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PERSPECTIVE

Consequences of changing water clarity on the fish and fisheries of the Laurentian Great Lakes

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Abstract: Human-driven environmental change underlies recent changes in water clarity in many of the world's great lakes, yet our understanding of the consequences of these changes on the fish and fisheries they support remains incomplete. Herein, we offer a framework to organize current knowledge, guide future research, and help fisheries managers understand how water clarity can affect their valued populations. Emphasizing Laurentian Great Lakes findings where possible, we describe how changing water clarity can directly affect fish populations and communities by altering exposure to ultraviolet radiation, foraging success, predation risk, reproductive behavior, or territoriality. We also discuss how changing water clarity can affect fisheries harvest and assessment through effects on fisher behavior and sampling efficiency (i.e., catchability). Finally, we discuss whether changing water clarity can affect understudied aspects of fishery performance, including economic and community benefits. We conclude by identifying generalized predictions and discuss their implications for priority research questions for the Laurentian Great Lakes. Even though the motivation for this work was regional, the breadth of the review and generality of the framework are readily transferable to other freshwater and marine habitats.

Résumé : Si des modifications de l'environnement causées par les humains sous-tendent les changements récents de la clarté de l'eau dans bon nombre des grands lacs de la planète, notre compréhension des conséquences de ces changements sur les poissons et les pêches qu'ils soutiennent demeure incomplète. Nous présentons un cadre pour organiser les connaissances actuelles, orienter la recherche future et aider les gestionnaires des pêches à comprendre l'incidence possible de la clarté de l'eau sur les populations qu'ils gèrent. En mettant l'accent, dans la mesure du possible, sur des constatations relatives aux Grands Lacs laurentiens, nous décrivons l'incidence directe que peuvent avoir les variations de la clarté de l'eau sur les populations et communautés de poissons en modifiant l'exposition au rayonnement ultraviolet, le succès d'approvisionnement, le risque de prédation, le comportement de reproduction ou la territorialité. Nous abordons également l'incidence que peuvent avoir les modifications de la clarté de l'eau sur les prises et l'évaluation des pêches par le biais d'effets sur le comportement des pêcheurs et l'efficacité d'échantillonnage (c.-à-d., la capturabilité). Enfin, nous tentons d'établir si les modifications de la clarté de l'eau peuvent avoir une incidence sur des aspects sous-étudiés de la performance des pêches, y compris les avantages économiques et pour les collectivités. Nous concluons en formulant des prédictions générales et discutons des questions de recherche prioritaires qu'elles font ressortir pour les Grands Lacs laurentiens. Même si l'intention à l'origine du présent article était régionale, la portée de la synthèse et le caractère général du cadre font qu'ils peuvent être transposés aisément à d'autres habitats marins et d'eau douce. [Traduit par la Rédaction]

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Introduction

Although scientists have increasingly documented changing water clarity in freshwater ecosystems worldwide, we do not fully understand its effects on aquatic food webs and the fisheries that they support. Through the 1970s, increasing anthropogenic eutrophication (i.e., excessive sediment and nutrient loading) tended to reduce water clarity in affected waters (e.g., Likens 1972; Schindler 1974). Similarly, during the 2000s, water clarity declined in some lakes, owing to "browning" associated with increases in terrestrially derived dissolved organic matter (Monteith et al. 2007; Solomon et al. 2015; Williamson et al. 2016*a*). By contrast, water clarity in a number of lakes in North America and Europe has increased during the last several decades as a consequence of the implementation of nutrient abatement programs (Ludsin et al. 2001; Jeppesen et al. 2005) and (or) the proliferation of filter feeders, such as invasive dreissenid mussels (*Dreissena polymorpha* and *Dreissena bugensis*), which have at least doubled phytoplankton filtration rates compared with pre-invasion levels (e.g., Mayer et al. 2014; Geisler et al. 2016).

These changes in water clarity can strongly influence lake ecosystems and the services that they provide. For example, reduced water clarity has been shown to degrade property values (Clapper and Caudill 2014; Liao et al. 2016) and erode recreational activities, including tourism associated with snorkeling, swimming, and boating (Keeler et al. 2012; Lee 2016). Likewise, altered water clarity holds great potential to affect the behavior, distribution, and production of fish populations and fisheries that they might support (e.g., Lester et al. 2004; Lehtiniemi et al. 2005; Tucker et al. 2012), which in turn, could have major social, nutritional, and economic consequences (McIntyre et al. 2016; Lynch et al. 2016). While much independent research, both experimental and observational, has been devoted to identifying linkages between water clarity and fish population and community dynamics in lake ecosystems, especially in small, shallow ones (e.g., Scheffer 1998), a comprehensive, unified understanding of how changing water clarity can affect the dynamics and performance of large-lake fish populations and fisheries, such as those found in the North American Great Lakes basin, is lacking. This information gap is concerning because it limits the ability of agencies to manage their fisheries in response to present-day and future changes in water clarity.

While many of the world's great lakes have been experiencing changes in water clarity, owing to human-driven environmental change (e.g., African Rift Lakes: Seehausen et al. 1997; Cohen et al. 1993; Lake Baikal: Izmest'eva et al. 2016), the Laurentian Great Lakes (hereinafter, Great Lakes) are illustrative of a suite of lakes that would greatly benefit from a conceptual framework that integrates existing knowledge to help agencies better understand how changing water clarity affects their diverse fish communities and valued fisheries. Not only do these lakes support fisheries that have been valued as high as US$2.2 billion annually (in terms of expenditures on recreational trips and equipment; US Department of Interior et al. 2018), some of these lakes have undergone major changes in water clarity during the last several decades (Barbiero et al. 2012; Binding et al. 2015; Yousef et al. 2017). For example, Secchi disk depth — a common measure of water clarity in lake ecosystems — has increased more than twofold since offshore monitoring began during the early 1980s in Lakes Huron, Michigan, and Ontario (Figs. 1*a*–1*c*; see online Supplementary material[1]). By contrast, other lakes and habitats within the Great Lakes basin have not undergone marked long-term changes (Fig. 1*d*) but are prone to nonpoint nutrient and sediment runoff or wind-driven sediment resuspension. Western Lake Erie (Richards et al. 2008; Niu et al. 2018) often experiences temporary (days to weeks), but large-scale, reductions in water clarity due to the formation of turbid sediment plumes in the spring (Reichert et al. 2010; Fig. 1*e*) and dense harmful cyanobacteria blooms in the late summer and fall (Stumpf et al. 2012; Fig. 1*f*). Improved understanding of how changing water clarity, in either direction, affects fish and fisheries in the Great Lakes, and large lakes in general, is needed.

Toward this end, we developed a framework (see Fig. 2) that seeks to synthesize and organize our collective understanding of how changing water clarity influences fish populations, the broader communities that they comprise, the fisheries that they support, and how these affect key aspects of fishery performance. This framework consists of several tenets, which are briefly outlined below and described in more detail through the remainder of this paper. First, we argue that changes in water clarity hold the capacity to drive change in fish population abundance, fish community composition, and fisheries production through a variety of ecological mechanisms, including potentially lethal exposure to ultraviolet radiation, foraging (energy intake), predation risk (survival), reproduction, and other behaviors (e.g., reproduction, schooling, territoriality), all of which can affect fitness. Second, we argue that altered water clarity can directly influence fisheries through nonecological mechanisms, such as altered catchability by fishing gears, which can affect both the success (e.g., catch per unit effort, CPUE) of fishers and the ability of agencies to assess fish populations, and altered fisher behavior (e.g., reduced fishing due to turbid algal blooms; Kotwicki et al. 2015; Nieman et al. 2020). Finally, we assert that the effects of water clarity on fish populations and their associated fisheries can ultimately influence fishery performance, defined as how well a fishery delivers community (e.g., social, cultural) and economic benefits in a biologically sustainable manner (see Anderson et al. 2015). Changes to water clarity in lake ecosystems, including the Great Lakes, can be expected to continue owing to climate change (e.g., Hayhoe et al. 2010), land-use change (e.g., LaBeau et al. 2014), and invasive species (e.g., Pagnucco et al. 2015). The need to continue to improve our understanding of how water clarity influences fish populations and fisheries is paramount given these continued expected changes.

We originally sought to develop our framework using examples only from large, deep lakes, such as the Great Lakes, where our expertise and experience is concentrated and where stakeholders, scientists, and managers have observed dramatic changes in water clarity. We realized, however, that less research existed in these systems than expected and that research from shallower systems, marine systems, and even controlled experiments would be required to understand and make predictions about the responses of fish in large, deep lakes. During this synthesis, we identified priority research needs for the Great Lakes and described them in Box 1. Given the broad swath of studies that we considered and that we are unaware of other frameworks or syntheses that have been developed to unpack the linkages among changing water clarity, fish, and fisheries, we anticipate that our framework will have application well beyond the Great Lakes, in both large and small ecosystems.

To help explain our framework, we organized this paper into several sections. First, we define water clarity and describe the key factors that attenuate sunlight in large, deep lakes. Second, we discuss how fish perceive light, which is critical to understanding the ecology of fish in relation to water transparency. Third, we compile existing knowledge on how changing water clarity can directly affect processes influencing fish, the fisheries they support, and ultimately fishery performance. Finally, we describe general predictions gleaned from the synthesis and discuss their implications for priority research in the Great Lakes. Collectively, our perspective offers a novel synthesis on how

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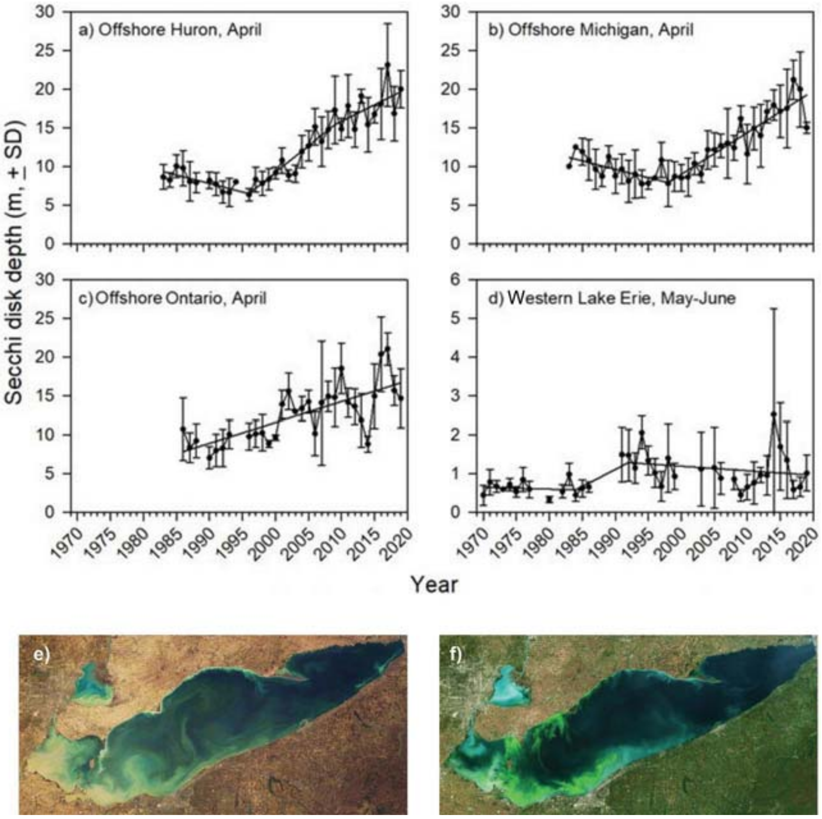
[1] Supplementary material is available with the article at https://doi.org/10.1139/cjfas-2020-0376.

