

SPECIAL SECTION: EFFECTS OF ECOSYSTEM CHANGE ON NORTH AMERICAN PERCID POPULATIONS

It's Complicated and It Depends: A Review of the Effects of Ecosystem Changes on Walleye and Yellow Perch Populations in North America

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Abstract

Walleye *Sander vitreus* and Yellow Perch *Perca flavescens* are culturally, economically, and ecologically significant fish species in North America that are affected by drivers of global change. Here, we review and synthesize the published literature documenting the effects of ecosystem changes on Walleye and Yellow Perch. We focus on four drivers: climate (including temperature and precipitation), aquatic invasive species, land use and nutrient loading, and water clarity. We identified 1,232 tests from 370 papers, split evenly between Walleye ($n = 613$) and Yellow Perch ($n = 619$). Climate was the most frequently studied driver ($n = 572$), and growth or condition was the most frequently studied response ($n = 297$). The most commonly reported relationship was “no effect” (42% of analyses), usually because multiple variables were tested and only a few were found to be significant. Overall responses varied among studies for most species–response–driver combinations. For example, the influence of invasive species on growth of both Walleye and Yellow Perch was approximately equally likely to be positive, negative, or have no effect. Even when results were variable, important patterns emerged; for example, growth responses of both species to temperature were variable, but very few negative responses were observed. A few relationships were relatively consistent across studies. Invasive species were negatively associated with Walleye recruitment and abundance, and higher water clarity was negatively associated with Walleye abundance, biomass, and production. Some variability in responses may be due to differences in methodology or the range of variables studied; others represent true context dependence, where the effect of a driver depends on the influence of other variables. Using common metrics of impact, publishing negative results, and robust analytical approaches could facilitate comparisons among systems and provide a more comprehensive understanding of the responses of Walleye and Yellow Perch to ecosystem change.

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Freshwater fisheries are threatened by multiple drivers of global change, including climate change, species invasions, and nutrient loading (Carpenter et al. 2011; Reid et al. 2019). Often, multiple ecosystem changes occur concurrently, making it difficult or impossible to identify causation using observational data alone—especially from a single system (Hilborn and Stearns 1982; Hilborn 2016). For example, climate change may increase habitat suitability for invasive species (Rahel and Olden 2008), while at the same time, warming temperatures and increased precipitation may increase nutrient loading in lakes (Collins et al. 2019; Ho and Michalak 2020), making it difficult to discern ultimate from proximate drivers of change. Ecosystem change may also have differential effects at different life stages of fish as a result of ontogenetic shifts in thermal tolerance, preferred prey, and other characteristics. In a world of unprecedented environmental change, it can be difficult to disentangle cause and effect from observational studies and messy data. Synthesizing information and comparing across studies to illuminate common patterns as well as differences in findings can help build common understanding and move beyond single-system narratives (Biggs et al. 2009).

The term “context dependence” is frequently used in ecology to describe variability in the existence, direction, or magnitude of a given relationship depending on other conditions (Catford et al. 2021). Relationships may vary among studies or ecosystems due to true context dependence (i.e., fundamentally different relationships under different ecological conditions) or due to apparent context dependence (i.e., the relationship appears to differ due to differences in statistical inference, sample size, range of values studied, or methodological differences; Catford et al. 2021). Higher-order interactions between variables can produce different relationships between driver and response variables, where the sign, magnitude, or functional form of a relationship varies based on levels of other environmental or biotic variables (Figure 1A). Additionally, unobserved system components, complexity, and ongoing change can alter relationships between components of a system (Figure 1B). These types of interactions and dynamics represent true context dependence. Recognizing and identifying the causes of context dependence can lead to greater insight into ecological processes and predictability of responses under changing conditions while also identifying areas of future study required to increase generalizability across systems (Catford et al. 2021). Conversely, observed effects can differ among ecosystems or populations due to nonmonotonic relationships, where a study encompassing one portion of the range of predictor values might be expected to identify a positive relationship, while at another range of variables we might expect a negative relationship or no relationship (Figure 1C). This apparent context dependence can be

resolved by studying relationships across a wide range of driver variables. Finally, a study may also identify a significant relationship between independent variables due to random chance, and such spurious correlations are unlikely to be consistent across studies (Figure 1D). The problem of spurious correlations is of particular concern when multiple relationships are tested. On the other hand, when observed effects are similar between studies, they may still have limited transferability to other systems if multiple ranges of conditions, contexts, and interactions have not been tested.

Here, we review the documented impacts of ecosystem change on Walleye *Sander vitreus* and Yellow Perch *Perca flavescens*—two economically, culturally, and ecologically important coolwater fish species that occur throughout North America (Bozek et al. 2011; Feiner and Höök 2015). We focus our review on four major drivers of ecosystem change: climate (including temperature and precipitation effects), aquatic invasive species, land use and nutrient loading, and water clarity. Although water clarity is inherently related to nutrients and land use, we included it as a separate driver for two reasons. First, water clarity (e.g., Secchi depth) is frequently measured in lakes throughout North America in the absence of nutrient or land use information, making it difficult to assess what might be causing differences in water clarity. Second, Walleye are physiologically adapted to low-light conditions (Ryder 1977) and the role of water clarity in determining Walleye abundance and production is well documented (Lester et al. 2004; Tunney et al. 2018; Hansen et al. 2019). Walleye and Yellow Perch exist across a wide range of climates, food webs, and productivity levels, and their responses may differ among ecosystems—that is, they may be truly context dependent. In this review we attempt to differentiate true context dependence from apparent context dependence, with the goal of identifying interactions between drivers that could lead to greater understanding of complex systems and the capacity to predict responses to future environmental change (Catford et al. 2021). At the same time, we recognize that management decisions cannot always wait for scientific certainty (or even robust statistical inference), and therefore this literature review will provide an up-to-date resource regarding the impacts of ecosystem change on Walleye and Yellow Perch, even when that information is based on one or a few studies.

METHODS

We used the Web of Science database to search for relevant literature up to May 27, 2021. A list of search terms was created for each major driver category for both Walleye and Yellow Perch. We used common names and scientific names for each species (including both *Stizostedion*

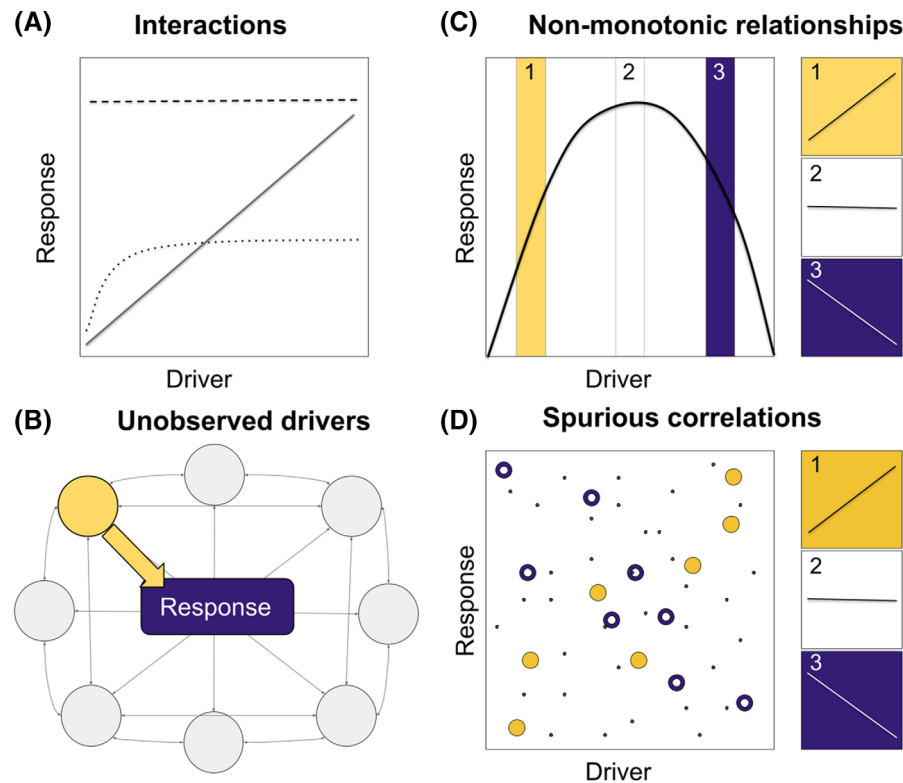


FIGURE 1. Documented responses to drivers of ecosystem change may vary across studies for many reasons. (A) Interactions among multiple drivers can produce different responses depending on the levels of other variables, representing true context dependence. (B) Complex systems with multiple interacting drivers that are frequently unobserved can produce different responses to the same drivers, and relationships themselves can change over time. (C) Nonmonotonic responses can result in opposite directional effects observed across different ranges of predictor variables (e.g., studies 1, 2, and 3 sample a different portion of the range of the driver variable and find different relationships). (D) Spurious correlations can produce statistically significant relationships that differ in direction just by random chance (e.g., studies 1, 2, and 3 sample a different subset of points due to random chance and find different relationships).

vitreum and *Sander vitreus* for Walleye) and excluded the terms “Pollack” or “Pollock” to eliminate hits from Walleye Pollock *Gadus chalcogrammus*. Searches were conducted using species names in combination with terms associated with our four categories of ecosystem change (using the Boolean operator “AND”). Search terms for climate change included any of the following (using the Boolean operator “OR”): climate change, climate, global warming, warming, or temperature. Search terms for nutrients and land use included the following: nutrient, nutrient loading, land use, land cover, pollute, run off, eutrophic, phosphoric, nitrogen, DOC, or dissolved organic carbon. Search terms for water clarity included the following: water clarity, turbid, Secchi, transparency, or light. Search terms for invasive species included the following: invasive species, AIS, invasive, non-native, non-indigenous, or alien.

