and freshwater (primarily Great Lakes) researchers ($n = 18$) whose expertise includes aquatic ecology, physical oceanography, limnology, climate modeling, and ecosystem modeling (including physical–biological modeling). Twelve people affiliated with management agencies also were invited to attend the workshop; however, most could not attend ($n = 10$). Consequently, the management perspective was only represented by the two people with fishery management experience, one from the Great Lakes and the other from outside of the region.

Within the general context of understanding how an altered ecosystem state, induced by climate variation and changed nutrient dynamics (i.e., oligotrophication, eutrophication), influences the role of physical–biological forcing in the fish recruitment process, attendees were asked to reflect upon five specific questions both before and during the workshop: (1) What physical processes should increase/decrease in importance as an ecosystem shifts to a new state? (2) As physical processes change, what are the implications for physically driven recruitment variations as compared to other processes important to population dynamics, such as predator–prey interactions and overlap with suitable habitat/prey resources? (3) To what degree can fish life-histories accommodate these changes in physical and biological processes? (4) What are the management implications of changes to the physical–biological forcing of recruitment variability? (5) Will physical forcing of recruitment vary the same way in response to nutrient state change as to climate state change, and will responses be similar in freshwater and marine systems?

All participants were required to complete a series of pre-workshop activities to ensure maximal progress during the meeting period. Attendees were first asked to recommend two relevant papers (e.g., peer-reviewed publications, gray literature reports, undrafted manuscripts), which were made available to all participants prior to the workshop. From this list, the workshop's steering committee selected a subset to be read prior to the workshop, with each participant asked to read four papers: (1) Ludsin et al. (2014), which discussed the importance of physical processes to fish recruitment in the Great Lakes; (2) Bunnell et al. (2014), which provided an overview of recent changes in Great Lakes ecosystems; (3) Magnuson et al. (1997), Najjar et al. (2010), or Ficke et al. (2007), each of which discussed climate change impacts on aquatic ecosystems; and (4) Massol et al. (2007), Winder and Schindler (2004), or Durant et al. (2007), each of which provided an example of how climate change and/or altered ecosystem productivity could influence fish recruitment. Participants also were required to craft short papers and presentations that illustrated the foundation/evidence for their views.

While numerous additional activities occurred at the workshop (e.g., small-group discussions, outlining manuscripts), two key activities led to the outcomes that we present below. First, after every five participant presentations, group discussions ensued, which integrated across individual views and sought broad consensus. Second, after the final presentation discussion period, participants were required to identify in writing (20 min allotted time) three needs that could most improve the ability of agencies to manage their fisheries in the face of ecosystem state change. These needs could have emanated from individual experiences, pre-workshop writing activities (writing, reading), the presentations, or the post-presentation discussions.

Below, we provide an overview of the key outcomes of this writing exercise, as several of these topics (or their combination) are being developed into independent manuscripts.

Workshop outcomes

A diversity of needs were mentioned in the writing exercise. Most of them focused on gaps in research and monitoring, as well as general modeling approaches and management considerations, which could *indirectly* improve fisheries management (Table 1). As a means to prioritize the importance of each need, we tallied the number of times each need was mentioned. These included seven areas of improvement that we grouped *post hoc* into two broad categories: (1) improved ecological understanding and (2) expanded research and management approaches.

Improved ecological understanding

A general consensus existed among workshop participants that better knowledge of fish recruitment mechanisms would improve our ability to understand how climate and changes in lake trophic state will influence fish population dynamics and fisheries production potential. While much progress has been made in this arena, our understanding of fish recruitment processes remains incomplete in most ecosystems, including the Great Lakes (Ludsin et al., 2014; Pritt et al., 2014). Within this context, three specific, but inter-related, information gaps were consistently mentioned by workshop participants: (1) a lack of understanding of the relative importance of and interactions among physical and biological drivers in the recruitment process; (2) a lack of knowledge concerning interspecific and intraspecific life-history variation and its plasticity; and (3) a lack of information on the impact of simultaneous human-driven stressors of fish populations.

