

# Forecasting the combined effects of anticipated climate change and agricultural conservation practices on fish recruitment dynamics in Lake Erie

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## Abstract

1. Many aquatic ecosystems are experiencing multiple anthropogenic stressors that threaten their ability to support ecologically and economically important fish species. Two of the most ubiquitous stressors are climate change and non-point source nutrient pollution.
2. Agricultural conservation practices (ACPs, i.e. farming practices that reduce runoff, prevent erosion, and curb excessive nutrient loading) offer a potential means to mitigate the negative effects of non-point source pollution on fish populations. However, our understanding of how ACP implementation amidst a changing climate will affect fish production in large ecosystems that receive substantial upstream sediment and nutrient inputs remains incomplete.
3. Towards this end, we explored how anticipated climate change and the implementation of realistic ACPs might alter the recruitment dynamics of three fish populations (native walleye *Sander vitreus* and yellow perch *Perca flavescens* and invasive white perch *Morone americana*) in the highly productive, dynamic west basin of Lake Erie. We projected future (2020–2065) recruitment under different combinations of anticipated climate change ( $n = 2$  levels) and ACP implementation ( $n = 4$  levels) in the western Lake Erie catchment using predictive biological models driven by forecasted winter severity, spring warming rate, and Maumee River total phosphorus loads that were generated from linked climate, catchment-hydrology, and agricultural-practice-simulation models.
4. In general, our models projected reduced walleye and yellow perch recruitment whereas invasive white perch recruitment was projected to remain stable or increase relative to the recent past. Our modelling also suggests the potential for trade-offs, as ACP implementation was projected to reduce yellow perch recruitment with anticipated climate change.

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5. Overall, our study presents a useful modelling framework to forecast fish recruitment in Lake Erie and elsewhere, as well as offering projections and new avenues of research that could help resource management agencies and policy-makers develop adaptive and resilient management strategies in the face of anticipated climate and land-management change.

#### KEYWORDS

climate warming, eutrophication, fisheries management, multiple stressors, percid

## 1 | INTRODUCTION

Many aquatic ecosystems are experiencing multiple anthropogenic stressors that threaten their ability to support fish populations. One of the most ubiquitous stressors is climate change, which has caused distributional shifts (Comte, Buisson, Daufresne, & Grenouillet, 2013; Filipe et al., 2013; Hansen, Read, Hansen, & Winslow, 2017; Van Zuiden, Chen, Stefanoff, Lopez, & Sharma, 2016), increased the spread of invasive fish species (Rahel & Olden, 2008; Van Zuiden et al., 2016), altered fish community composition (Alofs, Jackson, & Lester, 2014), affected reproductive dynamics (Farmer, Marschall, Dabrowski, & Ludsin, 2015; Hansen et al., 2017; Krabbenhof, Platania, & Turner, 2014), and changed fish production (Blanchard et al., 2012). Seemingly as pervasive has been non-point source (NPS) nutrient and sediment pollution, which can negatively affect fish populations by causing bottom hypoxia, harmful algal blooms, reduced water clarity, and altered food-web interactions (Breitburg, Hondorp, Davias, & Diaz, 2009; Caddy, 2000; Diaz & Rosenberg, 2008; Ludsin, Kershner, Blocksom, Knight, & Stein, 2001; Scavia et al., 2014). Although the observed and projected individual effects of climate change (e.g. Comte et al., 2013; Lynch et al., 2016) and NPS pollution (e.g. Leach & Nepszy, 1976; Ludsin et al., 2001) are well-documented and can be substantial, many fish populations are experiencing climate change and NPS pollution simultaneously, which could magnify or mitigate their independent effects. However, the effects of climate change combined with NPS pollution on fish populations remain largely unstudied, especially in lake ecosystems. Understanding the combined effects of multiple stressors is especially critical in ecosystems that support economically and ecologically important fisheries as it can help guide management and conservation strategies (DeVanna Collingsworth et al., 2017; Fussell et al., 2016; Lynch et al., 2016; Paukert et al., 2016).