For all papers generated from our database search, we reviewed each abstract to determine whether it included our species of interest and was relevant to our driver categories and search terms in any way. We then removed all

duplicates between our four searches, which resulted in 880 total papers for our initial literature review. We read each paper to identify if it was suitable for inclusion in the review. Inclusion required that investigators tested a relationship between some measure of climate, invasive species, nutrients and land use, or water clarity and some measure of Walleye and/or Yellow Perch individuals, populations, communities, or habitat (Figure 2). We also excluded studies that reported only time series with no statistical analysis of relationships between drivers and response.

For papers deemed suitable, we classified the direction of response based on results of statistical tests and visual examination of figures presented in the papers or supplementary materials. Response directions were classified as positive, negative, nonmonotonic or interactive, or no effect based on estimated coefficients and statistical significance based on the methods and interpretation of the original authors. Responses were classified as nonmonotonic or interactive only when identified as such by the original authors or based on graphical presentation of results.

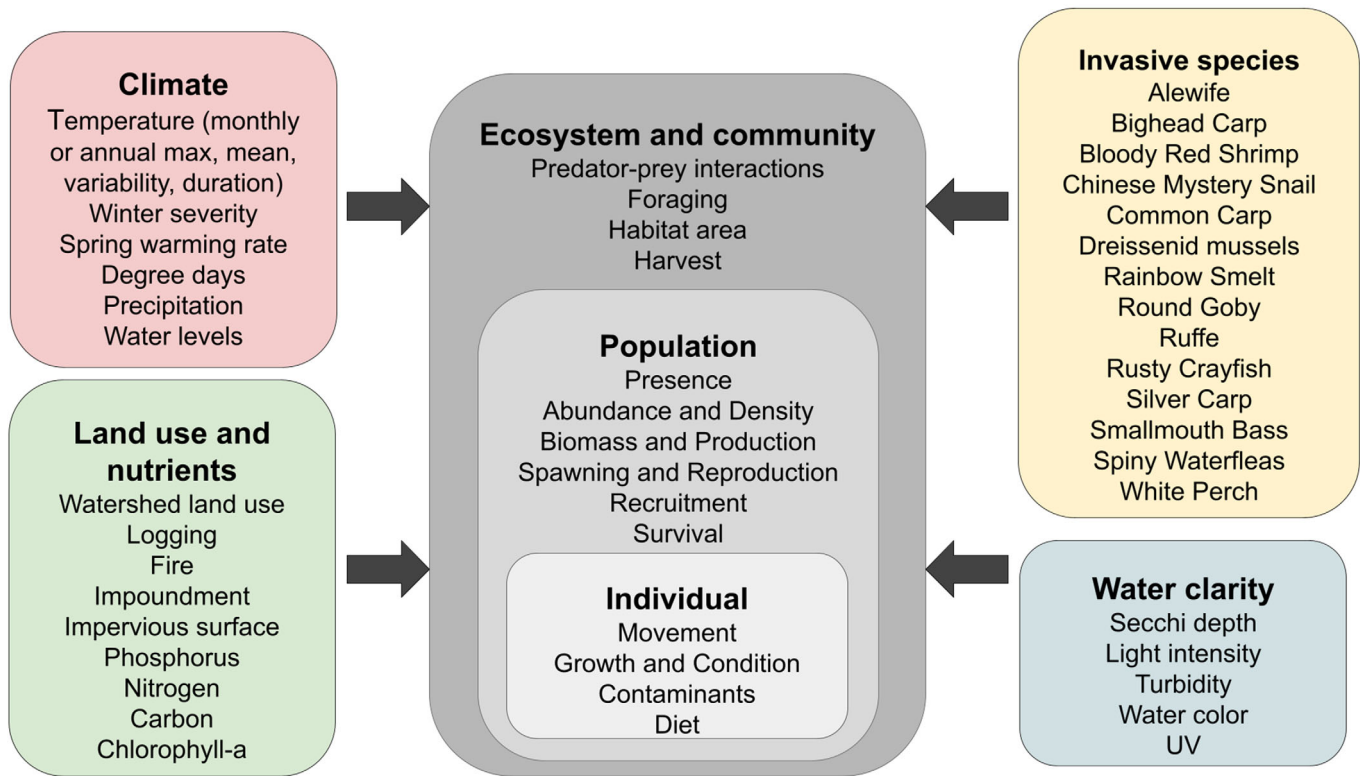


FIGURE 2. Drivers of ecosystem change included in each of the four major categories, and response variables recorded in the literature review. Invasive species included the following: Alewife *Alosa pseudoharengus*, Bighead Carp *Hypophthalmichthys nobilis*, bloody-red shrimp *Hemimysis anomala*, Chinese mystery snail *Cipangopaludina chinensis*, Common Carp *Cyprinus carpio*, dreissenid mussels, Rainbow Smelt *Osmerus mordax*, Round Goby *Neogobius melanostomus*, Ruffe *Gymnocephalus cernua*, rusty crayfish *Orconectes rusticus*, Silver Carp *Hypophthalmichthys molitrix*, Smallmouth Bass *Micropterus dolomieu*, spiny water flea *Bythotrephes longimanus*, and White Perch *Morone americana*.

When variables were selected for inclusion in a final model based on information theoretical approaches (e.g., Akaike 1973), we considered predictors not selected for inclusion in the final model to have no effect. We included studies that quantified simple correlations between variables and relied on the inference presented in the paper even if we questioned statistical methods or conclusions. We excluded review papers. We classified responses and drivers under major themes (Figure 2; Table S1 in the Supplement in the online version of this article) using Google Forms. Some responses were further combined for presentation here; for example, predator-prey interactions and diet studies were combined as “trophic interactions” and sparsely studied responses such as harvest, movement, diversity, and thermal habitat were grouped under “other” (Table S1). Results from studies with multiple drivers, responses, or species were recorded individually, meaning that multiple tests were often recorded from the same studies. This included studies where multiple metrics within the same category of driver were tested, for example, testing multiple climate metrics.

RESULTS

We identified 1,232 tests from 370 papers to include in our final literature review (Table S1). Results were split fairly evenly between Walleye ($n = 613$) and Yellow Perch ($n = 619$). We identified relatively few results prior to the late 1990s, and the majority of comparisons came from 2016 (Figure 3). In part, this spike is due to the publication of a book on systems change in Oneida Lake (Rudstam et al. 2016). Studies on a few locations were well represented in the literature; 11% of all analyses were from Lake Erie, and another 17% were from Minnesota (including Red Lake, Mille Lacs, and all other inland lakes; Figure 4). Climate change was the most frequently studied driver ($n = 572$) and growth/condition was the most frequently studied response ($n = 297$). The most commonly reported relationship was “no effect” ($n = 522$, or 42% of analyses), usually because multiple variables were tested and only a few were found to be significant. Overall responses varied among studies for most species-response-driver combinations, with approximately equal frequencies of

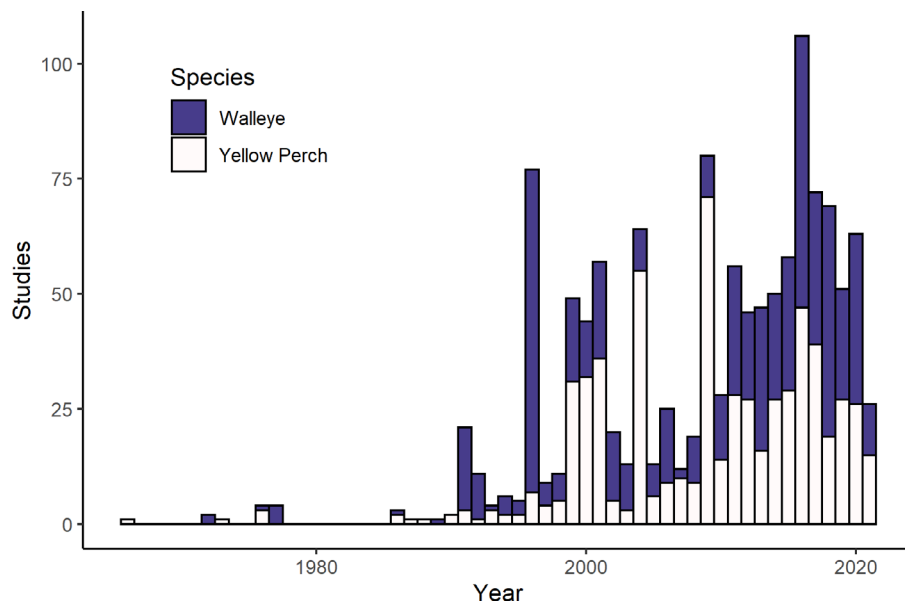


FIGURE 3. Number of analyses identified in the literature review by year of publication. Fill colors represent focal species.

positive and negative relationships documented in many cases (Figure 5).