Physical and biological drivers of recruitment

Participants reaffirmed the GLFC's goal of understanding the role that physical factors play in the recruitment process, especially through their effects on the spatial and temporal overlap between fish early life stages (e.g., larvae) and prey (zooplankton) availability (sensu Ludsin et al., 2014; Table 1). Marine scientists have long recognized the potential for physical processes (e.g., advection) to indirectly regulate fish recruitment by altering the match between first-feeding fish larvae and their planktonic prey (Hjort, 1914; Cushing, 1975, 1990). However, this mechanism was postulated as being unimportant to freshwater fish recruitment because many freshwater fishes have evolved a life-history in which larvae hatch at a larger size (and with more yolk) and spend a shorter time in a pelagic planktivorous stage, thus rendering them less vulnerable to starvation and predation relative to their marine counterparts (Miller et al., 1988; Houde, 1994; Myers, 1997). While probably true for the majority of fishes that occupy small freshwater lakes and lotic environments, many of the economically and ecologically important fishes in the Great Lakes Basin, including walleye *Sander vitreus* (e.g., Mion et al., 1998; Fraker et al., 2015), yellow perch *Perca flavescens* (e.g., Reichert et al., 2010; Brodnik et al., 2016), lake whitefish *Coregonus clupeaformis* (Freeberg et al., 1990; Pothoven et al., 2014), and alewife (e.g., Höök et al., 2007, 2008), do have pelagic, planktivorous larvae that exhibit high dispersal potential. Further, consumption, growth, survival, and recruitment of ecologically and economically important fishes in the Great Lakes have been shown to be indirectly regulated by processes that influence access to zooplankton (prey) resources during the pelagic larval stage (e.g., Freeberg et al., 1990; Bremigan et al., 2003; Dettmers et al., 2005; Redman et al., 2011; Pangle et al., 2012).

Research focused on biophysical regulation of the recruitment process also should enhance our ability to anticipate how human-driven changes in climate and ecosystem productivity might impact the dynamics of exploited fish populations. Temporal coincidence between fish larvae and their planktonic prey on seasonal time scales is expected to become increasingly important as changes in heating, cooling, and stratification alter their respective phenologies (e.g., Peeters et al., 2007; Platt et al., 2003; Winder and Schindler, 2004). For example, climate warming might indirectly reduce growth and survival of larval fish by affecting the temporal overlap of planktivorous larvae with their prey (Durant et al., 2005, 2007; Taylor, 2008; Ottersen et al., 2010), as plankton blooms in temperate ecosystems are expected to occur earlier in a warmer climate (Peeters et al., 2007), which may not be the case for fish spawning times (e.g., Farmer et al., 2015; but see Peer and Miller, 2014).

Changes in ecosystem productivity (i.e., increases or decreases in primary production) also can have large impacts on food availability to fish early life stages. While the response would be expected to be faster and perhaps more pronounced in shallow areas (e.g., nearshore embayments) and small systems (e.g., Lower Great Lakes) relative to deeper areas (e.g., main lake basins) and large systems (e.g., Upper Great Lakes), zooplankton biomass should increase as an ecosystem moves from a lower to higher trophic state (i.e., becomes more eutrophic), owing to "bottom–up" effects of enhanced phytoplankton availability (McCauley and Kalff, 1981; Bays and Crisman, 1983; McQueen et al., 1989). In turn, enhanced zooplankton prey availability could increase survival during the zooplanktivorous larval stage (Freeberg et al., 1990; Beaugrand et al., 2003; Roseman et al., 2005). However, as with temperature, ecosystem productivity can increase beyond a point that is optimal for a fish, at which point any benefits gained by enhanced zooplankton are offset by losses of other critical habitat features. For example, excessive phytoplankton production could lead to areas with low dissolved oxygen (hypoxic zones) or insufficient light, which can impair growth, foraging, and survival (Ludsin et al., 2001; Breitburg, 2002; Wellington et al., 2010; Pangle et al., 2012). The potential also exists that, in highly eutrophic ecosystems, zooplankton may not be available for consumption by fish. Zooplankton composition may change, for instance, which can result in incompatible sizes or low-quality prey resources (Miller et al., 1990). Or, zooplankton might use the hypoxic zone as a refuge from predation, thereby reducing availability to fish predators (Klumb et al., 2004; Ludsin et al., 2009; Vanderploeg et al., 2009).

Life-history variation

Workshop participants indicated that better knowledge of interspecific and intraspecific life-history traits of fishes (e.g., birth and death rates; reproductive timing, frequency, and location; age at maturation; and longevity), including their plasticity, would improve the ability of managers to understand and predict fisheries dynamics in a changing environment over the long-term (Table 1). Potential effects of ecosystem change on recruitment variation depend on the interaction

Table 1
Responses of workshop participants ($n = 20$) to the question, "What three needs could most improve the ability of Great Lakes agencies to manage their fisheries in the face of ecosystem state change?" The frequency that each response was mentioned is provided (out of 60 total responses). These responses were classified *post hoc* into two general categories: "Improved Ecological Understanding" and "Expanded Research and Management Approaches".