Highly productive coastal and large-lake ecosystems that receive substantial river-transported runoff from agricultural catchments are typically negatively affected by the combined impacts of climate change and NPS pollution (Buchheister, Bonzek, Gartland, & Latour, 2013). Because these ecosystems (e.g. Chesapeake Bay; Breitburg,

2002; Kemp et al., 2005; Buchheister et al., 2013; northern Gulf of Mexico: de Mutsert, Steenbeek, Lewis, Buszowski, & Cowan, 2016; Lake Erie: Ludsin et al., 2001) often support valuable commercial and recreational fisheries, which can be adversely affected by eutrophication, regulatory agencies and policy-makers have typically sought to improve habitat conditions (e.g. water quality) by altering farming practices in the catchment (Hagy, Boynton, Keefe, & Wood, 2004; Keitzer et al., 2016; Ohio EPA, 2013; Scavia et al., 2014; Wilson et al., 2019). Agricultural conservation practices (ACPs), which are farming practices that reduce runoff, prevent erosion, curb excessive nutrient loading, and mitigate ecosystem degradation, offer one potential means to reduce the negative effects of NPS pollution on fish production while, ideally, not compromising agricultural production (USDA Keitzer et al., 2016; NRCS, 2011). The benefits of such practices are well-documented and have been shown to limit in-stream nutrient and sediment loading, improve water quality, promote diverse stream-fish assemblages, and even reduce nutrient inputs into downstream recipient water bodies (Bosch, Allan, Selegean, & Scavia, 2013; Keitzer et al., 2016; Richards, Baker, & Crumrine, 2009). Even so, how ACP implementation amidst a changing climate would affect fish production in large ecosystems that receive substantial upstream nutrient and sediment loads remains a conspicuous information gap. Such information could help managers design more resilient and adaptive management strategies (Hansen et al., 2017; Lynch et al., 2016; Paukert et al., 2016).

Climate change and nutrient loading can directly and indirectly drive fishery dynamics by affecting the recruitment of individuals to the fishable population (Farmer et al., 2015; Hansen et al., 2017). Recruitment (herein, defined as the contribution of individuals to older ages that can be targeted by a fishery) responses can be complex—positive or negative, species-specific, variable across spatial and temporal scales, and life-stage dependent (Drinkwater et al., 2010; Ludsin, DeVanna, & Smith, 2014; Radinger et al., 2016). For example, climate change and NPS pollution can alter key habitat characteristics that affect early life growth and survival (Brochier et al., 2013; Brunel & Boucher, 2007; Lindegren et al., 2010; Mueter, Bond, Ianelli, & Hollowed, 2011). In many cases, the magnitude

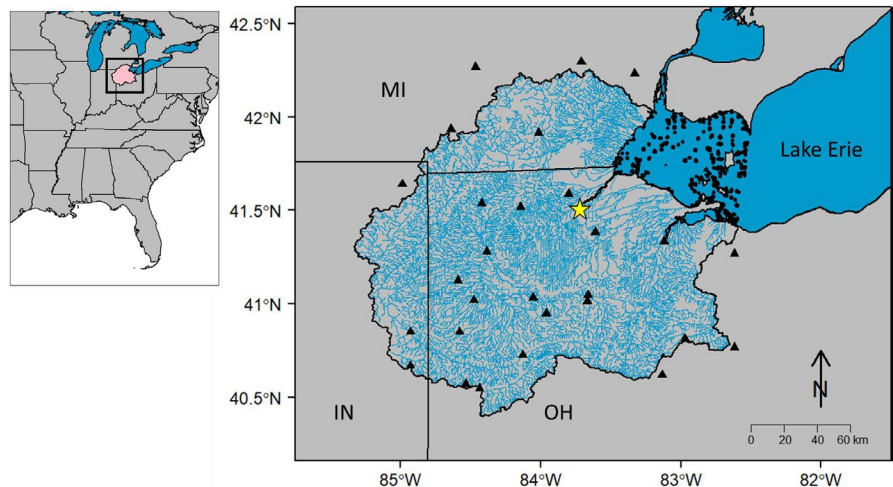
and direction of response to increasing temperature is linked to a species' thermal guild, with cool- and cold-water species showing negative responses to warming and warm-water species showing positive ones (Comte et al., 2013; Hansen et al., 2017; Lynch et al., 2016). Similarly, a species' tolerance, or lack thereof, of eutrophic, nutrient-rich waters can affect recruitment positively or negatively through top-down or bottom-up processes (Briland, 2018; Ludsin et al., 2001). Thus, understanding the response of fish recruitment, and ultimately fishery production, to climate change and the implementation of ACPs is a key component to future management and conservation (Pritt, Roseman, & O'Brien, 2014).