Climate Change

The effects of climate on Walleye and Yellow Perch populations were highly variable (Figure 5) and differed among systems. No single directional effect was documented in the majority of cases. Variability in some cases stemmed from the use of different climate metrics across studies. Summarizing climate variables in a way that is ecologically meaningful is nontrivial and oftentimes not straightforward (Sofaer et al. 2017). Metrics of temperature used in statistical analyses included annual measures of temperature such as growing degree-days (e.g., Venturelli et al. 2010; Haxton 2015; Dembkowski et al. 2017), temperature conditions related to specific months (e.g., Cyterski and Spangler 1996; Ward et al. 2004; Lyons and Oele 2018), metrics related to temperature variability (e.g., Henderson and Nepszy 1988; Lyons and Welke 1996; Eldridge et al. 2015), metrics related to winter severity or ice cover (e.g., Farmer et al. 2015; Feiner et al. 2018; Marcek et al. 2021), and many others (Figure 2). Numerous studies tested multiple climate metrics as potential predictors, and frequently, many variables were found to have no effect. For example, Cyterski and Spangler (1996) conducted 57 statistical tests relating a number of climate metrics to various measures of Walleye growth in Red Lake, Minnesota. They identified 6 positive relationships, while the other 51 relationships were not significant. Some studies examined thermal habitat directly as a function of climate—that is, quantified the amount of habitat area in a lake that falls within a specified preferred temperature

range for Walleye or Yellow Perch. Perhaps counterintuitively, thermal habitat for coolwater fishes was generally predicted to increase with warming temperatures throughout much of North America due to the positive influence of longer growing seasons outweighing the negative influence of high temperature exceeding upper thermal limits (Fang et al. 2004; Cline et al. 2013; Hansen et al. 2019).

Recruitment.—Recruitment was the second most commonly studied response to climate drivers, with variable results (Figure 5). Of the 88 analyses focusing on Walleye, the majority (72%) documented no effect. The effects of climate on Yellow Perch recruitment were less frequently studied (33 tests), and here the most frequently documented response was positive (42% of tests), followed by no effect (33% of tests). Recruitment was measured at different life stages in different studies and thus comprises natural reproduction, growth, and survival to different age-classes and in some cases includes stocked fish. Similarly, climate and temperature can be summarized in nearly infinite ways, and some variability in results may have been due to different definitions of recruitment and/or climate. Still, the influence of several climate variables on recruitment were commonly tested.

Warmer winters and earlier ice-out dates were associated with lower recruitment of Walleye and Yellow Perch in several populations in diverse systems, including Nebraska reservoirs (DeBoer et al. 2013), inland lakes of Minnesota (Schneider et al. 2010), and the Great Lakes (Farmer et al. 2015; Bunnell et al. 2016; Dippold et al. 2020; Marcek et al. 2021). However, winter duration was not significantly related to Walleye recruitment to age 0 in Wisconsin lakes (Hansen et al. 2015a, 2017). In

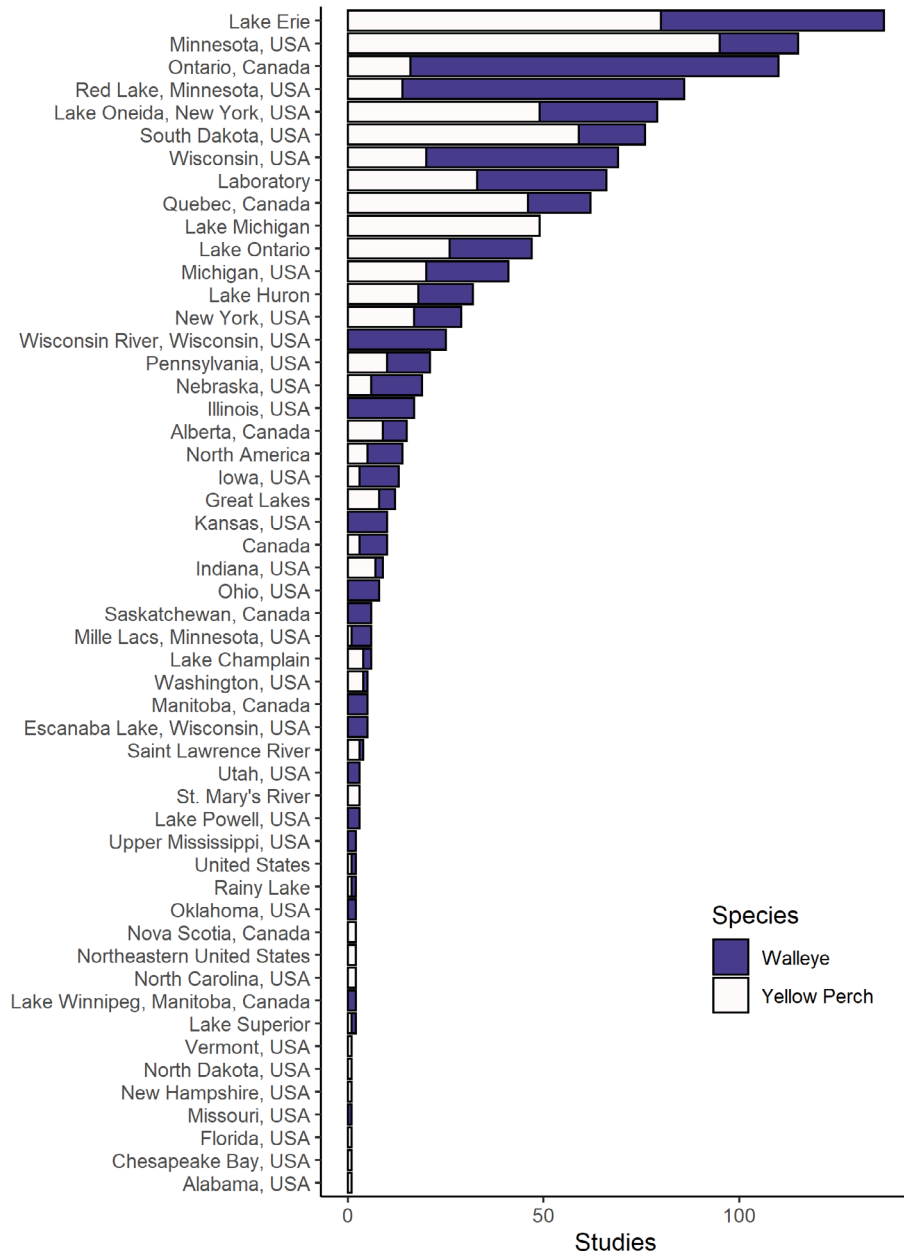


FIGURE 4. Number of analyses identified in literature review by location. Note that some specific locations are counted separately from the total from their state or province to highlight the number of studies on a single lake or river.

Minnesota's large lakes, no relationship was observed between recruitment and the severity of the winter preceding Walleye hatching, but winter severity in the year following hatching was negatively correlated with recruitment (Honsey et al. 2020).

Fast-warming springs were associated with higher Walleye recruitment in diverse ecosystems, including Lake Erie (Shuter et al. 2002; Zhao et al. 2013; but see Dippold et al. 2020), pools of the upper Mississippi River (Pitlo 2002), and South Dakota and Nebraska reservoirs (Graeb

et al. 2010; DeBoer et al. 2013). However, spring warming was not related to Walleye recruitment in Indiana reservoirs (Doll et al. 2015) or Wisconsin lakes (Hansen et al. 2015a). For Yellow Perch, spring warming rates negatively affected recruitment at swim-up larvae and pelagic juvenile life stages (Zhang et al. 2017), but overall, spring warming rates did not impact Yellow Perch recruitment in Lake Erie (Dippold et al. 2020). Variability in spring temperatures can negatively affect Walleye and Yellow Perch recruitment (Serns 1982; Hansen et al. 1998), although