Identified needs	Frequency
Improved ecological understanding	
Physical and biological drivers of recruitment	15
Inter- and intra-species life-history variation and its plasticity	8
Impacts of multiple human-driven stressors on recruitment	6
Expanded research and management approaches	
Approaches to assess the impact of ecosystem state change	12
Mechanistic management approaches	9
Monitoring programs	6
Robust predictive models of the physical environment	4

among life-history characteristics and several processes, including spatial restriction on movement due to lake size and orientation, limits on gene flow and genetic variation within populations due to movement restrictions among populations, and limits due to specific life-history characteristics.

Knowledge of life-history traits and related processes might help anticipate which species will increase or decrease their range (and/or population size) in the face of ecosystem state change (Olden et al., 2006). For example, while local populations of marine species with strict habitat requirements for spawning (Atlantic herring *Clupea harengus*) or for their nursery grounds (plaice *Pleuronectes platessa*) were predicted to be less resilient to climate-induced environmental variability than species with more general requirements (e.g., Atlantic cod *Gadus morhua* and European anchovy *Engraulis encrasicolus*; Petitgas et al., 2013), the connectivity provided by open-water habitat over a long latitudinal gradient (assuming the required habitat shifts north or south and is not location-specific) would be expected to allow marine fish to track preferred habitats over large distances. By contrast, Great Lakes species may be more limited in their potential to track shifting habitat by the existence of confining shorelines that will restrict latitudinal migration to the narrow connecting channels among the lakes. Most certainly, this limitation will vary among lakes, owing to size, lake orientation, and depth differences (e.g., Lake Erie has an east–west orientation, whereas Lake Michigan has a north–south orientation).

While a similar effort to understand the capacity of life-history traits to influence species persistence has not been attempted in the Great Lakes, species with a "periodic" life-history strategy (i.e., Winemiller and Rose, 1992) would be expected to fare poorly with continued climate change because of projected increases in the frequency of spring storm events, reduced ice cover, and likely mismatches between zooplankton prey and larval fish production (Kling et al., 2003; Durant et al., 2007; Hayhoe et al., 2010; J. Wang et al., 2012; H.Y. Wang et al., 2012) that could further reduce the frequency of already rare, strong recruitment events. If true, recruitment to the fishery of many of the Great Lakes' ecologically and economically important species (e.g., walleye, yellow perch, alewife, and lake whitefish) might decline and/or become more variable in the face of a new climatic regime unless plasticity exists in their life-history strategies that allowed for rapid adaptation.

Instead, species with more "opportunistic" life-history attributes that promote demographic resilience in the face of environmental change (i.e., Winemiller and Rose, 1992) would be expected to increase in abundance with continued environmental variability brought on by climate change. Similarly, species that develop their ovaries during winter and spawn the following spring (e.g., yellow perch) would be expected to be negatively affected by winter warming, which has been shown to impair reproductive success by reducing egg quality and hatching success, as well as larval size at hatch (Farmer et al., 2015). On the contrary, species that develop ovaries after the winter and spawn during summer (e.g., freshwater drum *Aplodinotus grunniens*, emerald shiner *Notropis atherinoides*) or that are vulnerable to overwinter mortality associated with low temperature (e.g., white perch *Morone americana*: Johnson and Evans, 1990; Fitzgerald et al., 2006; gizzard shad *Dorosoma cepedianum*: Fetzer, 2009; alewife: Höök et al., 2007) might be expected to actually benefit from a shortened winter and enhanced spring-through-fall growing season.