Fig. 1. Panels *a*–*d* represent time series of mean Secchi disk depth readings (±1 standard deviation) from selected sites and months in the Laurentian Great Lakes. The line in each panel illustrates the predicted best fit among four different model types: (*i*) an intercept-only model (i.e., no trend over time); (*ii*) a linear regression model with time as the predictor; (*iii*) a segmented regression model with a single change-point (two linear trends) in the time series; or (*iv*) a segmented regression model with two change-points (three linear trends). See Table S1 in the Supplementary material[1] for more details about sources of data and the slope(s) of the best-fit line(s). Note the *y* axis changes across panels. Temporary seasonal reductions in water clarity are common in Lake Erie during the spring, when sediment and nutrient runoff cause open-lake river plumes (panel *e*; MODIS true-colour satellite image from 15 April 2005), and during the late summer, when harmful algal blooms are most common (panel *f*; MODIS true-colour satellite image from 3 September 2011), owing to excessive nutrient runoff and high temperatures (image sources: NOAA Great Lakes CoastWatch Node, https://coastwatch.glerl.noaa.gov/).



changes in water clarity affect the fish populations and fisheries of large, deep lakes, while simultaneously offering advice to management that will help keep these fisheries sustainable in the face of continued ecosystem change.

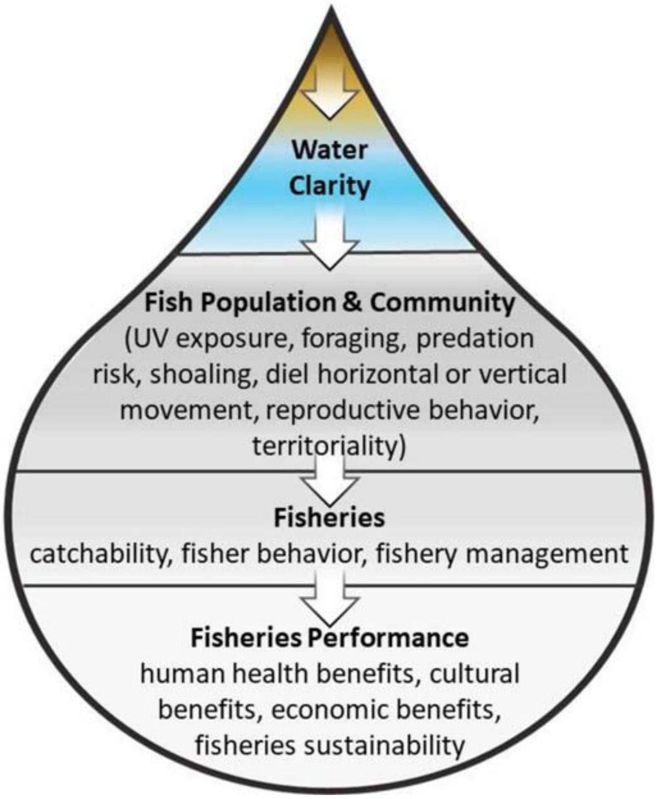
Defining water clarity and describing sunlight transmission into water

In this section, we provide a high-level overview of the optical principles of light penetration, absorption, and scattering within the water column to inform subsequent discussion on how changing water clarity can influence fish and fisheries. There is no commonly accepted definition of "water clarity" nor is there a single metric that has been consistently used to measure the clarity of water. However, because understanding the factors affecting transmission of light though the water (the fundamental physical basis of "clarity") is so important for many studies of biotic and abiotic aquatic processes, the literature is rich with works that describe different measures related to water clarity, and more detailed information on light in lakes can be found in Kirk (2011), Johnsen (2012), Neale et al. (2021), and Williamson and Neale (2021). In the discussion below, it is important to understand the electromagnetic spectral composition of sunlight, which includes not only the most commonly measured "light" visible to humans and used by phytoplankton and plants for photosynthesis (400–700 nm), but also shorter wavelength ultraviolet radiation (290–400 nm, hereinafter "UV") and infrared radiation (700–3000 nm). The wavelength-specific attenuation of sunlight determines the depths to which prey, predators, or mates can be seen, damaging UV can penetrate, as well as the heat distribution and thermal structure of the lake, all of which, in turn, regulate the distribution and abundance of all life stages of fish.

Water clarity and water transparency are two terms often used interchangeably to describe how deep light penetrates into a lake. The greater the water clarity or transparency, the less light is attenuated with depth. Light is attenuated with depth by two fundamental processes: absorption and scattering. Both processes are regulated by dissolved and particulate compounds in the water, as well as by absorption by water itself (Kirk 2011). Absorption involves the conversion of light (photons) into primarily heat energy, which influences vertical temperature gradients in lakes. By contrast, scattering is the redirection of photons from their original paths by molecular collisions without loss of photons and without any heat gain by the water. Although often used mistakenly to refer to water clarity, the term turbidity is a measure of only the scattering by the particulate components in the water, including both inorganic (e.g., sediments, glacial flour) and organic (e.g., phytoplankton, bacteria, detritus).

Major regulators of water clarity in large lakes include sediment and coloured dissolved organic matter (CDOM) plumes

Fig. 2. Conceptualization of how the effects of water clarity cascade down to affect fish populations and communities, fisheries, and fisheries performance of the Great Lakes or other large, deep lakes.



from terrestrial runoff, rivers, phytoplankton blooms, and wind-driven resuspension of sediments in shallower waters. The UV range is particularly sensitive to attenuation by CDOM, whereas absorption and scattering by sediments and phytoplankton blooms attenuate light more uniformly across all wavelengths. Water clarity in large lakes is often greater in offshore than in nearshore waters due to the influence of terrestrially derived CDOM and particulates in nearshore environments. Heavy precipitation events can cause CDOM, as well as inorganic silt and clay particles, to flow in from tributaries (Reichert et al. 2010; Howell et al. 2012). Similarly, riverine inflow of nutrients can contribute to nearshore phytoplankton blooms. Both sediment and nutrient-induced algal blooms can be advected substantial distances, reducing water clarity offshore as well. High wind events can also cause sediment resuspension in nearshore regions, as well as in shallow lakes (Mortimer 1987; Lick et al. 1994; Niu et al. 2018). Remote sensing techniques are now permitting large-scale assessment of not only water clarity and sediment plumes, but the relative contributions of attenuating substances such as CDOM versus harmful algal blooms (Kutser et al. 2015; Urquhart et al. 2017). In temperate lakes, ice cover can greatly reduce light levels and primary productivity, although type of ice, whether suspended sediments were included during freezing, and whether ice is covered with snow are key factors (Bolsenga and Vanderploeg 1992; Vanderploeg et al. 1992; Twiss et al. 2014). One other abiotic factor that can affect light attenuation is the precipitation of oversaturated minerals, such as calcium carbonate ($CaCO_3$), commonly referred to as “whiting events”. These events have been shown to dramatically reduce water clarity for days to weeks in lakes that have high $CaCO_3$ concentrations, such as Lakes Michigan, Ontario, and Erie (Strong and Eadie 1978; Hodell et al. 1998; Watkins et al. 2013). The effects of these whiting events, especially on fishes, however, remain largely unstudied.

Biological processes have also been shown to attenuate light in lakes. Grazing of primary producers by herbivorous zooplankton, for example, can cause a period of abrupt and sometimes prolonged high water clarity referred to as a clear-water phase during the spring and early summer (Lampert et al. 1986; Williamson et al. 2007; Sommer et al. 2012). Filter-feeding species also can modify light penetration and water clarity. Most prominent have been the effects of dreissenid mussels on small and large lakes throughout North America, wherein their filtration of phytoplankton has caused long-term increases in water clarity (e.g., Karatayev et al. 2002; Mayer et al. 2014; Rowe et al. 2015). The impacts of these mussels are stronger during isothermal periods, where they have access to plankton throughout the water column (Rowe et al. 2015). Mussels have also been hypothesized to reduce the intensity of whiting events, owing to their uptake of calcium (Barbiero et al. 2006; Binding et al. 2007; but see Watkins et al. 2013). However, the ability of mussels to regulate water clarity is low in shallow regions that receive high sediment inputs from rivers or are prone to sediment resuspension, such as western Lake Erie (Barbiero and Tuchman 2004; Niu et al. 2018) or certain shallow areas of Lake Ontario (Howell et al. 2012). This interaction has complicated our ability to model water clarity in dynamic ecosystems such as the Great Lakes, including its effects on other organisms.

Methods for measuring water clarity have advanced tremendously through the years. Despite these advances, the classic, but still most widely used, method of measuring water clarity is the black and white Secchi disc because of its low cost, simplicity of use, and availability of long-term data sets (see Fig. 1). For improved understanding of spectral composition, a submersible radiometer that measures changes in light at a given wavelength (λ) or a range of wavelengths is required. The commonly used photosynthetically active radiation (PAR) radiometer measures light in the 400–700 nm λ range, which is useful for studies of primary production and has also been used to quantify light availability to foraging plankton or fish. One commonly estimated parameter is the diffuse attenuation coefficient ($K_{d\lambda}$, m^{-1}) for a given λ, which can be estimated from the slope of the log-linear relationship between light intensity and depth and is used to estimate the penetration of a given λ to a given depth. For example, 1% light penetration depth for a given λ ($Z_{1\%\lambda}$, m) is often a depth of interest; $Z_{1\%\mathrm{PAR}}$ is the depth to which 1% of PAR penetrates and has often been used to estimate the photic compensation depth, the depth below which community respiration exceeds photosynthesis. One justification for collection of radiometer profiles is the common poor correlation between Secchi disk depth and $K_{d\mathrm{PAR}}$ in lakes (Kirk 2011).