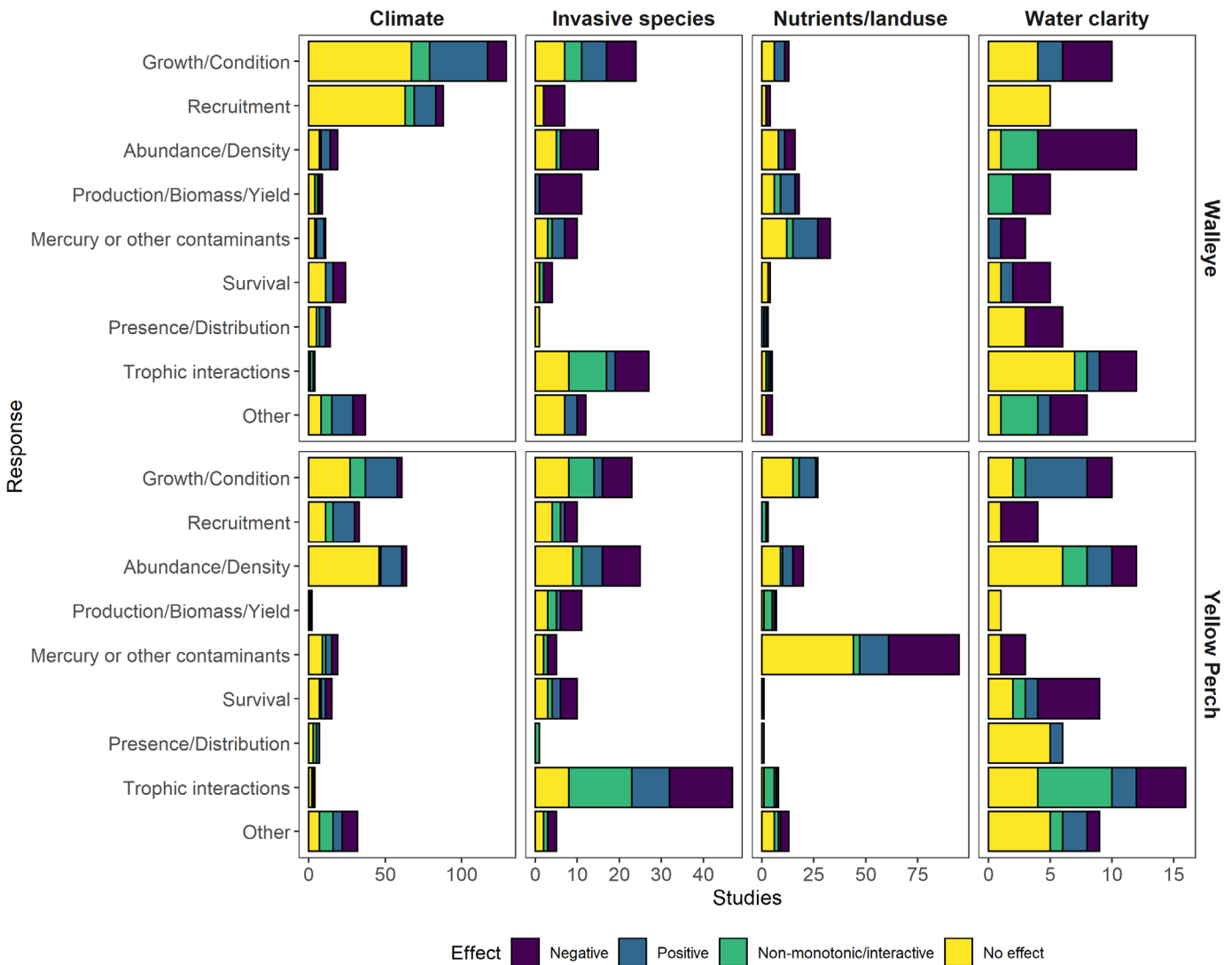


FIGURE 5. Summary of literature review results showing the number and direction of associations between ecosystem change drivers and various population or individual responses for Walleye (top panels) and Yellow Perch (bottom panels). Note the different horizontal axis scales.

again this effect appears to vary among systems (Kallemeyn 1987; Quist et al. 2003; Hansen et al. 2015a) and even among time periods within a single lake (Shaw et al. 2018). Laboratory studies showed mixed results of variability in temperature during critical periods on larval survival and growth of both Walleye and Yellow Perch (e.g., Jansen et al. 2009; Coulter et al. 2016).

Recruitment was also impacted by summer temperatures and growing degree-days, and this relationship varied among locations. Warmer temperatures and longer growing seasons positively affected Walleye recruitment in Minnesota's largest Walleye lakes (Schupp 2002; Honsey et al. 2020) and negatively affected recruitment to the fall of age-0 Walleye in small lakes (<500 ha) but had no effect in large lakes in Wisconsin (Hansen et al. 2015a), in

Lake Escanaba (Shaw et al. 2018), or in the Wisconsin River (Lyons and Oele 2018). Furthermore, the direction of the correlation between degree-days and recruitment varied depending on the abundance of Largemouth Bass *Micropterus salmoides* (Hansen et al. 2018). Modeling suggests that recruitment responses of Walleye in Lake Erie to temperature could be positive, negative, or nonexistent depending on other factors (Jones et al. 2006). Temperature was not related to Yellow Perch recruitment in Indiana lakes (Feiner et al. 2019) or in southern Lake Michigan (Beletsky et al. 2007; Redman et al. 2011; Forsythe et al. 2012), although warmer temperatures related to stronger Yellow Perch year-class strength in the St. Lawrence River (Hudon et al. 2010), in Lake Erie (Jarrin et al. 2015), in Lake Michigan (Bunnell et al. 2016), and

in stocks throughout the Great Lakes (Honsey et al. 2016). Various aspects of precipitation, water levels, and water flow were also related to recruitment for both Walleye and Yellow Perch but were frequently hypothesized to have modulating effects on the influence of temperature and spring warming rates on recruitment (Hudon et al. 2010; Doll et al. 2015). Where precipitation or river flow were reported to have more direct effects on recruitment, the mechanism was largely related to water levels (Bunnell et al. 2016; Dembkowski et al. 2017).

Abundance, biomass, and production.—As with recruitment success, the relationship between temperature and Walleye abundance, biomass, and/or production appears to be nonlinear and potentially interactive. Interactions among temperature, water clarity, dissolved oxygen, system productivity, and prey availability, as well as the temperature range studied, seemed especially important in determining Walleye and Yellow Perch abundance or biomass responses (e.g., Minns and Moore 1992; Pandit et al. 2013; Gutowsky et al. 2019; Hossain et al. 2019).

The most common response of Walleye biomass or abundance to climate was no effect (39% of tests), while positive and negative results were equally prevalent in the literature (25% of tests, each). Higher summer temperatures were associated with declining Walleye catch rates in some systems (e.g., Robillard and Fox 2006; Haxton 2015; Kraus et al. 2017), but in other cases, warmer temperatures led to higher Walleye catch rates (Schupp 2002; Berger et al. 2012). Spring warming rates were positively related to the abundance of age-0 Walleye in western Lake Erie (Roseman et al. 1999), while other studies detected no relationship between Walleye abundance and temperature, illustrating the complexity of this relationship (Hansen et al. 2019; Pennock and Gido 2021). Jarvis et al. (2020) found that Walleye production was lower in lakes with higher degree-days in Ontario, despite growth being higher in these lakes. They hypothesized that lower production and higher growth at high temperatures reflects a trade-off in life history traits at warmer temperatures (Lester et al. 2014). Walleye production in Ontario was also higher in lakes with lower annual precipitation (Jarvis et al. 2020), in contrast to earlier work relating Walleye abundance to higher water levels (Chevalier 1977). These differences may reflect the complex relationships among precipitation, river flow, runoff, and thermal habitat (Jarvis et al. 2020).

For Yellow Perch, the majority of tests examining climate effects on abundance or biomass did not identify any relationship (71%), though two-thirds of the tests came from a single study focusing on glacial lakes of South Dakota (Ward et al. 2004). When an effect of temperature on abundance or biomass was documented, it was more likely to be positive (21% of tests; e.g., Stacy-Duffy et al. 2020) than negative (6% of tests; e.g., Magee

et al. 2018). In contrast, precipitation and water levels were positively associated with Yellow Perch abundance (Gaeta et al. 2015; McLean et al. 2016) and recruitment (Bunnell et al. 2016).

Growth.—Growth and condition were the most commonly studied responses to climate change. Fish growth responses to temperature were highly variable among studies, although very few negative responses were observed for either species (Figure 5). For Walleye, the majority of studies reported a nonexistent relationship (52% of tests identified no effect; e.g., Hall and Rudstam 1999; Rudstam et al. 2016). When a relationship was present, it was more frequently positive (29% of tests) than negative (9% of tests). Some variability in results may be attributed to growth being measured in different ways and for different life stages. Furthermore, fish growth responses to temperature are decidedly nonmonotonic, with increasing positive responses up to a threshold (optimal) value, above which growth rapidly declines (Kitchell et al. 1977). Thus, we would expect positive effects of temperature on growth at temperatures below the optimum and negative effects above the optimum. Indeed, temperature negatively affected Walleye growth rate potential at very high temperatures, such as those observed in Utah reservoirs (Budy et al. 2011) and in power plant thermal discharges (Coulter et al. 2014). Conversely, temperature positively affected early life growth in diverse systems, including a reservoir in Nebraska (Uphoff et al. 2013), multiple lakes across Ontario (Shuter et al. 2002), and northern Wisconsin lakes (Pedersen et al. 2017).

Yellow Perch growth was more frequently positively than negatively related to temperature (34% and 5% of 61 tests, respectively), but again, many studies (44%) reported no effect (Figure 5). Similar to Walleye, Yellow Perch growth responses to temperature depended on life stage. For example, in Lake Ontario, temperature explained variation in growth of age-0 Yellow Perch but did not affect growth rates at older life stages (O’Gorman and Burnett 2001). We also observed context dependence within a single study. Summer temperature was negatively correlated with Yellow Perch body condition in Lake Ontario but positively correlated in Lake Erie during the same time period (Crane et al. 2015). The range of temperatures examined also influenced results. Manning et al. (2014) found that temperature was the least influential predictor of growth and starvation out of all predictors included in a simulation model. They hypothesized that growth was not sensitive to a 10% change in temperature because this is within the bounds of normal fluctuations.