Knowledge of life-history attributes also may help to guide predictions of within-species responses to ecosystem state change (Jones et al., 2006). Similar to non-Great Lakes fishes, both freshwater and marine (e.g., Leggett and Carscadden, 1978, Conover and Present, 1990; Conover et al., 1997), intraspecific variation in life-history attributes associated with growth and reproduction has been documented within and among the Great Lakes for ecologically and economically important fishes, including lake trout *Salvelinus namaycush* (Krueger and Ihssen, 1995), lake whitefish (Ihssen et al., 1981), walleye (Jones et al., 2006), and yellow perch (Feiner et al., 2015). However, information on the magnitude of plasticity that exists within and among Great Lakes populations remains scant, with only a few recent studies speculating on how HIREC has influenced life-history variation through space and time (e.g., Wang et al., 2008; J. Wang et al., 2012; H.Y. Wang et al., 2012; Feiner et al., 2015). Even more enigmatic are the consequences of altered or lost intraspecific life-history variation that is expected with continued HIREC through shifts in habit conditions (e.g., water temperature, water clarity, river flows) important to growth, reproduction, and survival (e.g., Jones et al., 2006). Because of the potential for lost intraspecific variation in life-history attributes to negatively affect fisheries production and sustainability (Hilborn et al., 2003; Schindler et al., 2010), we agree that a fuller understanding of the causes and consequences of intraspecific life-history variation would benefit the ability of managers to understand past, present, and future variation in their fisheries.

Multiple human-driven stressor impacts

Workshop participants fully recognized the need to consider the impact(s) of multiple human-driven stressors on fish populations (Table 1). This recognition may be partly due to the possibility of climate change and/or altered ecosystem productivity worsening the ability of managers to understand and forecast fisheries dynamics by weakening (through antagonistic effects; i.e., the combined effects of multiple stressors are less than the sum of stressors independently) or intensifying (through additive or synergistic effects; i.e., combined effects of two stressors are equal to or greater than the sum of the stressors independently) the impact of other anthropogenic stressors (Folt et al., 1999; Brook et al., 2008; Ormerod et al., 2010). Indeed, a meta-analysis of studies that manipulated two or more stressors in marine and coastal ecosystems showed that, while the cumulative effects of stressors were additive in 26% of the studies, synergistic in another 36%, and antagonistic in the remaining 38%, the addition of a third stressor doubled the number of synergistic interactions (Crain et al., 2008).

The combined effects of these multiple stressors may, in turn, lead to "ecological surprises" (Doak et al., 2008; Paine et al., 1998) that make management difficult. For example, multiple human-driven stressors (i.e., human population growth, intensive fishing, land cultivation, introduced species, and climate warming) have been implicated in Lake Victoria's (East Africa) transition into a new ecosystem state that is typified by reduced fish consumer biomass in the middle of the food web and high primary production, two changes that are unlikely to have occurred in the face of any single stressor alone (Hecky et al., 2010; Van Zwieten et al., 2016). Similarly, through an array of experimental manipulations, Christensen et al. (2006) showed how the non-additive, cumulative effects of increased temperature, acidification, and drought had unexpected synergistic and antagonistic effects on planktonic consumers and producers, respectively, in boreal lakes. Ecological surprises also have been observed in the Great Lakes, which have a long history of experiencing simultaneous human-driven stressors, including overexploitation, non-native species introductions, altered ecosystem productivity, and habitat destruction (Berst and Spangler, 1972; Christie, 1972; Hartman, 1972; Wells and McLain, 1972). In western Lake Erie, for instance, yellow perch recruitment and fishery harvest dynamics have (unexpectedly) come to depend on formation of turbid, open-lake river plumes that can provide a refuge for larvae from predators (Ludsin et al., 2011; Manning et al., 2013; Reichert et al., 2010; Carreon-Martinez et al., 2014). While these plumes have previously formed with no impact on yellow perch, their strong current impact apparently owes to the *combined* impacts of the following anthropogenic perturbations: (1) planned phosphorus abatement programs and unplanned dreissenid mussel introductions that increased water transparency in the west basin (Ludsin et al., 2001); and (2) the establishment of non-native invasive white perch, which have been shown to consume larval yellow perch more efficiently

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outside versus inside of turbid river plumes in western Lake Erie (Ludsin et al., 2011; Carreon-Martinez et al., 2014).

Examples such as these illustrate the need for investigations that explore interactions among multiple stressors. This need exists because continued disturbances associated with climate change and human population growth in the watershed are likely to promote species invasions that might magnify the incidence of unexpected interactions and synergies in the Great Lakes and the fisheries that they support (Byers, 2002; Rahel and Olden, 2008; Strayer, 2010). This need is further supported by the fact that studies on multiple stressors on aquatic ecosystems are lacking relative to single-stressor studies, yet freshwater science and management are replete with problems associated with multiple stressors (Crain et al., 2008; Ormerod et al., 2010).