Fish visual sensory capabilities

The portion of the electromagnetic spectrum perceived by a fish depends on characteristics of its eyes. Similar to humans, fish have both rods adapted to low light conditions and cones adapted to detect photons within a specific range of wavelengths. Cones allow fish to detect colour. Fish can be dichromatic (two types of cones), trichromatic (like humans), or even tetrachromatic with the ability to detect UV (Johnsen 2012). Eyes that are sensitive to UV are mainly found in young fish, including yellow perch (*Perca flavescens*; Loew and Wahl 1991), and the ability to detect UV can improve foraging (Loew 1999; Leech et al. 2009). Some species retain the ability to detect UV as adults (Harosi and Hashimoto 1983), perhaps as a means to help choose mates (e.g., Smith et al. 2002). Regardless, the properties of the eye interact with the spectral quality of available light to affect the brightness perceived by a fish.

Box 1. Priority Great Lakes research questions arising from synthesis of how changing water clarity affects fish and fisheries.

Ultraviolet (UV) exposure

- Can historical UV exposure be estimated with models that use predictor variables including DOC or turbidity?
- Can UV profiles be added to routine Great Lakes water quality monitoring?
- How does UV exposure vary across habitats (e.g., tributaries, drowned river mouths, coastal zone, embayments, offshore pelagic region)?
- For what species are the early life stages (e.g., eggs, larvae) most vulnerable to UV exposure?
- Which species can detect and behaviorally avoid UV exposure and (or) mitigate or repair any damage?

Fish foraging and risk of predation

- Do larger piscivores benefit more than smaller planktivores with increasing water clarity, as predicted?
- Given that fish species have evolved to optimally forage at different light levels, have the changes in water clarity benefited some key fish species more than others?
- How do organic versus inorganic components of turbidity differentially affect foraging success?
- Should decision-support tools that estimate salmonine consumption be revised to incorporate water clarity changes?
- How have changes in water clarity affected shoaling behavior or diel vertical or horizontal migration patterns?

Fish reproductive behavior and territoriality

- Have nonindigenous round goby increased territorial or aggressive behavior towards native benthic fishes in lakes with increasing water clarity?
- How do declines in water clarity associated with cyanobacteria blooms or sediment plumes affect mate selection or other aspects of reproductive behavior?

Catchability and fisher behavior

- How does changing water clarity affect the catchability of common assessment gears, including gillnets and daytime bottom trawls, and how does this response vary by fish species?
- How does incorporating changes in catchability affect estimates of stock size?
- How have recreational and commercial fishers responded to changes in water clarity, as expressed in assessment data that estimate distribution of effort, gear selection or modifications, fishing techniques, and which species are targeted?

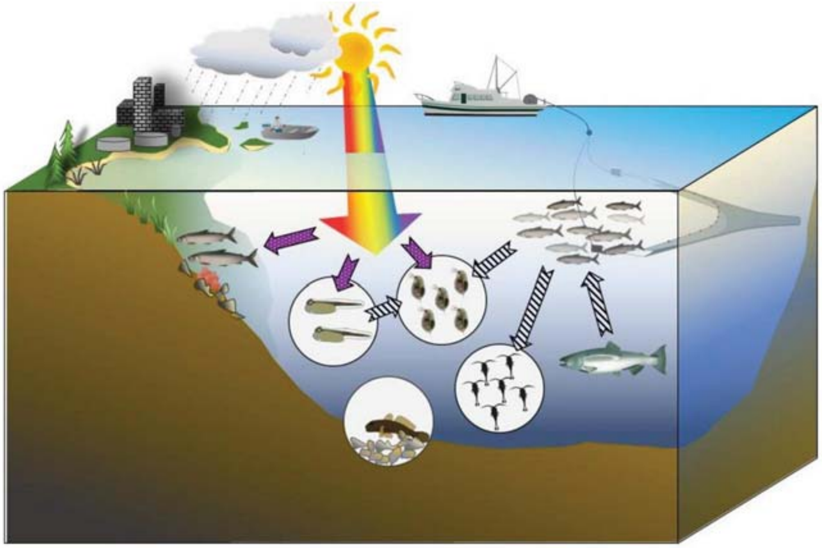
Fisheries performance

- How has changing water clarity, relative to other environmental or economic factors, affected where, when, and how people fish, within and among the Great Lakes?
- How have changes in water clarity affected the diversity of societal uses of waters of the Great Lakes?
- How has changing water clarity affected fishing license sales and local economies?
- Are the effects of reduced water clarity on fishing behavior (where, when, and how people fish) the same for organic and inorganic components of turbidity?
- Are there thresholds in water clarity, such that management for a diversity of societal uses becomes a key consideration in the Great Lakes?

Measuring the brightness perceived by fish or other aquatic animals is not as straightforward as using a radiometer to measure PAR. For humans, perceived brightness is measured in lux by photometric sensors that weigh the incoming light by a λ-specific luminosity function (defined for light- (photopic) or dark-adapted (scotopic)), which mimics the λ-specific sensitivity of the human eye. Thus, how appropriate lux is as a unit of brightness to a fish depends on how similar the fish eye is to the human eye. Ideally, one would measure the complete spectrum of available sunlight using a radiometer and apply a luminosity function specific for each species of interest (Johnsen 2012). Such functions have been derived for some species, including some in the Great Lakes, with new units of brightness being defined as a result (e.g., the "alelux" for alewife (*Alosa pseudoharengus*) (Boscarino et al. 2010); the "mylux" for the invertebrate *Mysis diluviana* (Gal et al. 1999)). Using these species-specific units has allowed for improved predictions of feeding rates (for alewife; Boscarino et al. 2010) and distributions (for mysids; Gal et al. 1999) in the Great Lakes, yet remain surprisingly rare in the freshwater literature.

The ability of aquatic animals to detect an image depends on the ambient brightness, how light scatters, and the size of the image (Johnsen 2012). In general, visual fish foragers can detect larger prey from a further distance than they can detect smaller prey (Wright and O'Brien 1984). In turbid water, however, the scattering of light by particulates can reduce the sharpness of an image and make it more difficult to detect a prey even though the amount of light may be sufficient. Because image deterioration associated with scattering increases with distance, planktivorous fish that rely on detecting small, nearby prey are less affected by turbidity than predatory fish, which typically detect larger prey at a longer distance (Breck 1993; De Robertis et al. 2003). Hence, with reduced water clarity owing to turbidity, foraging by a piscivore is more negatively affected than foraging by a planktivore (De Robertis et al. 2003). As we discuss more fully below, this interaction among fish size, prey size, and turbidity-

Fig. 3. Illustration of different effects of changing water clarity on fish and fisheries. Black and gray diagonal-lined arrows depict effects on reactive distance and foraging success (or predation risk). Purple arrows show that ultraviolet radiation can affect the survival or distribution of early life stages of fish (e.g., eggs, larvae) and invertebrate fish prey (e.g., zooplankton). Other relevant processes affected by changing water clarity include schooling behavior, reproductive behavior, territoriality (see inset of benthic fish guarding rock pile), behavior of fishers, and catchability of fisheries assessment gear (e.g., trawls, gill nets). One prominent external factor that can influence water clarity is the climate or watershed-driven external loading of sediments, dissolved organic matter, or nutrients that stimulate algae blooms (see the plume in upper left). The extent of light penetration can affect the magnitude and depth of peak primary production, including benthic vegetation that affects fish habitat. Some images authored by Tracey Saxby, Diana Kleine, and Emily Nastase courtesy of Integration and Application Network, University of Maryland Center for Environmental Science (ian.umces.edu/imagelibrary/). Other images authored by Cory Brant, US Geological Survey.



induced scattering can influence both habitat use and foraging behavior and success.

Water clarity effects on fish, fisheries, and fisheries performance: a synthesis

Changes in water clarity can affect processes relevant to individual fishes and aspects of the fisheries that they support, as illustrated in Fig. 3. For example, direct effects of changing water clarity on fish include alteration of foraging success, predation risk, and other behaviors such as schooling, movement (both vertical and horizontal), and territoriality. Furthermore, reduced attenuation of UV or visible light can affect reproductive behavior or the distribution and survival of fish eggs and larvae. With respect to effects on fisheries, changing water clarity can also directly affect catchability in assessment gear used to inform fishery management decision-making, as well as the behavior of fishers, which can influence both fishing effort and harvest. Finally, Fig. 3 illustrates an example of an "indirect" effect of changing water clarity on fish — the growth of benthic macrophytes. Unless one is studying a fish that consumes macrophytes (e.g., Wiley et al. 1984), we consider changes in macrophyte abundance to have more indirect effects on fishes in the context of spawning habitat (e.g., Lane et al. 1996) or refuge from predation (e.g., Savino and Stein 1982). Another similar example of a more indirect effect is how changing water clarity can influence phytoplankton production and distribution. Even though most fish species do not directly feed on phytoplankton, spatiotemporal distribution of phytoplankton can affect other aspects of the food web (e.g., zooplankton, benthic invertebrates) that more typically can influence fish foraging. Although these and other indirect effects are potentially important for fish growth, reproduction, and survival, our synthesis only focused on the more direct effects of changing water clarity, given their greater relevancy to our objectives and the need to limit the length and scope of this paper.

Effects of changing water clarity on fish

Effects of UV exposure

The effects of exposure to UV can vary with life stages of fishes and can cause a wide range of physiological effects, including DNA damage, a decrease in epithelial mucous cells, reductions in metabolic and growth rates, suppression of the immune system, or damage to the eyes, liver, gonads, and spleen (see review by Alves and Agustí 2020). Similarly, an earlier ecologically oriented review documented how UV damage to DNA holds the potential to kill fish rapidly (in a few days) during early life when they are highly transparent, especially in lakes with high water clarity (Zagarese and Williamson 2001). For example, exposure to UV can be lethal to the eggs and larvae of yellow perch (Williamson et al. 1997; Huff et al. 2004; Boily et al. 2011) and the larvae of bluegill (*Lepomis macrochirus*), pumpkinseed (*Lepomis gibossus*), and largemouth bass (*Micropterus salmoides*; Williamson et al. 1999; Olson et al. 2006; Tucker and Williamson 2014).