Many growth studies relied on bioenergetics models (Kitchell et al. 1977; Hanson et al. 1997; Deslauriers et al. 2017), in which the effect of temperature on growth was, by definition, nonmonotonic. In reality, growth responses to temperature depend on behavioral thermoregulation,

prey availability, magnitude of temperature increase, and individual species tolerances. Growth response could be positive or negative depending on prey availability and whether species track preferred temperatures by changing behavior (Kao et al. 2015). Madenjian et al. (2018) concluded that temperature is less important than food availability in explaining variation in Walleye growth in Lakes Erie and Huron. Bioenergetics models also predict seasonal differences in responses of growth to temperature. The overall response of fish growth to increasing temperatures may depend on whether they can survive potential periods of summer thermal stress in order to experience the growth benefits of warming in other seasons (Quist et al. 2002; Budnik et al. 2021).

Diet and trophic interactions.—Trophic interactions were the most infrequently investigated responses to climate change (Figure 5). However, both direct and indirect impacts of climate on Walleye and Yellow Perch were described. Direct responses to changes in temperature included shifts in prey type (Goto et al. 2017) and volume consumed (Kocovsky and Carline 2001) as well as digestion rates (Legler et al. 2010) of prey items. Increased instances of predation on Yellow Perch (by Northern Pike *Esox lucius* and Largemouth Bass) in response to increased temperatures were also reported (Breeggemann et al. 2016). However, climatic shifts were also found to have a moderating effect on other driver relationships; for example, changes in water levels and temperatures shifted habitat availability for prey species that then increased in Walleye diets due to opportunistic feeding (Bryan et al. 1995).

Mercury and other contaminants.—Climate affects mercury concentrations in aquatic environments and bioaccumulation rates in the tissues of fish (Macdonald 2005; Balogh et al. 2006; Sumner et al. 2020). Both temperature and precipitation or water levels were associated with mercury concentrations in Walleye and Yellow Perch, once again with variable results. Of the 11 tests that focused on climate impacts on contaminants in Walleye, 45% found positive relationships and 36% found no relationship. For Yellow Perch, 47% of 19 analyses reported no relationship between climate variables and contaminants, and positive and negative relationships were reported at equal frequencies (21% of tests, each). Higher temperatures were associated with higher mercury concentrations in both Walleye and Yellow Perch in locations around the Nearctic (Evans et al. 2005a; Chen et al. 2018; Sorensen 2019), but the opposite was true in northern Minnesota lakes (Kolka et al. 2019). The connection between temperature and fish growth muddies the relationship between temperature and mercury bioaccumulation. For example, warmer winters can increase growth rates of Walleye, which results in lower concentrations of mercury in their tissues (Lucotte et al. 2016). However, higher summer temperatures can

increase mercury methylation and availability as well as fish metabolic rates, thus increasing concentrations of mercury in fish tissues (Harris and Bodaly 1998; Evans et al. 2005b).

Climate impacts include both precipitation/water levels and temperature. Higher water levels were associated with higher mercury in Walleye tissues across hundreds of Wisconsin lakes (Watras 2020). Water level effects on mercury concentrations in Yellow Perch were inconsistent. Sorensen (2019) reported higher mercury concentrations at higher water levels across Minnesota, contrary to findings by Riggs et al. (2017). The relationship between water levels and mercury concentrations in Yellow Perch was inconsistent even within a single system (Larson et al. 2021).

Aquatic Invasive Species

The most consistent responses of Walleye and Yellow Perch to ecosystem change were observed for aquatic invasive species (Figure 5). Negative responses were common among diverse systems and invasive species. Many different invasive species were studied (Figure 2), and as a result, there are few cases of replication to assess context dependence on an individual species level. We report below on the most commonly studied invasive species and responses.

Recruitment.—We documented relatively consistent negative relationships (five of seven tests) between Walleye recruitment and multiple different invasive species (e.g., dreissenid mussels [Hoyle et al. 2008], Rainbow Smelt *Osmerus mordax* [Mercado-Silva et al. 2007]). Yellow Perch recruitment responses to invasive species were more variable among both invasive species and locations (40% no effect, 30% negative, 20% positive, 10% nonmonotonic). For example, Yellow Perch recruitment in Lake Michigan was negatively associated with invasive Alewife *Alosa pseudoharengus* (Redman et al. 2011; Forsythe et al. 2012) but not related to Round Goby *Neogobius melanostomus* (Forsythe et al. 2012). Variable responses to dreissenid mussels were also observed in different basins of Lake Erie (Zhang et al. 2018) and in Oneida Lake (Rutherford and Rose 2016).

Abundance, biomass, and production.—Walleye abundance, biomass, and/or production was negatively associated with the invasion of multiple invasive species (73% of 26 tests identified negative effects), including dreissenid mussels (e.g., Hoyle et al. 2008; Nienhuis et al. 2014; Irwin et al. 2016; Hossain et al. 2019), Rainbow Smelt (Roth et al. 2010; McDonnell and Roth 2014), and Alewife (Makarewicz et al. 2016). In some cases, the impacts of the same invasive species varied among systems. The occurrence of nonnative Smallmouth Bass *Micropterus dolomieu* was negatively correlated with Walleye abundance in Ontario lakes (Van Zuiden and Sharma 2016),

though no effect of Smallmouth Bass on Walleye abundance or other population parameters was found in South Dakota lakes and reservoirs (Wuellner et al. 2011; Galster et al. 2012).

Reported relationships between Yellow Perch abundance and invasive species were more variable than those of Walleye. Negative relationships between Yellow Perch abundance and invasive species were reported in 53% of 36 tests and included negative impacts of Alewife (O’Gorman and Burnett 2001; Madenjian et al. 2002; Bunnell et al. 2006) and dreissenid mussels (Irwin et al. 2016; Rutherford and Rose 2016; Hossain et al. 2019). As with Walleye, the impacts of some invasive species on Yellow Perch populations varied. For example, Round Goby influence on Yellow Perch abundance in Lake Michigan varied with life stage (Stacy-Duffy et al. 2020), whereas the presence of Round Goby led to increases in Yellow Perch abundance in Lake Ontario (Hoyle et al. 2017). Similarly, in Oneida Lake, both positive and negative effects of zebra mussels *Dreissena polymorpha* were reported depending on measure of impact, life stage, and time period (Rutherford et al. 1999; Mayer et al. 2001; Irwin et al. 2016). Invasive species did not affect Yellow Perch abundance in 33% of tests, including Common Carp *Cyprinus carpio* in South Dakota (Weber and Brown 2011, 2018), White Perch *Morone americana* in Lake Erie (Guzzo et al. 2013), and Round Goby in St. Marys River (Schaeffer et al. 2017).

Growth.—The influence of invasive species on growth was approximately equally likely to be positive, negative, or have no effect for both Walleye and Yellow Perch (Figure 5). Negative effects were reported in 29% of the 24 tests examining the influence of invasive species on Walleye growth, including slower growth of young Walleye in the presence of dreissenid mussels (e.g., Roseman et al. 1999; Hansen et al. 2020). In 29% of tests, no effect was reported on Walleye growth. The effects of some invasive species varied by life stage and/or location. For example, Walleye body condition was generally unaffected by Round Goby invasion in Lakes Erie and Ontario, with the exception of the largest Walleye in Lake Ontario, for whom body condition increased (Crane et al. 2015).

The impacts of invasive species on Yellow Perch growth exhibited a range of different responses, with a similar proportion of the 23 tests showing a negative effect (30%), nonmonotonic/interactive effect (26%), or no effect at all (35%). Studies that reported a negative or nonmonotonic relationship mostly involved invasive fish (e.g., Ruffe *Gymnocephalus cernua* [Fullerton et al. 2000] and Rainbow Smelt [Hrabik et al. 2001]). The effects of invertebrate invasive species, including dreissenid mussels and spiny water flea *Bythotrephes longimanus*, on Yellow Perch growth were documented to be negative (e.g., spiny water flea; Staples et al. 2017), positive (e.g., dreissenid mussels; Mayer et al. 2000), or showed no effect (e.g., dreissenid mussels and

spiny water flea; Hansen et al. 2020). Only two studies (9%) reported a positive relationship between species invasion (i.e., zebra mussels) and Yellow Perch growth (Thayer et al. 1997; Rutherford and Rose 2016).

Diet and trophic interactions.—Diet, stable isotope composition, and trophic interactions (e.g., foraging success) were by far the most frequently examined responses to species invasion (Figure 5). As with other responses and drivers, results varied, showing that Walleye and Yellow Perch diets changed (e.g., Sheppard et al. 2015; Prestie et al. 2019) or did not change (e.g., Mayer et al. 2000; Kreps et al. 2016) in the presence of invasive species. Diet changes could result from direct consumption of the invasive species; for example, Walleye diets in the north basin of Lake Winnipeg consisted almost entirely of invasive Rainbow Smelt (Sheppard et al. 2015). In other cases, competition or exclusion from certain habitats resulted in diet shifts. For example, age-0 Yellow Perch decreased their consumption of benthic prey items, such as chironomids and amphipods, in the presence of Round Goby (Houghton and Janssen 2015). In some cases, the presence and density of invasive species also influenced foraging success (e.g., Cobb and Watzin 2002) or predation risk (Morbey et al. 2007) of Yellow Perch. The wide variety in measures of impact and the diversity of invasive species examined makes it difficult to assess context dependence in this case.