In particular, we encourage agencies to support multi-faceted, multi-scale, mechanistic research investigations. While the exact approach employed will depend on a host of factors (e.g., monetary support, existing data and knowledge, complexities associated with the study system, species, and question asked; spatial and temporal scales of interest), we recommend a combined field, experimental, and modeling approach. At the outset, qualitative (e.g., Last et al., 2011) or quantitative (e.g., Bunnell et al., 2014) analysis of long-term research and monitoring data could be conducted, ideally in an integrative ecosystem assessment framework (e.g., Choi et al., 2005). Such analyses could help to identify shifts in fisheries and the broader ecosystem, and in turn, allow for plausible hypotheses to be developed regarding the causal relationships. Afterwards, controlled laboratory or manipulative field experiments could be used to test predictions specific to the hypotheses generated. Ideally, these experiments would be conducted in such a fashion that any antagonistic, additive, or synergistic effect could be detected (e.g., Folt et al., 1999). Finally, we would recommend combining these empirical approaches with mechanistic modeling, which can further test the hypotheses and their associated predictions. Ideally, sufficient field and experimental data would exist to both calibrate any models developed, as well as to test their performance in mimicking nature. In the best-case scenario, tractable questions would be asked with the initial model conceptualization, long-term data collection design, and analytical approach developed simultaneously so as to help ensure that appropriate data are being collected to address the question at hand (Lindenmayer and Likens, 2009).

Expanded research and management approaches

The second broad category of identified management needs centered on approaches that could benefit the ability of agencies to understand the impacts of HIREC on ecosystems. It also focused on ways to improve the ability of fisheries management agencies to quantify population size and trajectory, as well as to improve their ability to develop harvest control rules that could establish meaningful stock rebuilding thresholds and strategies to ensure stock persistence in the face of a changing environment (Table 1). Also identified was the need for better predictive models of the physical environment and monitoring programs, both of which could support the suggested research and management efforts.

Research approaches

Multiple approaches were mentioned that could improve understanding of how HIREC can alter fish recruitment through effects on coupled physical and biological processes. Meta-analytic approaches, which have had a long history in marine fisheries science, but with little history of application to the Great Lakes fishery, were specifically mentioned by workshop participants. Meta-analyses have been recommended for use in fisheries science when long time-series data are lacking, as the addition of datasets on similar fish populations can reduce uncertainty in model predictions and also provide necessary contrasts that can allow for patterns to emerge (Myers and Mertz, 1998; Planque and Frédou, 1999; Myers, 2001). Planque and Frédou (1999), for example, showed the value of such an approach in their examination of the effects of temperature on North Atlantic cod stocks. When each stock was examined individually, temperature was unrelated to inter-annual variation in recruitment. However, when individual stocks were combined into a meta-analysis, cold-water cod stocks were found to respond differently to fluctuations in water temperature than warm-water stocks or those located in the region between the stocks (Planque and Frédou, 1999).

In addition to pattern identification that can come from quantitative meta-analyses, workshop participants highlighted the value of conducting more general ecosystem comparisons. Such comparisons are considered valuable because they can help identify general responses to a perturbation to the ecosystem, which then potentially could be applied broadly to other ecosystems. This approach was successfully used in the Great Lakes to elucidate the impact of a different set of human-driven stressors (i.e., overfishing, invasive species, eutrophication) on Great Lakes fisheries (e.g., Smith, 1968; Christie, 1974), with only limited use of this approach for fisheries management purposes in recent decades (e.g., Bunnell et al., 2014). Indeed it was the hope of identifying similarities in the response of fisheries within the Great Lakes and marine ecosystems to ecosystem state change that motivated this workshop's steering committee to have both marine and freshwater scientists attend this workshop. This same motivation also in part underlies the development of programs that fund comparative ecosystem research (e.g., the National Science Foundation's and National Oceanic and Atmospheric Administration's now discontinued Comparative Analysis of Marine Ecosystem Organization [CAMEO] program; http://cameo.noaa.gov/).