Some large, deep lakes are highly transparent, creating the potential for fish to be exposed to damaging UV. In Lake Tahoe (California–Nevada, USA), for example, 1% of the most potentially damaging, short-wavelength (320 nm) UV-B routinely penetrates to 20 m or more in the water column (Williamson et al. 2016*b*). Penetration depths of longer wavelength (380 nm) UV-A can be greater than those of visible light, with 1% of UV-A reaching depths close to 50 m (Rose et al. 2009; Williamson and Rose 2010). Although UV measurements are limited in the Great Lakes, measurements collected during 2000 in Lakes Huron, Erie, and Ontario demonstrated the $Z_{1\%325\ \mathrm{nm}}$ was 5 to 10 m in the offshore waters and only 1 to 2 m in embayments and tributaries (Smith et al. 2004). This finding suggests that Great Lakes species that spawn offshore and have pelagic larvae, including deepwater ciscoes or deepwater sculpin (*Myoxocephalus thompsonii*), may be exposed to more UV than those that spawn in shallow, nearshore waters or tributaries, including walleye (*Sander vitreus*), alewife, yellow perch, lake whitefish (*Coregonus clupeaformis*), and rainbow smelt (*Osmerus mordax*) (Scott and Crossman 1973). One important caveat is that larvae of some nearshore spawning species, including alewife (Weber et al. 2015) and yellow perch (Dettmers et al. 2005), can be advected offshore.

In the Great Lakes, UV exposure as a source for egg or larval mortality has not been evaluated for key fish species. It could, however, provide an alternative explanation for observed patterns of differential larval survival in areas of higher versus lower turbidity. For example, yellow perch recruitment in western Lake Erie has been shown to be higher in turbid areas with lower water clarity (e.g., river plumes) relative to less turbid areas of higher water clarity (non-plume areas), with the presumed mechanism that turbid, open-lake river plumes provide a refuge from predation on larvae (Reichert et al. 2010; Ludsin et al. 2011; Carreon-Martinez et al. 2014). Alternatively, low water clarity could provide protection from damaging UV (Williamson et al. 1997; Huff et al. 2004). In Lake Tahoe, for example, nearshore areas with low water clarity provided refuge from lethal UV exposure for non-native centrarchid larvae that need to spawn in the warmer surface waters (Tucker et al. 2010; Tucker and Williamson 2014).

Some species of fish have developed effective defenses against UV, including photoprotection and photoenzymatic repair of UV-damaged DNA (Olson and Mitchell 2006), as well as behavioral avoidance. The need to understand this capability is especially important for vulnerable life stages such as larvae, if they are attracted to visible light. Despite limited study, there is evidence that larvae and juveniles of some species can detect and avoid UV, even if they are attracted to visible light (Kelly and Bothwell 2002; Ylönen et al. 2004; Guggiana-Nilo and Engert 2016). If Great Lakes fishes do not have the ability to detect and avoid UV during early life, the attraction to well-lighted areas to find prey may cause these individuals to swim to their death, or experience reduced growth, owing to inadvertent exposure to high levels of UV (i.e., the Solar Ambush Hypothesis; Williamson 1995).

To summarize, in lakes where water clarity is increasing, several lines of research are needed to assess changes in UV as well as PAR in the lakes. More information is also needed on (*i*) the UV tolerance of different species and their ability to detect and avoid UV, (*ii*) their ability to reduce UV damage with photoenzymatic repair or photoprotection, and (*iii*) the extent of sublethal as well as lethal effects.

Effects on fish foraging

Foraging enables the acquisition of energy for the maintenance of basal metabolic needs, growth, and reproduction. As with other animals (Holling 1959), foraging by fishes has been conceptualized as consisting of five components: search, prey encounter, pursuit, capture, and handling (Diana 2004). Changes in water clarity have the potential to affect both the search volume (or area) of a forager, as well as its encounter rate with prey. If one considers the search volume of an individual forager as a cylinder, with its length equal to the distance swum and its basal area a function of the reactive distance of foragers to prey, the effect of water clarity on search volume can be estimated (Park et al. 2007). Using this approach, small changes in water clarity can have a disproportionately large effect on the volume searched (Fiksen et al. 2002; Utne-Palm 2002). For example, a 50% increase in reactive distance will lead to a 225% increase in the volume capable of being searched in the same amount of time. Furthermore, increased water clarity will generally improve the ability of visual foragers to detect prey by increasing light intensity (Eiane et al. 1999) and enhancing the contrast between prey and its background (Lythgoe 1979). As a result of larger search volumes and prey detection capabilities, encounter rates with prey would be expected to increase with increasing water clarity, potentially benefiting energy intake per unit of foraging time (e.g., Gardner 1981; Sweka and Hartman 2001). Indeed, the functional feeding response of predators (e.g., number of prey ingested per unit time) has been shown to increase with increasing water clarity across a wide range of prey densities (e.g., Ljunggren and Sandström 2007). Likewise, increased water clarity may allow some foragers to continue to feed at relatively high rates even when prey densities decrease. For example, while the invasion of dreissenid mussels into Oneida Lake (New York, USA) led to declines of some zooplankton taxa, yellow perch growth did not decline (Mayer et al. 2000; Manning et al. 2014). Instead, the concomitant increase in water clarity potentially contributed to more successful foraging and increased growth of age-0 yellow perch that improved overwinter survival (Irwin et al. 2009; Rudstam et al. 2016). Collectively, these results highlight the need to consider water clarity when estimating fish foraging capabilities, as it can greatly alter energy intake and resultant development, growth, survival, and reproductive fitness.

While increased water clarity has *generally* been shown to positively affect fish foraging (e.g., Mahon and Holanov 1995; Boscarino et al. 2010; Weidel et al. 2017), both the magnitude and direction of its effect can vary across species, trophic levels, and ecosystems (Fiksen et al. 2002; Utne-Palm 2002; De Robertis et al. 2003). These differential responses are a consequence of species-specific differences in reactive distances and visual acuity, the relative ability to forage nonvisually, the type and behavior of prey targeted, and the physical properties of the environment contributing to reduced water clarity. Such effects can lead to variation among species and ecosystems on the amount of prey consumed at any given level of turbidity (e.g., Bonner and Wilde 2002; De Robertis et al. 2003). They can also affect the type and size of prey targeted. For example, three-spined sticklebacks (*Gasterosteus aculeatus*) reduced their size selection for *Daphnia magna* with elevated turbidity (Sohel et al. 2017). These findings indicate that a "one size fits all" approach to modeling fish foraging is likely to be inappropriate in many cases and highlights the need to explore and develop species-specific, and in some cases context-specific (sensu Pangle et al. 2012), foraging curves in relation to water clarity.

This need for species- or context-specific modeling of foraging becomes even more paramount when considering that some species can continue to forage even under low light conditions. For example, although Boscarino et al. (2010) found that alewife feeding rates on mysids in Lake Ontario increased with increasing light intensity, feeding continued in complete darkness, likely owing to their use of lateral line sensory cells to detect prey (Janssen et al. 1995). In other species, foraging efficiency has been shown to be higher under elevated turbidity and low to intermediate light levels than in clearer water (Boehlert and Morgan 1985; Gregory and Northcote 1993; Miner and Stein 1993), with Lake Erie yellow perch exhibiting a unimodal foraging response curve with higher consumption at intermediate turbidity levels (Pangle et al. 2012).

Walleye, an ecologically and economically important top predator across the Great Lakes basin, is another species that exhibits a unimodal foraging response to water clarity (light intensity), with greatest activity at intermediate light levels (~30 lx; Ryder 1977; Lester et al. 2004). The eyes of walleye are morphologically adapted for low light conditions, similar to the congener pikeperch (*Sander lucioperca*), which can feed at similar turbidity levels during both daytime and nighttime (Ljunggren and Sandström 2007). Although intermediate light levels will be present at dawn and dusk in clear lakes, the foraging window is likely longer in lakes with lower water clarity, perhaps including the whole daylight period at deeper depths. Elevated foraging success at intermediate light levels can have important implications for Great Lakes walleye populations, potentially affecting the distribution of its biomass across ecosystems (Lester et al. 2004) and its relative reliance on nearshore versus offshore production pathways in lakes of varying water clarity (Tunney et al. 2018).

Fish foraging is also affected by the type of particulate (e.g., organic or inorganic) causing turbidity. Wellington et al. (2010) showed that larval and juvenile yellow perch consumption of zooplankton prey was more strongly negatively affected by phytoplankton than sediment components. This finding can help explain why prey consumption by larval yellow perch remained similar in western Lake Erie between a turbid river plume dominated by sediments versus another river plume with lower sediment concentrations and higher water clarity (Reichert et al. 2010; Ludsin et al. 2011). Modeling work in Lake Erie has suggested that the differential components of turbidity can have important ramifications for larval cohort survivorship and ultimately recruitment potential (Manning et al. 2014). Moreover, other species and life stages may display similar responses, as the reaction distance of adult walleye and emerald shiner (*Notropis atherinoides*) declined more severely with organic turbidity than inorganic turbidity, suggesting reduced foraging success during algal blooms (Nieman and Gray 2019, 2020; but see Briland et al. 2020). The need to consider the primary component of turbidity is important, given that harmful blooms dominated by algae and cyanobacteria are becoming commonplace in many areas of the Great Lakes, from small embayments to whole lake basins (Stumpf et al. 2012; McKindles et al. 2020; Sterner et al. 2020).

Should UV penetration increase in lakes where water clarity is increasing, the effects on visual acuity should be considered within the context of foraging. Based on current knowledge, fish larvae have the highest visual acuity in the UV-A region (Britt et al. 2001; Siebeck and Marshall 2007). Mesocosm experiments in an oligotrophic lake with 15 mm largemouth bass demonstrated enhanced feeding rates on zooplankton in the presence of UV, relative to when it was blocked (Leech et al. 2009). At the same time, laboratory experiments with a variety of other fish species under more highly controlled conditions suggest that UV may not be important to foraging success (Leech and Johnsen 2006; Zukoshi et al. 2018). Interspecific differences may contribute to these contrasting results, but more research is needed to determine the importance of UV to foraging success.

In summary, increasing water clarity should improve foraging opportunities for visual predators by increasing the reactive distance for prey. In reality, however, foraging success cannot be simply predicted based on water clarity alone, given that some species have evolved to optimally feed at different light levels, some use UV, and some actually reduce foraging activity under high water clarity conditions if predation risk is heightened (see next section). Conversely, when water clarity declines, how much foraging is reduced depends on the primary component driving the increased turbidity (e.g., organic versus inorganic) and species likely differ in their ability to forage under these different turbidity conditions.