Mercury and other contaminants.—Species invasions were associated with changing contaminant loads in 7 out of 10 cases for Walleye and in 3 out of 5 cases for Yellow Perch (Figure 5). For Walleye, increased and decreased contaminants were associated with species invasions at equal frequencies (30% of tests). For Yellow Perch, sample size was low and no positive relationships were observed. The relationship between species invasion and chemical contamination in Walleye and Yellow Perch tissues appears to be a function of bioaccumulation as invasive species contribute to the diets of fishes at multiple trophic levels. For example, PCB levels in Walleye decreased when their diets switched from primarily higher-contaminated Alewife to lower-contaminated Yellow Perch (Jude et al. 2010). However, dreissenid mussels did not affect the bioaccumulation of polybrominated diphenyl ethers (flame retardants) or α - and γ -chlordane levels in Walleye and Yellow Perch in Lake Erie (Azim et al. 2011; Perez-Fuentetaja et al. 2015). In both cases, invasive prey were not found to accumulate high levels of contaminants.

Nutrients and Land Use

We documented inconsistent responses of Walleye and Yellow Perch to specific nutrient and land use drivers (Figure 5). The effects of changing nutrient loading and land use practices were difficult to summarize and to interpret due to differences in metrics used to define them and relationships between land use and nutrients. For example,

increased forested land cover could influence phosphorus or dissolved organic carbon (DOC) inputs and concentrations in lakes and rivers, but measurements may not have been taken for all parameters to determine the specific mechanisms influencing Walleye and Yellow Perch.

Recruitment.— Documented relationships between land use or nutrients and recruitment were rare, with low sample sizes for both Walleye and Yellow Perch (four and three tests, respectively; Figure 5). No positive relationships were observed between any nutrient or land use variable and recruitment of either species. Of the information available, external nutrient loading, specifically total phosphorus, was found to negatively impact Walleye and Yellow Perch year-class strength (Culver et al. 2009; Fielder and Baker 2019). Agricultural land use in a watershed was also linked to eutrophication and was found to have a nonmonotonic (dome-shaped) relationship with Yellow Perch recruitment in Lake Erie (Dippold et al. 2020).

Abundance, biomass, and production.— Land use and nutrient loading effects on abundance, biomass, and/or production were commonly studied, and the most common result was no effect (41% and 37% of tests for Walleye and Yellow Perch, respectively). Phosphorus, eutrophication, and agricultural land use were commonly studied drivers, and their effects on Walleye and Yellow Perch abundance and biomass were variable depending on the range of values studied and interactions with other drivers. When directional effects were observed, they were approximately equally likely to be positive or negative for both species (29% positive and 21% negative for Walleye; 22% positive and 22% negative for Yellow Perch). The range of values studied was important in determining results. For example, phosphorus was positively associated with Walleye catch rates within and across lakes in Ontario (Robillard and Fox 2006) but negatively associated with Walleye catch rates at extremely hypereutrophic levels in Lake Moses, Washington (Welch 2009). Similarly, in Ontario lakes, DOC exhibited a nonlinear relationship with Walleye production, with production peaking at intermediate levels (Jarvis et al. 2020). The strength and direction of the relationship between phosphorus and both Walleye and Yellow Perch biomass varied based on life stage, nutrient management regimes, and invasive species statuses in both Lake Ontario and Lake Erie (Zhang et al. 2016; Hossain et al. 2019).

Other nutrients and measures of land use were also related to Walleye and Yellow Perch abundance in variable ways. Dissolved organic carbon concentrations were negatively related to Walleye and weakly negatively related to Yellow Perch relative abundance in Quebec lakes (Benoit et al. 2016). Neither fire nor logging influenced Walleye or Yellow Perch catch rates in Quebec lakes (St-Onge and Magnan 2000). Land cover alone had no effect on Walleye biomass, but declining forest cover amplified the effect of

climate change and decreased the negative effect of zebra mussels in Ontario lakes (Gutowsky et al. 2019).

Growth.— Growth responses to nutrients and land use were most frequently nonexistent for Walleye (46% of 13 tests) and Yellow Perch (56% of 27 tests; Figure 5). Overall, the effects of nutrient loading and eutrophication on Walleye growth appear to be nonmonotonic, such that growth increases with increasing productivity to a point then declines as hypereutrophic conditions are reached (Hayward and Margraf 1987). For example, total phosphorus was associated with increased lengths and weights of Walleye in treatment groups with phosphorus additions (Fox et al. 1992), yet Walleye growth was also negatively related to phosphorus at very high levels (Budy et al. 2011).

The effects of nutrients and land use on growth were more commonly studied for Yellow Perch than for Walleye. Here, most tests showed no effect, though positive responses were frequently identified (30% of tests). For instance, Yellow Perch growth was positively related to total phosphorus in Minnesota lakes (Kolka et al. 2019) and in Lake Ontario (O’Gorman and Burnett 2001). The effects of nutrients other than phosphorus on growth were infrequently studied, but a few examples exist. Walleye growth was negatively related to DOC concentrations in Quebec lakes, but no such relationship was observed for growth of Yellow Perch (Suns and Hitchin 1990; Benoit et al. 2016). Reductions in forest and wetland land cover were associated with reduced terrestrial inputs and subsequent reduced weight of age-0 Yellow Perch in Ontario (St-Onge and Magnan 2000; Tanentzap et al. 2014).

Diets and trophic interactions.— Very few studies examined the impacts of nutrient loading on Walleye ($n = 5$) or Yellow Perch ($n = 8$) trophic interactions, making generalizations difficult. Nonmonotonic or interactive effects of nutrients or land use on trophic interactions were most commonly observed for Yellow Perch (62% of tests). Various aspects of diet composition were impacted in Yellow Perch, including larval and juvenile diet diversity decreasing in logged versus unperturbed systems in Quebec lakes (Leclerc et al. 2011). In Ontario lakes, the proportion of offshore-derived carbon in Walleye diets was negatively related to DOC but not related to total phosphorus (Tunney et al. 2018). However, phosphorus was related to an increase in prey biomass in Walleye stomach contents in rearing ponds (Fox et al. 1992).

Mercury and other contaminants.— Mercury concentrations were the most frequently documented response to nutrients and land use for both Walleye ($n = 33$) and Yellow Perch ($n = 95$; Figure 5). Mercury methylation depends on water chemistry, and specifically DOC, pH, and oxygen availability (Korthals and Winfrey 1987; Gilmour and Henry 1991; Watras et al. 1995). For both species, the most common relationship between nutrients or

land use and contaminants was no effect (36% and 46% of tests for Walleye and Yellow Perch, respectively). Positive relationships between contaminants and nutrient levels were frequently identified for Walleye (36% of tests), whereas negative relationships were frequently observed for Yellow Perch (36% of tests). Several papers quantified positive correlations between DOC and mercury in fish tissues (Wren et al. 1991; Parks et al. 1994; Rencz et al. 2003), though negative correlations were found between DOC and mercury concentrations in Yellow Perch eggs in Wisconsin lakes (Hammerschmidt et al. 1999). Nonmonotonic (quadratic) relationships between DOC and Walleye mercury levels were also observed in northern Ontario lakes (Sumner et al. 2020). To add further complexity, Driscoll et al. (1995) found that very high concentrations of DOC were associated with decreased mercury in Yellow Perch because mercury will bind better to DOC at high concentrations, leading to decreased availability of mercury in the system.

Separating the direct effects of nutrients and land use on mercury per se from indirect effects via influences on fish growth is challenging and requires innovative statistical methods and experimental design. For example, Thomas et al. (2020) used structural equation modeling and concluded that in stratified lakes, DOC was directly positively related to Walleye mercury levels but indirectly negatively related to mercury concentrations due to negative effects on fish weight. Decreased forest cover was associated with increased DOC and higher mercury in Walleye in Quebec lakes (Garcia and Carignan 2005). Greater wetland area was found to be positively correlated with mercury for both Walleye and Yellow Perch (Simonin et al. 2008; Dittman and Driscoll 2009). Greenfield et al. (2001) found a similar relationship between mercury and wetland area but also found that water chemistry and fish growth had a greater impact on mercury concentrations.

Phosphorus and eutrophication were related to mercury concentrations of Walleye and Yellow Perch in variable ways. For instance, mercury concentrations in Walleye were highest in the least agricultural watersheds in Iowa, suggesting a negative relationship between nutrient loading and mercury (Mills et al. 2019). In contrast, system phosphorus was not related to mercury concentrations in fish tissues in a variety of systems (Parks et al. 1994; Ethier et al. 2008; Stone et al. 2011; Kolka et al. 2019). Indirect effects of nutrients on mercury via fish growth may also confound these relationships as higher ecosystem productivity can lead to higher fish weight or biomass and therefore higher mercury concentrations (Essington and Houser 2003; Miller et al. 2012).

Water Clarity

Water clarity was related to Walleye and Yellow Perch populations through a variety of pathways, with few

positive effects of water transparency documented, especially for Walleye (Figure 5). Walleye are low-light specialists due to their specialized retinal structure, and these structures develop when Walleye are approximately 60 mm long (Vandenbyllaardt et al. 1991). Therefore, direct impacts of water clarity on Walleye populations are expected to be stronger after they reach this size. Yellow Perch do not have a similar retinal structure, and therefore we expected fewer direct effects of water clarity on Yellow Perch populations a priori. At high levels of water transparency, exposure to UV radiation can cause significant mortality at egg and larval stages of Yellow Perch (Huff et al. 2004), although the effects of UV on Walleye and Yellow Perch populations have not been widely studied (but see Williamson et al. 1997).