With continued climate change, the Great Lakes are expected to experience substantial changes in temperature and precipitation during the course of the 21st century. For example, Hayhoe et al. (2010) predicted that the weather of Illinois during summer will feel like a summer in Oklahoma by 2050 and that of Texas by 2090 under a business-as-usual emissions scenario. Workshop participants suggested that, in addition to the current approach of using general circulation model (GCM) climate scenarios to force physical and biogeochemical models into the future (e.g., Sahoo et al., 2013; Cousino et al., 2015), developing “spatial translation” approaches that consider the entire life cycle and species interactions could benefit our ability to predict the impacts of climate change or altered ecosystem productivity on fish populations and the fisheries that they support. Such approaches have been used to predict fish growth during portions of the year in early Great Lakes climate studies (Magnuson and DeStasio, 1997). This same approach also has been effectively used to estimate the impacts of anticipated climate change on economically important blue crab (*Callinectes sapidus*) populations in Chesapeake Bay, where sea surface temperature in 2100 is expected to be similar to that of Georgia/South Carolina under a low greenhouse gas emission scenario and that of eastern Florida under a high emissions scenario (Boesch et al., 2008). Essentially, by modeling Chesapeake Bay blue crab populations under the expected thermal regime of South Carolina (for example), it was predicted that individual growth rates and developmental rates would increase, maturation would occur earlier, and the overall rate of population growth would increase because temperatures would exceed 11 °C during the winter, a temperature threshold that has been shown to delay developmental rates and maturation schedules by 4–6 months (Brylawski and Miller, 2006). In turn, the increase in blue crab production that is expected to occur under a South Carolina thermal regime in Chesapeake Bay also should allow for higher rates of exploitation that are still sustainable, a longer fishing season, and have major impacts on food web interactions (Hines et al., 2009).

Management approaches

Workshop participants expressed the need for agencies to adopt more mechanistic approaches in their management (Table 1), including

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those that consider the impacts of ecosystem state change on the recruitment process and sub-population (i.e., stock) diversity that can arise from life-history differences. This reflects the general shift in the goal of fisheries science from trying to eliminate variability in fish recruitment to trying to better understand this variation and use it to better manage the fishery (Houde, 2008, 2009). Workshop participants indicated that the use of mechanistic modeling approaches is appropriate because human-driven ecosystem state change can alter interactions within and among species in complex ways, which are not easily captured by traditional statistical approaches that rely solely on fisheries-dependent and fisheries-independent catch rates and demographic attributes. While we fully recognize that mechanistic models will always be imperfect, owing to insufficient data, unaccounted for phenomena, and/or missing ecosystem understanding, they can benefit fisheries management by allowing hypotheses concerning HIREC-induced ecosystem change to be tested and by helping identify critical information gaps that require further study and/or monitoring (Jones et al., 2006; Miller, 2007; Ludsin et al., 2014). Further, owing to the various ways in which HIREC can alter ecosystems, including interactions within and among species, traditional, non-mechanistic management practices may lead to strategies that unintentionally harm a resource (Hofmann and Powell, 1998). This unintended consequence can arise due to the use of a short-term management perspective driven by concerns among stakeholders in the level of uncertainty in model predictions. In turn, the use of mechanistic, physical–biological models to understand the recruitment process has been encouraged in fisheries science and management in both marine ecosystems (de Young et al., 2010; Hofmann et al., 2010; Miller, 2007; North et al., 2009) and the Great Lakes (Jones et al., 2006; Ludsin et al., 2014).

Recognition by some workshop participants that management agencies need to consider stock structure was not unexpected, given that identifying stock structure has long been a goal of marine fisheries management and conservation (Begg and Waldman, 1999; Hilborn et al., 2003; Schindler et al., 2010). It also has recently been recognized as a vital need in large freshwater ecosystems such as the Great Lakes (Kutkuhn, 1981; Glover et al., 2008; Sepulveda-Villet and Stepien, 2011; Ludsin et al., 2014; DuFour et al., 2016). Each stock (i.e., local spawning population) likely has diverse life-history characteristics and adaptations to the habitat in which it spawns (Hilborn et al., 2003). For example, Sockeye Salmon (*Oncorhynchus nerka*) stocks that support the Bristol Bay, Alaska fishery—one that has remained fairly stable over the last 20 years despite substantial variation in climate—spend varying amounts of time at sea as an adult, migrate to different rivers to spawn, and spawn at different times of the year (Hilborn et al., 2003; Schindler et al., 2010). The resilience of this fishery to environmental variation has been attributed to this diversity of reproductive tactics (life-histories), which allows different stocks to do well under different environmental conditions (Schindler et al., 2010). This finding reinforces our previous suggestion to understand species' life-histories points to the need to maintain stock diversity, and recommends against strategies that only manage for stocks that are currently doing well or that manage a known multi-stock fishery as a single stock (Hilborn et al., 2003; Schindler et al., 2010; DuFour et al., 2016). Therefore, the need to identify and manage for a diverse assemblage ("portfolio") of fish stocks in the Great Lakes, which is now occurring in some populations (e.g., Ryan et al., 2003) but not others (DuFour et al., 2016), is likely to increase with continued climate change (Höök et al., 2008; Sesterhenn et al., 2014).