Effects on predation risk

The concepts and theories that predict how changing water clarity will affect fish foraging can be used to help understand the effects of changing water clarity on fish under threat from predation by piscivores or other top predators (e.g., cormorants (*Phalacrocorax* spp.)). Research on age-0 fishes exposed to predators has revealed that reduced water clarity, often associated with increasing turbidity, is a net benefit. For several freshwater fish species, enhanced turbidity reduces their time spent hiding in predation refuges (Miner and Stein 1996; Engström-Öst and Mattila 2008; Snickars et al. 2004), potentially allowing them to increase the frequency of their attacks on prey. Similarly, using empirical data collected from ponds, reservoirs, and Lake Erie, as well as a laboratory experiment, Pangle et al. (2012) provided theoretical and empirical support for a unimodal optimal foraging rate curve for zooplanktivorous age-0 fish in the presence of predation risk, which suggests that intermediate levels of water clarity allow larvae to be less vigilant of predators (i.e., less responsive to cues), ultimately resulting in enhanced foraging success relative to lower and higher water clarity levels. Furthermore, both theoretical and empirical evidence has been produced to indicate that recruitment of larvae to older life stages can be enhanced if predation risk can be reduced without compromising foraging. Fiksen et al. (2002), for example, used numerical simulations to show that increased turbidity can more strongly reduce predation pressure from piscivores than impede foraging by larval fish, ultimately enhancing the recruitment potential of their modeled larvae. These same advantages may explain why some species of planktivorous fish, including a variety of small-bodied and juvenile (age-0) forage species (e.g., yellow perch, white perch (*Morone americana*), emerald shiner, gizzard shad (*Dorosoma cepedianum*)) appear to use harmful algal blooms dominated by cyanobacteria as a refuge from predation, despite such areas being potentially suboptimal for growth and survival because of cyanotoxins (Briland et al. 2020) and relatively low food quality (Engström-Öst et al. 2006).

For many fish species, horizontal or diel vertical migration (DVM) and schooling or shoaling (hereinafter shoaling) are well-studied behaviors that theoretically balance multiple factors that could affect future fitness, including predation risk, potential energy acquisition, and growth (Eggers 1976; Mehner 2012; Pitcher 1986). Because predation risk typically increases with increasing water clarity, one might expect these behaviors to increase with increasing water clarity, even if these would reduce foraging opportunities (Gregory 1993; Utne-Palm 2002; Abrahams and Kattenfeld 1997). Despite numerous studies that have explored how light availability affects these behaviors (see reviews by Magurran 1990; Mehner 2012; Pavlov and Kasumyan 2000), fewer studies have explicitly investigated the effects of changing water clarity. For these few, behaviors associated with predator avoidance (e.g., use of vegetation, dimly lit bottom waters, and the surface as cover; reduced horizontal migrations) declined in the presence of reduced water clarity or enhanced turbidity (e.g., Abrahams and Kattenfeld 1997; Jacobsen et al. 2004; Lehtiniemi et al. 2005). As expected, predators increase their activity and movement with increasing light levels, even undergoing diel horizontal migrations between the littoral and pelagic zone (Nakayama et al. 2018).

While numerous studies have documented the effects of turbidity or water clarity on the DVM behavior of zooplankton (e.g., Horppila et al. 2004; Castro et al. 2007), evidence for these effects on the movement behavior of fishes is less common. In fact, we only found one experimental study conducted with Lake Superior cisco (*Coregonus artedi*) larvae (Swenson and Matson 1976) and a few field observational studies focused on non-Great Lakes fish larvae (Netsch et al. 1971; Johnston and Wildish 1982; Matthews 1984) that documented any sort of effect of turbidity or water clarity on fish vertical movement behavior. In all four studies, larvae were found closer to the surface when these waters were turbid relative to when they were clear, suggesting that, as with zooplankton prey, small-bodied fishes will alter their DVM behavior in response to water clarity. This result is consistent with general DVM patterns for planktivorous fish in large lakes that are deeper during the day (higher light) and shallower at night (lower light; Eshenroder and Burnham-Curtis 1999; Simonin et al. 2012; Riha et al. 2017). Future research could also explore how changing water clarity has affected horizontal movements of fishes in the Great Lakes.

The few studies that have explored the impact of turbidity on shoaling behavior consistently report declines in shoaling behavior with increasing turbidity. For example, experiments revealed guppies (*Poecilia reticulata*) form smaller schools and are found alone more frequently in turbid conditions relative to clear-water conditions (Borner et al. 2015). Similar reductions in shoal size and relaxed aggregations have been shown for other fishes, both freshwater (Fischer and Frommen 2013) and coastal marine (Ohata et al. 2014), in lower clarity waters. We suspect that these declines in shoaling behavior are related to perceived decreases in predation risk. However, because the regularity of spacing and movement of individuals in a school depends on vision, impaired vision that emanates from reduced water clarity could be the ultimate cause of the loss of school formation (Partridge 1982). For Great Lakes fishes, it is well documented that fish shoaling is far more common during the daytime in the Great Lakes than it is during the night (e.g., Yule et al. 2007; Riha et al. 2017), but future research should evaluate whether aspects of daytime shoaling (e.g., size, tightness of aggregations) have increased in lakes with long-term increases in water clarity.

Collectively, this body of research shows that the effect of changing water clarity on predation risk is complex and context-dependent. Most conspicuous is the need to consider the characteristics of the predator and prey, including their body size, their sensory capabilities, their morphology and functional anatomy, and their general feeding preferences. Most of the relevant research synthesized for this study illustrated how reductions in water clarity tend to reduce behaviors that reduce predation risk (i.e., DVM, shoaling). This work provides testable hypotheses for future research applicable to systems where water clarity is increasing: that diel horizontal or vertical migrations or shoaling should become more frequent to reduce the risk of predation mortality.

Effects on fish reproductive behavior

Water clarity has been shown to affect multiple aspects of reproductive behavior, including mate selection and spawning behavior, which could influence reproductive success and survival to older life stages and the fishery. The effects of water clarity on mate selection are relatively well-studied, particularly within the deeper lakes of eastern Africa, with the common finding of an impaired ability to assess mates and relaxed sexual selection when turbidity increases. For example, in Lake Victoria, female cichlids from populations occupying low-clarity waters demonstrated a reduced preference for colourful males relative to those from populations occupying high-clarity regions (Mann et al. 2010). Reduced mate selection has also been documented in other ecosystems with reduced water clarity, suggesting it to be a common phenomenon. For example, in a coastal marine fish (sand goby, *Pomatoschistus minutus*), sexual selection decreased with decreasing water clarity, leading to the distribution of males that successfully competed for mates in low-clarity waters to be more evenly distributed than in clearer waters (i.e., mate selection was less skewed toward large males; Jarvenpaa and Lindstrom 2004). Similar negative effects of low water clarity on the strength of sexual selection were shown in Baltic Sea three-spined stickleback populations, where the costs of courtship behavior (e.g., time spent displaying) increased with increasing algal cover (Candolin et al. 2007). Finally, low UV penetration, which we would expect to accompany increases in turbidity, can weaken sexual selection for fish species that can use UV to improve colour discrimination of potential mates (Smith et al. 2002).

A reduction in the ability of individuals to assess and select mates in ecosystems that are experiencing reduced water clarity is important, as it could lead to loss of species diversity through hybridization or transfer of suboptimal genes to the next generation, both of which could lead to reduced population fitness and viability. Support for this hypothesis derives from the endemic haplochromine cichlid assemblage in Lake Victoria, which uses colour signals to distinguish individuals among species. When water clarity declined, this distinguishing ability declined and sexual selection was relaxed, which led to an increase in interspecific breeding and a loss of species diversity (Seehausen et al. 1997). While high turbidity has been suggested as a mechanism to explain high levels of hybridization in centrarchids (e.g., *Lepomis* spp., *Pomoxis* spp.) living in turbid environments, such as reservoirs, definitive tests of this hypothesis have not been conducted (Bolnick 2009). If and how changes in water clarity affect mate selection in Great Lakes species remains unstudied.

Changing water clarity can also influence other aspects of spawning behavior, including spawning site selection and spawn timing. In lakes with low levels of dissolved organic carbon (DOC), yellow perch spawned in deeper waters than in lakes with higher DOC, perhaps avoiding exposing their eggs to damaging UV-B in the lower DOC lakes (Williamson et al. 1997; Huff et al. 2004). Whether this relationship between UV and spawning habitat is due to behavioral choices made in response to high water transparency and putative UV damage, or to fidelity to natal habitat, remains unknown. Nile tilapia (*Oreochromis niloticus*) in a Sri Lankan reservoir system not only spawned in deeper waters when water clarity was higher, but also increased nest density with increasing turbidity (Sandun et al. 2017). Perhaps in conditions of low water clarity, nesting individuals are less able to perceive nearby nests leading to greater density of nest sites. Young and Woody (2007) showed that sockeye salmon (*Oncorhynchus nerka*) in a glacial lake timed their spawning period to coincide with a seasonal decrease in lake turbidity, potentially to offset negative effects associated with spawning in highly turbid waters, such as egg smothering (Muncy et al. 1979).

In summary, spawning behaviors that have evolved in lakes with relatively high water clarity are generally altered when water clarity becomes reduced. For lakes that are undergoing oligotrophication (perhaps following a period of eutrophication), one might expect an improved ability to discriminate mates and increasing reproductive isolation for species with high morphological similarity. Although these patterns are not derived from Great Lakes studies or from fishes that are common in the Great Lakes, they provide predictions upon which future research could be based.

Effects on territoriality

Territoriality is a common behavior exhibited throughout the year for several families of fishes that can occur in different habitats throughout the Great Lakes, including Cottidae, Percidae, Gobiidae, Centrarchidae, and Cichlidae. However, the body of research that has explored the effects of changing water clarity on territoriality remains scant and clearly is an area in need of more research. One generalization that has emerged from limited research is that reduced water clarity suppresses territorial behavior. For example, Berg and Northcote (1985) showed that in turbid conditions, juvenile coho salmon (*Oncorhynchus kisutch*) ceased defending previously established territories and reduced aggressive behaviors towards conspecifics. Likewise, territorial behavior was shown to decline in juvenile Atlantic salmon (*Salmo salar*) as turbidity increased (Robertson et al. 2007). Finally, high turbidity caused a shift in the behavior of rock-dwelling cichlids in Malawi, with individuals reducing the time and effort invested in territory defense and increasing their foraging behavior (Gray et al. 2011). Given that several common species of native (e.g., smallmouth bass (*Micropterus dolomieu*)) and invasive (e.g., round goby (*Neogobius melanostomus*)) fishes demonstrate territoriality in the Great Lakes (Ridgway et al. 1991; Balshine et al. 2005), the need to better understand the effects of water clarity change remains high.