Recruitment.—Investigations of the effects of water clarity on recruitment were limited for both Walleye ($n = 5$) and Yellow Perch ($n = 4$; Figure 5). However, in every case, water clarity was found to have no effect on Walleye recruitment. The paucity of information on water clarity and Walleye recruitment could be because the effects of clarity have not been well studied or could reflect that the foraging advantage of Walleye in turbid waters is not present until later life stages (Vandenbyllaardt et al. 1991). The only documented effects of water clarity on Yellow Perch recruitment in our review came from three studies documenting higher recruitment associated with the turbid Maumee River plume in Lake Erie (Reichert et al. 2010; Carreon-Martinez et al. 2015; Jarrin et al. 2015), which may have limited transferability to other ecosystems.

Abundance, biomass, and production.—The documented relationships between water clarity and abundance, biomass, and/or production were among the most consistent in our review (Figure 5). Walleye responses to water clarity were primarily negative (65% of 17 tests). Increased water clarity has been associated with reduced habitat area and abundance of Walleye in large, productive lakes such as Lake Erie (Roseman et al. 2005; Pandit et al. 2013) and Minnesota's Mille Lacs (Hansen et al. 2019), as well as smaller, inland lakes of varying productivity in Ontario (Robillard and Fox 2006; Tunney et al. 2018). In general, Walleye production is highest at low to moderate Secchi depths, although the effect of clarity depends on lake morphometry and temperature (Lester et al. 2004; Geisler et al. 2016; Jarvis et al. 2020).

Yellow Perch abundance and production responses to water clarity were more variable (Figure 5). In a majority of cases (54%), water clarity had no effect on Yellow Perch abundance or biomass (e.g., Tremblay and Richard 1993; Bertolo et al. 2012; Parker et al. 2012). Higher water clarity was associated with higher abundance in only two cases across both species; both were Yellow Perch in Lake Erie (Reichert et al. 2010; Collingsworth and Marschall 2011).

Growth.—Water clarity influences on Walleye and Yellow Perch growth were inconsistent (Figure 5). Water clarity was equally likely to negatively influence Walleye growth or to have no effect (40% of tests in both cases). Negative effects of water transparency on larval Walleye growth were documented in several laboratory studies (e.g., Bristow et al. 1996; Rieger and Summerfelt 1997; Clayton et al. 2009); however, no effect of clarity on Walleye growth was documented in several field-based studies (Craig and Babaluk 1989; Uphoff et al. 2013; Pedersen et al. 2017; but see Rudstam et al. 2016). Positive relationships between water clarity and Yellow Perch growth were somewhat more consistent across systems (50% of tests; e.g., Manning et al. 2013, 2014; Withers et al. 2015), although effects may depend on life stage and water clarity (Boisclair and Rasmussen 1996; Manning et al. 2014). The effects of water clarity on fish growth are not always straightforward and it can be difficult to disentangle the effects of nutrients, land use, invasive species (e.g., zebra mussels), and water clarity on fish growth. To this end, Giacomazzo et al. (2020) used structural equation modeling to separate direct from indirect effects and estimated a positive relationship between water clarity and Yellow Perch growth, despite no effect of nutrient loading on growth.

Diet and trophic interactions.—The influence of water clarity on diet and trophic interactions was once again variable for both Walleye and Yellow Perch (Figure 5). The specialized retinal structure in the eyes of Walleye increases their visual acuity in dim light, and as a result, Walleye feeding efficiency and foraging success increases in turbid water (Vandenbyllaardt et al. 1991; Bristow et al. 1996; Einfalt et al. 2012). Cannibalism was also reported to be reduced in turbid waters (Bristow et al. 1996), but in another case, rates of cannibalism were not affected by water clarity (Rieger and Summerfelt 1997). The superior foraging capacity of Walleye in turbid water can translate into differences in diet and resource use across a clarity gradient (Tunney et al. 2018), but many studies (58%) reported no differences in Walleye diets or resource use as a function of water clarity (e.g., Stasko et al. 2015; Edmunds et al. 2019; Nanayakkara et al. 2021).

Many different effects of water clarity on Yellow Perch foraging and diets were reported, with context-dependent results. Yellow Perch selected for smaller prey in both lab and field studies in Oneida Lake as clarity increased (Mills et al. 1986). Laboratory studies showed that different types of turbidity (e.g., sediment versus algal) influenced foraging in opposing directions: larval feeding rates increased with increasing sediment-driven turbidity but decreased with algal-driven turbidity (Manning et al. 2014). Other studies demonstrated that Yellow Perch diets and foraging rates were nonlinearly related to turbidity and depended on factors such as life stage, the presence of

predators, and zebra mussels (Mayer et al. 2001; Wellington et al. 2010; Pangle et al. 2012).

Mercury and other contaminants.—Relatively few studies examined the impacts of water clarity on contaminants—only three tests were identified for both Walleye and Yellow Perch (Figure 5). Two of the three studies on Walleye identified negative relationships between mercury content of tissues and water clarity in inland lakes (Parks et al. 1994; Simonin et al. 2008), although a positive correlation was documented in the Laurentian Great Lakes (Lepak et al. 2018). Mercury concentrations in Yellow Perch were negatively correlated with water clarity in two studies on Minnesota lakes (Riggs et al. 2017; Kolka et al. 2019) but were not related in New York lakes (Simonin et al. 2008).

DISCUSSION

The published literature assessing the effects of ecosystem change on Walleye and Yellow Perch populations is substantial. In the majority of driver–response combinations, we documented positive, negative, nonlinear, and no relationships, in many cases in roughly equal proportions. However, a few relationships between ecosystem change and Walleye and Yellow Perch populations were relatively consistent. Invasive species were more negatively associated with Walleye recruitment, abundance, and production/biomass, despite the numerous different invasive species considered. This could reflect publication or funding bias—researchers are perhaps more likely to examine the effects of invasive species in scenarios where negative impacts are suspected a priori. However, published Yellow Perch responses to invasive species were more variable, so it is possible that the consistent response of Walleye is a reflection of their higher sensitivity to invasive species. Water clarity effects on Walleye abundance, biomass, and production were also consistently negative or nonlinear, perhaps reflecting the physiological adaptation of Walleye to turbid conditions (Brackevelt et al. 1989; Vandenbyllaardt et al. 1991).

Small sample sizes for many driver–response combinations made it difficult to distinguish true context dependence resulting from higher-order interactions from nonmonotonic responses across environmental gradients or from apparent context dependence due to differences in statistical methodology or spurious correlations. One challenge was that ecosystem change drivers were defined and quantified differently among studies. For example, the effect of temperature or climate was assessed in different seasons and was quantified using different metrics (e.g., maximum, mean, variability). Of course there is no single measure of “temperature” that an organism living in a fluctuating environment experiences, and it is reasonable that different researchers quantify temperature effects in different ways.

However, such variability makes it difficult to assess similarities and differences among systems. Our review suggests that future investigators may want to choose metrics for quantifying environmental change and species responses that are consistent with those reported in the literature to enable comparisons among studies and identification of true context dependence. Commonly identified drivers and responses are documented in our results, and we refer the reader to the relevant driver–response combinations for specific metrics that have been commonly studied. For example, degree-days are a common measure that were used in many studies of temperature. For nutrients and land use, direct measurements of nutrient concentrations are likely to provide greater mechanistic understanding. Otherwise, identifying plausible mechanisms to explain relationships as they relate to water chemistry when land cover is used as a surrogate may facilitate greater comparability. Responses of Walleye and Yellow Perch were also quantified in numerous ways. For example, abundance might be measured using mark–recapture population estimates or population estimates generated from statistical catch-at-age models or as relative abundance quantified by catch per unit effort of different gears. Such differences are in part due to variability in monitoring programs and are unlikely to be standardized across locations. In contrast, growth measurements are more consistent across studies and also provide high statistical power for detecting the effects of ecosystem change (Carpenter et al. 1995).

Some drivers of ecosystem change were consistently defined and revealed nonlinear or context-dependent responses of Walleye or Yellow Perch. Temperature effects are especially variable in strength and magnitude even when defined similarly, which may be indicative of the nonlinear relationship between temperature and most population parameters. For example, growing degree-days are an integrative measure of temperature that has been linked to Walleye and Yellow Perch recruitment (e.g., Redman et al. 2011; Hansen et al. 2015a; Honsey et al. 2020) and growth (e.g., Post and McQueen 1994; Venturelli et al. 2010; Stacy-Duffy et al. 2021) across a variety of systems. The effect of growing degree-days on Walleye recruitment appears to be both nonmonotonic and context dependent in that the direction of effect varies with lake size and location (Hansen et al. 2015a; Honsey et al. 2020). Similarly, the effects of nutrients, including total phosphorus and DOC, on Walleye and Yellow Perch growth and abundance vary in direction depending on nutrient concentrations and other factors such as invasive species (e.g., Zhang et al. 2016; Hossain et al. 2019).