Physical models and monitoring

The final identified need in this second category included more accurate predictive models of the physical environment and the expansion of ecosystem monitoring programs (Table 1). While current GCMs have been fairly successful and precise when predicting climate patterns at a large scale, they do not provide the detail needed for accurate regional-scale models that usually come from long-term direct measurements (Christensen et al., 2007; Karl and Trenberth, 2003). Likewise, existing regional climate models currently are lacking in several ways, including their spatial resolution, how they are coordinated among scientific studies, and their reproducibility (i.e., different models provide different results) (Christensen et al., 2007). Thus, continued effort to increase the predictive capabilities of down-scaled climate models was strongly supported by workshop participants. This need is only further heightened by the fact that climate (e.g., temperature, wind, precipitation) drives many of the key physical processes in the Great Lakes (e.g., thermal stratification, heating, cooling, and tributary discharge) that, in turn, can influence the fish recruitment process (reviewed by Ludsin et al., 2014). Further, the general consensus among workshop participants was that, if we cannot achieve reliable physical models of the Great Lakes, we stand little chance of correctly predicting biological (including fisheries) responses to ecosystem state change. In addition, while finer scales are necessary to develop more accurate physical and biological models, methods of reconstituting predictions at the broader spatial and temporal scales useful to management (e.g., seasonal and annual time septs) also are necessary. These predictions, however, should not be too far into the future, given that Great Lakes managers/policymakers show a strong preference for near-term forecasts (5–10 years out) over longer-term ones (>20 years out) (Mulvaney et al., 2014).

To help improve the predictive capability of climate models, as well as linked physical–biological models that might be developed to support fisheries management (see above), workshop participants strongly encouraged the expansion of monitoring of key environmental variables. This need was mentioned because climate and physical–biological models are typically data "hungry," requiring data for calibration and independent data for evaluation. Most prominently, workshop participants identified the need for monitoring programs that are conducted at biologically relevant spatial and temporal scales in the same system through time which can allow scientists to understand spatial and temporal heterogeneity in ecosystem attributes. In particular, a gap in our understanding of the dynamics of the lower food web (e.g., phytoplankton, zooplankton), water quality, and biogeochemical parameters was identified during early spring, a period when larval fish are typically in high abundance in the ecosystem and require plankton to survive (Ludsin et al., 2014).

Caveats

Most of the needs identified in our workshop offered *indirect* support for fisheries management by improving our ability to understand and model the ecosystem, as well as its fisheries. With exception of the recommendation to implement strategies that can protect stock diversity, no direct, "on-the-ground" management regulations or policies (e.g., stocking practices, harvest quotas, habitat restoration plans) or harvest considerations were mentioned by any of the workshop participants. Because researchers outnumbered fishery managers by a ratio of 9:1, despite our failed attempt to have a more balanced set of participants (see Workshop topic and approach), the possibility exists that the findings from our workshop's writing exercise were biased by the makeup of the participants. A comparison of our results to a recent study that independently surveyed Great Lakes fishery researchers and Great Lakes fishery managers/policymakers about climate change (Mulvaney et al., 2014) lends support for and against the notion that our results are biased. Similar to our own findings, Mulvaney et al. (2014) found that fishery managers/policymakers saw value in improving ecosystem understanding (i.e., food web interactions in particular), using biophysical modeling to assess the impacts of climate change on fisheries (but only in the short-term, not also at longer temporal scales), and monitoring physical data and processes over the long-term. However, Mulvaney et al. (2014) made no mention of the need to better understand the recruitment process, life-history variation, or multiple-stressor impacts; neither was the need for new

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analytical approaches (e.g., meta-analysis, comparative, spatial translation) insinuated. Given that our workshop asked a different set of questions than Mulvaney et al. (2014), we see value in repeating our exercise with a larger set of fishery managers/policymakers.

One additional limitation to having only a couple of fishery managers present at our workshop is that most participants likely did not know whether existing indices of fish recruitment are satisfactory in the Great Lakes. While we cannot know for certain, we presume that all of the workshop participants were working under the assumption that satisfactory indices of fish recruitment already exist and are being monitored. Such indices would be essential for any meaningful assessment of the impact of ecosystem change on fisheries, with their importance superseding the need for quality data on the physical environment or lower food web.