Effects of changing water clarity on aspects relevant to fisheries

Catchability

Formally, catchability is the proportion of a homogeneously distributed fish stock that will be caught by one unit of fishing effort. Catchability is often assumed to be constant, allowing fisheries scientists and managers to assume a linear relationship between stock abundance and CPUE. In reality, however, catchability varies with availability of fish and capture efficiency of fishing gear (Godø 1994). For example, with respect to a sampling gear like a bottom trawl, availability is the proportion of the targeted population within reach of the trawl (e.g., the proportion below the maximum height of the bottom trawl, relative to the total population). In turn, the capture efficiency is the proportion of the available fish that is captured by the trawl and not able to avoid it through some escapement behavior or size selectivity of the mesh. As we describe more fully below, the availability and capture efficiency of fish are influenced by water clarity, which in turn can affect the ability of fishers (e.g., recreational anglers, commercial fishers) to catch fish, as well as the ability of fisheries scientists and managers to properly assess catch rates and estimate the demographics of fish populations.

The vertical or horizontal distribution of fish can directly affect the availability of fish to fishing gears that target specific areas of the water, such as trawls, gill nets, and traps. Numerous physicochemical variables (e.g., light, temperature, dissolved oxygen) likely operate in concert with biotic factors (e.g., prey and predator distributions) to affect the distribution of fish in lakes (Neilson and Perry 1990; Wootton 1990). In most studies, temperature (Magnuson et al. 1979), prey (Eklöv 1997), and dissolved oxygen (Kramer 1987) have been primary variables underlying distribution (e.g., Rudstam and Magnuson 1985; Rowe and Chisnall 1995; Mehner et al. 2007), although some have speculated how light affects distributions as a consequence of affecting optimal foraging conditions (e.g., Baldwin et al. 2002; Lester et al. 2004). Some of these same variables have been shown to be important in the Great Lakes, affecting the distributions of both predators and their prey alike (Brandt et al. 1980; Roberts et al. 2009; Vanderploeg et al. 2009), with consequences for fisheries (e.g., Dippold et al. 2020). Unfortunately, none of these Great Lakes studies have explored the effect of changing water clarity on fish distributions. However, owing to the sensitivities of both predators and prey to light conditions (see sections **Effects on fish foraging** and **Effects on predation risk,** above), we fully expect water clarity (through its effect on light transmission) to hold the potential to modify the effects of other habitat variables on fish distributions and vulnerability to fishing gears.

Despite the potential for changing water clarity and resultant light penetration to affect the distribution of fish and their resultant availability to sampling gears, research on this topic is rare for freshwater lakes. One example is from a shallow lake in the Netherlands (Lake IJssel, mean depth = 5 m), where bottom trawl catches of ruffe (*Gymnocephalus cernua*) and age-0 pikeperch declined with increasing light levels, whereas the catch rates of three other species (*Osmerus eperlanus*, *Rutilus rutilus*, *Abramis brama*) were unrelated to light (Buijse et al. 1992). A well-studied marine species is walleye pollock (*Gadus chalcogrammus*), which is commercially fished through bottom trawling. Research has revealed that individuals alter their vertical distribution to optimize light conditions for foraging (Kotwicki et al. 2009), and when light conditions are sufficiently high near the bottom, walleye pollock availability to the bottom trawl increases (Kotwicki et al. 2015).

The efficiency of a sampling gear can also depend on water clarity when light conditions mediate escapement. For example, under low light conditions ($<10^{-6}$ lx) fish may not be able to detect an approaching trawl (Glass and Wardle 1989), whereas under intermediate light levels, bottom trawls (or their disturbance) can startle a fish on the bottom as it nears and cause them to be "herded" and potentially caught in the net (Ryer and Barnett 2006). However, under higher light levels ($>$1 lx), fish on the bottom may be more likely to detect the net soon enough such that their reaction allows them to avoid being captured (Wardle 1986). For passive gears, such as gill nets, efficiency can also vary with light levels. For example, for pelagic clupeids in the Baltic Sea, catch rates declined with increased Secchi disk depth, possibly owing to net avoidance (Hansson and Rudstam 1995).

Most fishery-independent surveys consider the effect of light on CPUE either in the design or interpretation of results. For example, many semipelagic planktivorous fish that are monitored annually in the Great Lakes (e.g., alewife, *Coregonus* spp.) demonstrate DVM behavior, being near the bottom during high light conditions (daytime) and migrating up in the water column during low light conditions (nighttime; Janssen and Brandt 1980; Jensen et al. 2006). As such, common assessment methods include daytime bottom trawling that can sample benthic and semipelagic species, as well as nighttime acoustics and midwater trawling that can sample pelagic species when the schools are more dispersed and individual fish targets can be more easily detected and counted (Yule et al. 2007, 2008). During the past two decades, studies have begun comparing catch rates from the bottom trawl during different times of the day and night (e.g., Stapanian et al. 2007; Yule et al. 2008). Surprisingly, catch rates of age-0 fishes from several species in western Lake Erie were more abundant in bottom trawls at night than during the morning or afternoon (Stapanian et al. 2007), which is opposite from the conventional DVM pattern expected for some species. The authors speculated that these age-0 fishes moved nearshore into the sampling region at night (i.e., increased availability), but an alternative explanation is increased efficiency of the trawl at night. In a more comprehensive modeling effort, Stapanian et al. (2009) found that catchability of age-0 yellow perch declined more during the day than during the night after 1990, coinciding with increased water clarity following the invasion of dreissenid mussels and consistent with reduced trawl efficiency in the daytime. In western Lake Superior, Yule et al. (2008) conducted bottom trawling during the day and night and reported higher catch rates of benthic-oriented species during the night, presumably owing to higher gear efficiency under lower light conditions. For semipelagic species, however, they reported higher catch rates during the day than at night, consistent with DVM behavior that would reduce their availability to nighttime bottom trawls.

Because light may both increase the avoidance of trawls and either increase or decrease an organism's use of trawled habitat, we expect the effect of altered light (or water clarity) on trawl catchability to be species-specific. For example, nighttime trawl catches of age-0 yellow perch are lower than daytime catches in Oneida Lake, whereas the opposite has been shown to be true for white perch (Forney 1974). These findings are consistent with marine studies that have found light levels to explain variation in the bottom trawl catch of targeted species (Bradburn and Keller 2015; Kainge et al. 2015; Kotwicki et al. 2015). These findings also highlight the importance of quantifying species-specific relationships among light and fish catches and reevaluating them as changes in the ecosystem occur. A lack of understanding of these relationships can lead to inaccurate estimates of population size (stock abundance) and a false understanding of how ecosystem change has been affecting resident fish populations and fisheries dynamics (Bohlin and Sundström 1977; Peterman and Steer 1981; Arreguín-Sánchez 1996). For this reason, time-varying catchabilities have been recommended in ecosystems that demonstrate nonstationarity or changes in assessment gears (Wilberg et al. 2009; Thorson and Berkson 2010). The need to consider time-varying catchabilities seems especially appropriate given both the long-term (decadal) and short-term (seasonal) changes in water clarity that have occurred in the Great Lakes (see Fig. 1).

Fisher behavior

In addition to affecting fish distributions and catchability, environmental conditions such as water clarity (Eiswerth et al. 2008) can influence fisher (*i*) perceptions about the availability, catchability, and edibility of fishes, (*ii*) decisions (both before the trip and in situ) about fishing sites and fishing tactics (Hunt 2005), and (*iii*) attitudes regarding their ability to attain fishing trip objectives (Provencher et al. 1997; Arlinghaus 2006; Beardmore et al. 2011; Carlin et al. 2012). Ultimately, all of these factors may govern whether to fish or not (Hunt 2005). While catching fish is important to trip satisfaction for some fishers but not others, we do know that catch expectation drives fisher satisfaction for many (Schramm et al. 2003; Arlinghaus 2006). In the Great Lakes, which supports one of the largest freshwater charter boat fisheries in the world (Kuehn et al. 2005), water clarity can affect fishing strategies. For example, Lake Huron charter boat captains adapted to increased water clarity by using planer boards when trolling and shifting effort to low-light periods (O'Keefe et al. 2015). In Lake Erie, recreational anglers change lure colours from white in clearer waters to black in more turbid waters while fishing for walleye (Nieman et al. 2020). Accordingly, water clarity is an important consideration of fishers when weighing expectations of achieving desired outcomes against incurred costs (expenditures, time) from a fishing trip (Hunt 2005).

Water clarity influences both spatial and temporal aspects of distribution and intensity of fisher effort in large lakes. The availability of waters of desired clarity, the suitability of those areas for attracting targeted fish species, the expected duration of water clarity conditions in those areas, travel options and costs to reach those areas, and fisher preferences or objectives can affect the distribution of fishery effort within lakes (Hunt 2005; Hunt et al. 2007). If a preferred fishing area has pervasive turbidity from suspended sediments or algal production, fishers may shift effort to clearer waters or to other species or avoid fishing until conditions improve, especially if they perceive clear water to indicate low levels of environmental pollution and contaminants in fish flesh (Schramm et al. 2003). Alternatively, turbid river plumes or nearshore areas in otherwise clear lakes may attract targeted fish species and concentrate fishery effort. As water clarity increased in Lake Erie during the 1990s, for example, walleye catchability declined and recreational fishery effort increased on smallmouth bass in nearshore areas (Lichtkoppler and Hushak 2001). Shore-bound anglers are more likely to be constrained by changes in water clarity than mobile (boat) fishers, although effort from either group can be affected. Temporally, angler effort may shift between diurnal and low-light periods in response to changes in water clarity. Commercial fisheries are generally more affected by spatial than temporal aspects of water clarity, with gill nets or trap nets often fished over an entire 24 h period (or longer) of varying light conditions. Ultimately, water clarity effects on fish and fisher behavior may shift fishery effort among species or areas of a large lake, driven initially by fisher expectations of increased catchability for preferred species or areas, and then reinforced by trip outcomes.