Ecosystem change means that multiple components of connected systems are changing simultaneously, and as a result it can be difficult to disentangle the impacts of multiple variables. Overwinter mortality can be negatively correlated with winter severity, but this effect depends on size,

prey availability, and metabolic rate (Hurst 2007). Additionally, multiple stressors and their interactions can produce unexpected effects. For example, Gutowsky et al. (2019) found that lower forested land cover in a watershed reduced the negative impact of zebra mussels on Walleye biomass but amplified the effect of climate change. Ecosystem change might also impact different life stages differently. Total phosphorus and temperature influenced growth of age-0 Yellow Perch but did not affect older life stages, even for the same lake and years (O’Gorman and Burnett 2001). It is also important to consider interactions between Walleye and Yellow Perch when evaluating the effects of ecosystem change on either population. For example, predation by Walleye can be a major source of mortality for juvenile Yellow Perch and Walleye (Chevalier 1973; Forney 1974), and the impacts of ecosystem change on Yellow Perch may be either compounded or counterbalanced by the impacts of the same change on Walleye (Rutherford et al. 1999). Finally, the importance and impact of system change may vary over time within a population, as was the case for the impact of river discharge on Yellow Perch recruitment in Lake Erie (Marcek et al. 2021).

As documented in this review, we may observe different relationships in different locations or time periods, but it is unclear whether these differences result from apparent context dependence related to statistical methods, the range of variables studied, or mechanistic context dependence due to ecologically relevant interactions. In a recent review of context dependence in ecological relationships, Catford et al. (2021) offer several useful suggestions for designing experiments to increase mechanistic understanding of context dependence, including clearly identifying the range of variables studied, incorporating interactions into statistical models, and focusing on effect sizes rather than statistical significance. We add to those suggestions here, recognizing that the bulk of our understanding of the effects of ecosystem change on Walleye and Yellow Perch come from observational studies rather than controlled experiments. We also recognize that in many cases, Walleye and Yellow Perch fisheries are managed at the lake or stock level, and understanding the dynamics of a single system and predicting responses to management or environmental change is the primary goal. Still, single-system studies frequently rely on correlation, and the strength of inference can be much improved by assessing the consistency of relationships across systems (Hilborn 2016). Furthermore, in a rapidly changing world, relationships themselves may be changing (Walker and Salt 2006; Biggs et al. 2009), and what worked for fisheries management in the past may not work under these new conditions (Hilborn 1992).

Avoid Publication Bias

In order to assess the generalizability of relationships, it is necessary to base conclusions on an unbiased assessment

of relationships between environmental drivers and fish populations. Publication bias, or the tendency to only publish significant results, means that certain results are not represented in the literature (Møller and Jennions 2001). Funding and research bias may also come into play if studies are only conducted when negative relationships are suspected. The use of *P*-hacking is a related phenomenon whereby researchers repeatedly try different statistical tests until a statistically significant result is produced (Head et al. 2015). In both cases, statistically insignificant results showing a lack of relationship are underrepresented in the literature, potentially distorting our collective understanding of the strength, direction, and existence of effects.

Investigators can commit to avoid *P*-hacking and publication bias by reporting nonsignificant results. This includes reporting variables that were tested and determined to have no effect—sometimes the lack of relationship can be important to understand. As documented in this review, a lack of relationship (no effect) was the most commonly observed effect across all drivers and responses. In the review process, identifying which variables were tested and found to have no effect was often not straightforward and required significant effort to track down. Clearly documenting all variables that were tested (and why) and reporting all results, even when no relationship is found, could enable an unbiased assessment of the consistency of relationships. For example, Honsey et al. (2016) report that Yellow Perch recruitment in the Great Lakes region is positively correlated with spring–summer air temperatures but NOT correlated with winter air temperatures, contrary to results from Lake Erie (Farmer et al. 2015). In this case the lack of relationship is important and it is noted in the abstract. Journal editors and peer reviewers can also help reduce this potential bias by supporting the publication (and clear reporting) of negative or nonsignificant results and by calling out *P*-hacking when it is suspected.

Considering a Broader Context

Advancing our understanding of the effects of climate and other drivers on fish populations will require scientists and resource agencies to think about experimental design in a larger context. In some instances, this may be accomplished by merely including and testing metrics that have been used in previous assessments, allowing for easier comparison and generalization among studies. Furthermore, researchers may acknowledge and highlight the range of values studied of any given driver of ecosystem change, relative to the range of values that exists (or could exist) in the real world. For example, researchers documenting the effects of temperature on Walleye or Yellow Perch populations could interpret their results in the context of the gradient of temperatures that the species

experience throughout their ranges, as nonmonotonic relationships are likely. At a larger scale, to fully understand the effects of climate and other landscape-level drivers across broad gradients will require greater collaboration across jurisdictional boundaries, including more fluent sharing of both project funding and data.

Interpret Correlations with Caution

Despite the general understanding that correlation does not equal causation, in many cases correlation is the best tool we have to understand fisheries systems (Hilborn 2016). Correlation can be interpreted as evidence for causation, albeit weak. Consistency of correlations across multiple studies increases the evidence for causation (Hilborn 2016), but publication bias clouds interpretation of any observed consistency. We advise researchers to entertain multiple working hypotheses when evaluating relationships in their data (Hilborn and Stearns 1982). Furthermore, to increase the predictive capacity of ecological models and attempts to avoid spurious correlations, models can be validated using independent data (Hurvich and Tsai 1990). When truly independent data are unavailable, withholding data nonrandomly for validation can improve the transferability and generalizability of models (Olden and Jackson 2000; Wenger and Olden 2012). Results from model selection approaches that are known to produce biased results, such as all-subsets regression models for choosing between multiple predictors (Olden and Jackson 2000), may be interpreted with caution.

Use Appropriate Analytical Methods

Although in fisheries we are often limited by data, we are often not limited in our choice of statistical techniques. We encourage investigators to consider methods other than simple linear regressions when evaluating relationships between variables. Hierarchical Bayesian techniques are particularly well suited for ecological questions because they account for multiple sources of uncertainty and can identify cross-scale interactions (Clark 2005; Wagner et al. 2007; Soranno et al. 2014). Multispecies models that account for species dependencies are effective at quantifying responses of multiple species to environmental change simultaneously (Clark et al. 2014; Tikhonov et al. 2017; Wagner et al. 2020). Nonlinear models, such as generalized additive models, are useful for modeling the frequently nonlinear relationships we observe in fish responses to environmental change (Jacobson and Anderson 2007; Jacobson et al. 2017; Pedersen et al. 2017). Fisheries data are often spatially or temporally autocorrelated, and a number of methods exist for dealing with such nonindependence, such as Bayesian integrated nested Laplace approximation (Zuur et al. 2017) and autoregressive integrated and moving averages methods (e.g., Pang et al. 2018; Ryan et al. 2019). A recent analysis of Walleye somatic growth across a landscape of lakes in

Alberta, Canada, demonstrates the power of accounting for both spatial and temporal correlations in a mechanistic framework to avoid bias in interpretation of results (Cahill et al. 2020). Structural equation modeling can account for multicollinearity (Graham 2003) and identify interactions and indirect effects (e.g., Hossain et al. 2019). Machine learning methods, such as artificial neural networks and random forest models, can handle multiple predictors with less risk of overfitting and can identify complex relationships and interactions (Olden et al. 2008; Hansen et al. 2017). Although these methods may be outside the expertise of many fisheries scientists, collaboration with quantitative ecologists and statisticians can facilitate greater learning and stronger inference, enabling effective responses to drivers of ecosystem change.

Benefits of Adaptive Management

Manipulation is the gold standard for understanding causation. Management experiments can provide insight into the effectiveness of management strategies as well as key uncertainties in mechanisms underlying responses (Walters 1986). Lake-rich landscapes offer abundant opportunities for learning about system change effects on fisheries systems across a gradient of conditions through adaptive management (Hansen et al. 2015b). To avoid spurious correlations and false certainty (Hilborn 1992), management experiments can be replicated, evaluated against unmanipulated reference systems, and applied as randomly as possible (Hilborn 2016). Despite stated commitments to adaptive management, adhering to these basic tenets of experimentation are difficult or impossible to achieve in complex socioecological systems such as managed fisheries, where the pressure to act often outweighs the desire to learn (Walters 2007). Still, even passive adaptive management can facilitate learning when systems are monitored following standardized protocols to facilitate comparisons among systems. Particularly in regions where multiple stocks are managed and cannot be monitored annually, standardized data collection and stratified sampling can allow for robust inference that would be impossible when relying on single systems (Lester et al. 2003, 2021; Fayram et al. 2009) and enable more robust understanding of Walleye and Yellow Perch responses to ecosystem change.

Conclusion

The majority of documented effects of ecosystem change on Walleye and Yellow Perch populations are inconsistent across systems. We view these inconsistencies as opportunities for developing a greater mechanistic understanding of responses to ecosystem change. Here, we provide an overview of the documented effects of climate, invasive species, land use and nutrient concentrations, and water clarity on Walleye and Yellow Perch populations via multiple pathways. We also provide ideas for distinguishing between true

context dependence that results from interactions among environmental drivers and apparent context dependence that is due to nonmonotonic relationships or methodological choices (Catford et al. 2021). Cooperative studies and synthesis may broaden understanding by identifying drivers of context dependence (Biggs et al. 2009). We intend for this review to stimulate synthesis and discussions across systems to enable more rapid learning and effective management responses to environmental change.

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SUPPORTING INFORMATION

Additional supplemental material may be found online in the Supporting Information section at the end of the article.