Summary and conclusions

Workshop participants identified several key research, management, and information needs that could help agencies better understand, predict, and ideally manage variation in fish production in the Great Lakes in the face of future ecosystem change. Most prominent was the need for fishery managers to conduct or support multifaceted mechanistic research into how physical processes, multiple interacting forms of HIREC, and life-history variation within and among species influence recruitment to the fishery and fishery dynamics. Physical processes are expected to play a more prominent role in the recruitment process with continued climate change (Ludsin et al., 2014), and other forms of simultaneous HIREC are expected to cause more ecological surprises. In turn, fisheries management should become more difficult as 1) fishery managers do not possess levers to readily control climate and nutrient inputs (or invasive species for that matter), 2) the ability to influence recruitment via biological controls (e.g., harvest regulations on the spawning stock) is likely to lessen with recruitment being driven even more by stochastic, physical processes (e.g., storm events, ice cover duration, river inflows), and 3) ecological surprises cannot (by definition) be anticipated, thus increasing the difficulty of long-term planning. The difficulty in managing fisheries will only be exacerbated by possible climate-driven reductions in the frequency of strong recruitment events for the many ecologically and economically important fishes with periodic life-history strategies (e.g., walleye, yellow perch, lake whitefish, and alewife), barring any rapid life-history variation. Such changes most definitely would influence how these fisheries are managed, with the most likely scenario being reducing fishing quotas to protect spawning stock biomass. The need for such protective measures would only be heightened if other forms of HIREC are operating that can reduce prey (e.g., zooplankton) availability, especially during early life stages. Such forms might include the establishment of a new invasive planktivore (e.g., bighead and silver carp or a predatory invertebrate), reduced river flows during the spring (sensu Reichert et al., 2010), or altered land-use practices in the watershed that reduce nutrient availability to plankton during the larval production period.

Our workshop also identified the need for mechanistic modeling approaches that explore the effects of ecosystem state change on fisheries (or stocks) in a hypothesis-driven (scenario-testing) framework. The need for expanded monitoring programs, which could generate data to support model calibration and testing was deemed critical to the successful development of robust physical models of the environment (e.g., regional climate models), as well as biophysical models that were viewed as important for understanding the impact of multiple stressors on fisheries. Importantly, to maximize the value to management of modeling endeavors that seek to develop mechanistic understanding, the researchers and managers will need to formally evaluate how the information will be incorporated into the management decision-making process.

Achieving all of these ends will require continued and perhaps even increased investment in both research and ecosystem monitoring. While we cannot offer solutions that will increase funding, we believe more coordination and communication among regional, state, provincial, and federal agencies in both the US and Canada could increase sampling coverage and fill research gaps while also minimizing redundancy in data collection and research. The Cooperative Science and Monitoring Initiative (CSMI) in the Great Lakes is an attempt at providing such coordination (e.g., Weidel et al., 2014). Unfortunately, CSMI sampling only occurs once every 5 years in each lake, which our workshop participants indicate is too course of a resolution to fully understand the impacts of multiple interacting forms of HIREC on Great Lakes fisheries. Fortunately, many state, provincial, and federal fisheries management agencies have voluntarily committed resources to filling in these temporal gaps (e.g., lower food web data are being collected multiple times per year by Lake Erie agencies via the GLFC's Lake Erie Forage Task Group, http://www.glfc.org/lakecom/lec/FTG.htm), given recognition that these data appear important to managing fisheries resources. "Adaptive monitoring", which requires periodic evaluation of ongoing monitoring and assessment practices and a willingness to alter what is being monitored in an ecosystem (Lindenmayer and Likens, 2009), also could offer a means to free up resources to support some of the suggested mechanistic research, or fill vital information gaps. Because many of the current human-driven stressors in the Great Lakes were non-existent at the time that long-term monitoring programs were established, adaptive monitoring offers a means for new data-streams to be generated, which could heighten our ability to understand the impact of HIREC on Great Lakes fisheries. We know that such assessments occur regularly for some (if not all) agencies in the Great Lakes Basin (e.g., Ohio Department of Natural Resources-Division of Wildlife; J.T. Tyson, co-author, personal communication). We also have no doubt that continued support for comparative research programs (Ludsin et al., 2014) and workshops such as this one, which foster communication and ideas between scientists and the management community, can help to better understand the world's ecosystems and sustainably manage their valued fisheries resources in the face of human-driven ecosystem change.

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