Effects on fisheries management considerations

Unlike small or shallow lakes, where water clarity could potentially be manipulated through biomanipulation (Meijer et al. 1999; Lathrop et al. 2002; Yu et al. 2016), larger lakes are more challenging for fisheries managers to directly manipulate water clarity because the underlying drivers require interventions at landscape scales (Wehrly et al. 2013) or are caused by a widespread invasive species (e.g., dreissenid mussels) for which control options may be limited. In the Great Lakes, ongoing research is at the early stages of exploring the feasibility of control measures for invasive mussels that could be delivered at the scale of a large lake (e.g., Weber 2015), while efforts to reduce point- and non-point-source nutrient and sediment pollution would require the involvement of federal and state regulatory agencies to help implement regulations. Although point-source nutrient abatement regulations successfully led to increased water clarity in western and central Lake Erie to the benefit of valued fish populations (Ludsin et al. 2001), it is uncertain whether efforts to control non-point sources will prove effective. This uncertainty exists because weather, including both precipitation and temperature, is a key uncontrolled driver of sediment and nutrient delivery to streams that drain into the recipient lake and can interact with and overwhelm the effects of agricultural conservation practices (Dippold et al. 2020; Fraker et al. 2020). Furthermore, droughts may increase water clarity, whereas heavy precipitation may reduce water clarity by reducing penetration of UV and visible light (Williamson et al. 2016*b*). In western Lake Erie, for example, frequent and intense spring storms have contributed to increased phosphorus loadings and summer algal blooms, and summer wind patterns affect the spatial extent of the blooms (Tian et al. 2017). Even so, past successes in improving water clarity through nutrient and land management, to the benefit of fisheries (Ludsin et al. 2001), offer some hope to fishery managers that collaborative efforts with land managers can provide an option to attempt management of water clarity under the right circumstances rather than simply managing the response to water clarity change.

Given the difficulty implementing simple, direct levers to alter water clarity, managers could benefit from improved understanding of how changing water clarity affects fish and fisheries and ultimately fishery performance. First, managers could adapt fishery assessment programs (e.g., creel, trawl, and physicochemical surveys) that can describe spatial–temporal changes in fish and fisher behavior. Fish surveys, when combined with physicochemical data collection, can allow managers and cooperating researchers to identify and understand fish–habitat associations that can help discern the effects of altered water clarity on their valued populations. Likewise, creel surveys can offer the opportunity to understand whether water clarity change has been underlying any observed changes in harvest or catch rates through its effects on the ecosystem versus fisher behavior. Second, managers could be better informed by implementing protocols to assess whether catchability has been changing through time, owing to altered water clarity or other factors. Such protocols are critical to interpreting both fishery-dependent and fishery-independent assessment data, which are vital to making informed decisions about harvest quota management (Wilberg et al. 2009; Thorson and Berkson 2010). To this end, Lake Erie managers conducted modeling simulations to explore how fishery-independent gill net surveys could be affected by changes in catchability, due to changing water clarity and other factors (e.g., Wagner et al. 2009), and revised their stock assessment model used for setting annual harvest quotas for walleye (Kayle et al. 2015). This study offered a framework to explore how shifts in catchability of assessment gear that are associated with water clarity change can be used to inform management decision-making (also see Wilberg et al. 2009; Thorson and Berkson 2010). Third, because the use of lakes is likely to increase with enhanced water clarity (Vesterinen et al. 2010; Keeler et al. 2015), conflict among different user groups (e.g., fishers versus boaters or jet skiers; recreational versus commercial fishers; swimmers versus anglers) should be expected (e.g., Meyerhoff et al. 2019). Fishery managers could anticipate the potential for dissatisfaction, tension, or conflict through education as well as voluntary or regulatory actions on specific user groups. Fourth, managers could use an understanding of how fish respond to water clarity to inform management priorities or decisions (Hansen et al. 2019). For example, understanding how water clarity affects fish reproduction (e.g., spawning timing or locations) could inform assessment of habitat availability to identify limiting habitats, prioritize fish habitat restoration projects, and provide fisheries managers the opportunity to partner with other environmental managers where possible. Furthermore, managers could use this knowledge to better inform permitting for in-water projects (e.g., dredging, diking, shoreline alterations, pipelines) that affect water clarity in localized areas important to fish habitat or fisheries.

As water clarity conditions change, managers may seek to prepare constituents for the possibility that the fish community, and hence set of harvestable species, will change as well. Fish communities in the Great Lakes have changed coincident with changes in nutrient loading (e.g., Ludsin et al. 2001; Ivan et al. 2014), but the individual contribution of water clarity in driving these changes remains unclear. In the Great Lakes, fishers have historically primarily valued and targeted species that are well-suited for moderate to high water clarity (e.g., percids, centrarchids, percichthyids, esocids, salmonids, and coregonids). In other ecosystems of normally low to moderate water clarity levels (relative to the Great Lakes), fishery interests may involve other well-suited species (e.g., ictalurids, cyprinids, or lepisosteids). Refined understanding of potential water clarity thresholds that influence fish community shifts in various aquatic systems, and the rates (years) at which shifts occur, could help fisheries managers better accommodate changes in water clarity of their lakes into their communications and management plans. In turn, managers could ensure that the expectations of their constituents for a desired fish species–community matches the fish community present in different water clarity conditions. Given that continued water clarity change is to be expected with continued human-driven environmental change (Jeppesen et al. 2005; Williamson et al. 2008), this outcome seems especially important.

Effects of changing water clarity on fishery performance

Although the conventional assessment of a fishery is based on the ecological health or sustainability of the stocks, "fishery performance" also considers the ability of a fishery to deliver economic and community benefits (Anderson et al. 2015; Heck et al. 2016). We assert that changing water clarity, through its effects on fish and fisheries, can also influence economic and community indicators of fishery performance (see Fig. 2). Unfortunately, studies that evaluate linkages between changing water clarity and the economic benefits of a fishery are uncommon for the Great Lakes or large, deep freshwater systems. Eiswerth et al. (2008) provide a case study that estimated a steep reduction in angling trips to Delavan Lake, Wisconsin (area = 770 ha, maximum depth = 16 m) when water clarity was reduced by 70%, leading to annual economic losses of US$520 000. Fishers in this lake associated reduced water clarity with a less desirable fish community, dominated by common carp (*Cyprinus carpio*) and bigmouth buffalo (*Ictiobus cyprinellus*), as opposed to preferred walleye and northern pike (*Esox lucius*). In another example across 53 Canadian lakes, Geisler et al. (2016) predicted that invasion of dreissenid mussels (and subsequent increases in water clarity) would affect the yield in the recreationally important walleye fishery, with predictions ranging from a 20% decline to a 50% increase, depending on the mixing depth of the lake.

Similar to economic benefits, community benefits offer a second broad indicator of fishery performance for which few linkages to changing water clarity have been documented. Community benefits of healthy freshwater ecosystems can include access to clean drinking water, beaches for recreation, and fisheries that support local economies and provide healthy, edible sources of protein and contribute to cultural enrichment (e.g., Smyth et al. 2009; Great Lakes Water Quality Agreement 2012; LaRiviere and Crawford 2013). Traditional fisheries that can enrich cultures typically develop because desired species are reliably abundant and catchable in certain areas during specific seasons (e.g., spring or fall spawning runs), as fishers draw from their successful experiences (Adamowicz 1994; Hunt 2005). Should changes in water clarity alter fish (or fisher) behavior and catchability of preferred species at traditional areas and times, harvest and effort by local communities could be reduced and potentially threaten the continuance of established traditions (Criddle et al. 2003).

In conclusion, consideration of fishery performance indicators (e.g., economic and community benefits) provide another context through which fisheries managers can consider how changing water clarity can affect large lake ecosystems such as the Great Lakes. Additional research is needed, however, to further understand how changing water clarity affects fishery performance for species of cultural or economic importance in the Great Lakes. Increased collaboration with social scientists that can measure economic, community, and ecosystem benefits associated with changing water clarity could accelerate scientific understanding and enhance the ability of fisheries managers to make more informed decisions to enhance fishery performance.

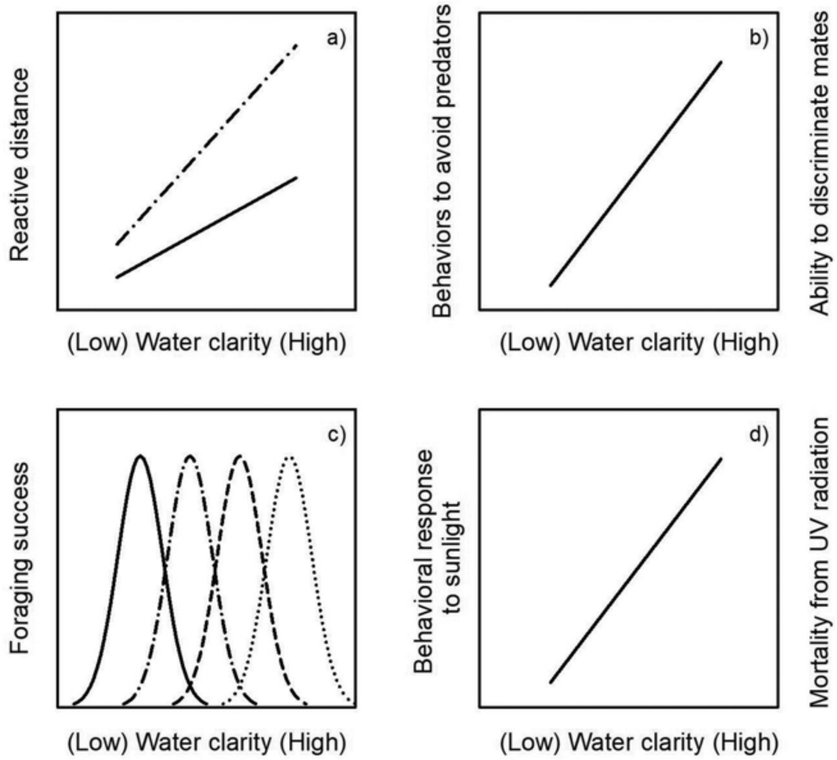
General predictions and implications for priority research in the Great Lakes

This paper was motivated to improve limited understanding of how (*i*) dramatic long-term increases in water clarity in Lakes Michigan, Huron, and Ontario during the past several decades and (*ii*) seasonal reductions in water clarity owing to the increasing frequency of sediment plumes and cyanobacteria blooms in Lake Erie affect fish and the fisheries that they support. As we compiled existing knowledge, we summarized some of the general predictions that emerged (see Fig. 4) and recognized how these predictions could inform priority research needs for the Great Lakes that could be useful for funding agencies (see Box 1).

The first general prediction arising from this synthesis is that the reactive distance to enhance fish foraging will increase with increasing water clarity (Fig. 4*a*). Because larger prey can always be detected over a greater distance and tend to be less transparent than smaller planktonic prey, piscivorous fish may experience increased foraging success relative to planktivorous fish with increasing transparency (Breck 1993; De Robertis et al. 2003). In turn, this prediction affords a greater predation risk to prey fishes than to zooplankton as lakes become clearer. Applied to prey fishes in Lakes Michigan, Huron, and Ontario, we would predict that top-down regulation (i.e., predation) to be even more important in the 2000s than during the 1980s and 1990s when the water was less clear. As a result, the already strong evidence for top-down control (e.g., Murry et al. 2010; Tsehaye et al. 2014; He et al. 2015) could be bolstered by enhanced foraging efficiency in systems with increasing water clarity. Planktivorous fishes, in turn, could seek to mitigate increased predation risk via several potential behavioral responses (Fig. 4*b*), including more time spent migrating to refugia (e.g., dark bottom waters, vegetation patches) or shoaling (hence potentially increasing competition for prey), both of which could reduce foraging time and energy intake.

Another general prediction is that different fish species, even within a trophic level, will experience optimal foraging success under different levels of water clarity (Fig. 4*c*). Species-specific differences are a consequence of varied anatomical (e.g., eye structure) and behavioral (e.g., feeding preferences, DVM behavior) adaptations, yet relatively few Great Lakes fish species have been studied to identify optimal water clarity conditions. Percid species are one exception, given that previous research has documented walleye to optimally feed in intermediate levels of water clarity (Ryder 1977; Lester et al. 2004) and that the foraging of walleye and yellow perch is more impeded by organic components of turbidity than inorganic ones (Wellington et al. 2010; Nieman and Gray 2019, 2020). Scientists should consider developing feeding experiments for other key Great Lakes species that likely have experienced dramatic changes in water clarity. For example, while Chinook salmon (*Oncorhynchus tshawytscha*) and lake trout (*Salvelinus namaycush*) are generally the most abundant piscivores in Lakes Michigan, Huron, and Ontario, we are unaware of

Fig. 4. Generalized expected relationships based on our review of how changing water clarity (increasing clarity from left to right) affects fish and fisheries. In panel *a*, reactive distance increases with increasing water clarity for both piscivores (dash-dotted line) and planktivorous (solid line) fish, but increases faster for piscivores because they have larger prey (i.e., prey fish versus zooplankton), and zooplankton are more transparent and are difficult to detect than a more opaque prey fish. Panel *b* depicts the general response of increased frequency of behaviors to avoid predators (e.g., schooling, protecting territories with shelters) and the increased ability to discriminate mates with increasing water clarity. Panel *c* illustrates that the level of water clarity that optimizes foraging should vary among species (each with a different unimodal curve), leading to the expectation that changes in water clarity will differentially affect energy intake by species with different eye physiology (e.g., ratio of rods to cones) or behavioral adaptations. Panel *d* depicts the general finding that behavioral responses to higher light exposure (e.g., swimming to deeper depths) and direct mortality from ultraviolet (UV) light exposure are expected to increase with increasing water clarity and increasing depths of UV radiation penetration.



any experiments with these species that can help agencies understand how each component of foraging (search, prey encounter, pursuit, and capture) might have changed with the dramatic increases in water clarity (see Fig. 1) or whether one species has benefitted more than the other. Likewise, while extensive foraging experiments that simulate organic turbidity have been conducted for some key Lake Erie species, similar investigations have not been conducted for other ecologically and economically important species (e.g., white perch, white bass (*Morone chrysops*), rainbow smelt, but see Nieman and Gray (2019, 2020)) that may be exposed to cyanobacteria blooms in Lake Erie or other productive embayments in the Great Lakes.

Improved knowledge of whether changing water clarity has affected the foraging efficiency of key species could help fishery management agencies determine the appropriate stocking rates of top predators. For example, a series of Lake Michigan stock assessment models that use a type II functional response to estimate the consumption of alewife by salmonines are used to inform salmonine stocking rates (Tsehaye et al. 2014). This functional response curve, however, does not account for varied water clarity, which is predicted to affect the foraging efficiency and energy intake per unit time (Gardner 1981; Sweka and Hartman 2001; Ljunggren and Sandström 2007). Given that water transparency in Lake Michigan has doubled since 2004 (see Fig. 1) and likely increased the foraging efficiency of piscivores especially (De Robertis et al. 2003; Fig. 4*a*), incorporating water clarity is a logical step in a revised model, which could reduce the risk of overstocking.

Another emerging general prediction is that as water clarity increases, visible light and even UV will concomitantly penetrate deeper in the water column, which could influence spawning behaviors, the distribution and abundance of larval fishes, and even their zooplankton prey (Fig. 4*d*). Unfortunately, because UV is not commonly measured in water profiles in Great Lakes monitoring, we do not know whether increased water transparency in Lakes Huron, Michigan, and Ontario has led to deeper penetration of UV. If we assume that UV now penetrates deeper in these lakes, species that have evolved in a high UV environment may have an advantage over other species because they can (*i*) use UV to improve foraging success or (*ii*) mitigate potential damage from UV through behavioral responses (e.g., migrating to deeper waters), morphological adaptations (e.g., protecting pigments), or DNA repair mechanisms (Zagarese and Williamson 2001). One hypothesis for future research is that the pelagic larvae of native Great Lakes species (e.g., *Coregonus* spp., deepwater sculpin) evolved in relatively high UV exposure environments before human activities increased nutrient inputs and reduced water clarity during the 20th century. By contrast, we would expect the early life stages of nonindigenous, naturalized species, such as alewife (dominant in Lakes Michigan and Ontario), rainbow smelt (abundant in all five lakes), and white perch (dominant in western and central Lake Erie), which evolved to spawn in tributaries or embayments of the Atlantic Ocean — where UV exposure was likely more limited — to have a lower tolerance to UV. Could low tolerance and increased UV exposure be contributing to the declines of alewives and rainbow smelt in Lakes Michigan, Huron, and Ontario over the past several decades?

As water clarity increases, a review of previous studies predicts that fish will defend territories more aggressively and discriminate mates more successfully (Fig. 4*b*). Because we found no research on these behaviors for common Great Lakes species, whether these behaviors have become more prevalent in Lakes Huron, Michigan, and Ontario during recent decades remains unknown. Such knowledge is important as it could help explain recruitment variation (via the ability to defend territories beneficial to reproduction and shelter; sensu Berg and Northcote 1985), highlighting the need for species-specific research. By contrast, in lakes or areas of lakes where water clarity becomes reduced for days or a few weeks (e.g., cyanobacteria blooms, wind-driven resuspension events, precipitation-driven sediment plumes out of river mouths) that happen to coincide with spawning periods, research from the African Great Lakes suggests fish may be more vulnerable to selecting suboptimal mates or even to hybridization. This latter question seems most relevant to nest-guarding Great Lakes species such as round goby, sculpins, and centrarchids, but also could be important to broadcast spawners such as yellow perch, which appear to use spawning areas that are defined by water clarity (Reichert et al. 2010; Carreon-Martinez et al. 2015) or that might rely on visual cues to maintain fine-scale population structure (Kocovsky et al. 2013).

A final general prediction is that as water clarity increases, catchability from gill nets and daytime trawls will decline, although the responses likely vary by species (Stapanian et al. 2007, 2009). Future research in Lakes Huron, Michigan, and Ontario could evaluate whether increased water clarity has changed the distribution of key planktivorous fishes that have traditionally undergone DVMs (e.g., alewife, rainbow smelt). Have they responded by increasing time spent in dark, bottom refuges during daytime or by intensifying daytime shoaling behavior? Their response may be mediated by the decline in energy-rich *Diporeia* spp. on the bottom of these lakes that would reduce daytime foraging opportunities in the benthos. With potential changes in fish distribution, future research could investigate whether increased water clarity has reduced the sampling efficiency of gears, especially if fish are able to detect and avoid the oncoming trawl earlier. Similar investigations into water clarity effects on catchability are relevant to western Lake Erie and other shallow areas of the Great Lakes that have been experiencing increased sediment plumes or cyanobacteria blooms (see Fig. 1). Beyond assessment, how are anglers and commercial fishers changing behaviors when these plumes or blooms occur? Catchability in these areas could increase due to fish aggregating in these areas to find prey or seek refuge (e.g., Briland et al. 2020) or by reducing the ability of fish to detect and avoid sampling gears. Finding that catchability has changed in either set of examples (increased or reduced water clarity) would have consequences for management agencies, which use long-term assessment data to inform fish stocking decisions or to estimate population sizes of fish and set harvest levels.

Conclusions

In developing our framework to improve understanding of how changing water clarity could affect fish and the fisheries they support in the Great Lakes, we derived general predictions (see Fig. 4) that can guide future research in the Great Lakes (Box 1) and beyond. Given that the responses of fish to altered water clarity will be species-specific (and perhaps even population-specific), we should expect that some species or populations will benefit more than others. Our ability to forecast these "winners" or "losers", or at a minimum understand the role of water clarity in driving fisheries performance, will hinge on our future success in estimating how changing water clarity affects these vital rates (e.g., foraging, predation risk), as well as our ability to accurately assess whether altered catchability could be affecting our ability to document real changes in population demographics. With respect to fisheries performance (i.e., Anderson et al. 2015), our framework development illuminated the need for additional Great Lakes research in the nascent field. Most obvious is the need for fisheries biologists and researchers to partner with social scientists and economists to evaluate nonbiological responses (e.g., cultural value, economic value) of fish and fisheries to changing water clarity. Doing so could help agencies better inform stakeholders about shifts in valued fish populations, as well as ensure that the values of these stakeholders are considered when forming future policies (e.g., harvest quotas, stocking rates). Furthermore, our research highlighted numerous ways in which improved understanding of the linkages among water clarity, fish, and fisheries could benefit efforts to conserve, rehabilitate, and sustain valued populations, or perhaps control nuisance populations (e.g., invasive species such as sea lamprey (*Petromyzon marinus*) and white perch). This understanding seems especially important given that recent changes in water clarity, both increases (as observed in Lakes Michigan, Huron, and Ontario) and decreases (as observed in Lake Erie), are not expected to be reversed and can be expected to interact with other anthropogenic stressors (e.g., climate change, invasive species, habitat modification; Smith et al. 2019). Such understanding can potentially offset ecological surprises (sensu Paine et al. 1998) that would make fisheries management even more difficult than it currently is. Finally, by offering (*i*) a new framework with which to view the effects of water clarity on fish populations, communities, and fisheries, (*ii*) a set of priority research questions that highlight important information gaps in the Great Lakes, and (*iii*) general (testable) predictions on how water clarity can be expected to influence fish, we are hopeful that more attention is paid to water clarity change, which is common to aquatic ecosystems worldwide, both freshwater and marine. Continued research into the impacts of water clarity change on lake fishes and fisheries, combined with a future synthesis of this research (like what we provided herein), would advance our ability to form general predictions that can be applied to ecosystems where data and (or) ecological understanding is lacking. In addition, findings from this research could improve the ability of management agencies to guide the expectations of their stakeholders such that they are well-matched with biological reality, as well as help managers keep their valued fish populations and fisheries sustainable in the face of continued ecosystem change.

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