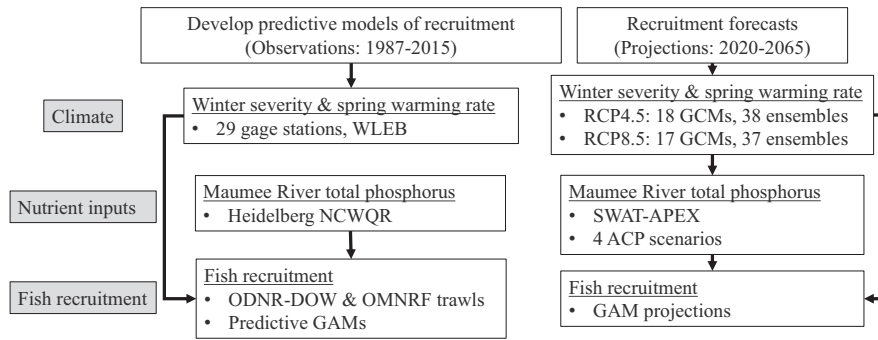
Towards this end, we explored how anticipated climate change and the implementation of realistic ACP scenarios might alter the recruitment dynamics of three ecologically and economically important fish populations (walleye *Sander vitreus*, yellow perch *Perca flavescens*, and white perch *Morone americana*) in the highly productive and dynamic west basin of Lake Erie (Figure 1). The recruitment dynamics of these species have been shown to respond to climate-related factors (e.g. winter and spring temperatures: Busch, Scholl, & Hartman, 1975; Clady, 1976; Farmer et al., 2015; Hokanson, 1977; Johnson & Evans, 1990) and factors associated with NPS inputs from rivers (Carreon-Martinez, Wellband, Johnson, Ludsin, & Heath, 2014; Jones, Shuter, Zhao, & Stockwell, 2006; Ludsin et al., 2011; Mion, Stein, & Marschall, 1998; Reichert et al., 2010). We focused on western Lake Erie for several reasons. First, ACPs designed to reduce phosphorus loading are being proposed and implemented in the surrounding western Lake Erie basin (WLEB) catchment to mitigate Lake Erie's eutrophication problem and its potentially harmful effects (e.g. bottom hypoxia, harmful algal blooms, reduced water clarity; Kane, Conroy, Richards, Baker, & Culver, 2014; Ohio EPA, 2013; Scavia et al., 2014; Watson et al., 2016). Second, projected climate change, which is characterised by short, warm winters (Farmer et al., 2015; Jones et al., 2006) and frequent, high-magnitude precipitation events in temperate ecosystems (Bartolai et al., 2015; Hayhoe, VanDorn, Croley, Schlegal, & Wuebbles, 2010; Maghrebi, Nalley, Laurent, & Atkinson, 2015), has occurred in the WLEB and has been linked to the recruitment

dynamics of important Lake Erie species such as yellow perch and walleye (e.g. Farmer et al., 2015; Fedor, 2008). Finally, the west basin of Lake Erie provides spawning and nursery areas for many of Lake Erie's ecologically and economically important species, including walleye (Jones, Netto, Stockwell, & Mion, 2003; Zhao, Jones, Shuter, & Roseman, 2009), yellow perch (Carreon-Martinez et al., 2014; Ludsin et al., 2011; Reichert et al., 2010), and white perch (Boileau, 1985; Schaeffer & Margraf, 1986).

We forecasted walleye, yellow perch, and white perch age-0 (juvenile) abundance, which has been shown to be a strong predictor of future recruitment to the fishery at age-2 (Farmer et al., 2015; WTG, 2017), under different combinations of anticipated (2020–2065) climate change and varying levels of ACP implementation in the WLEB catchment. Our specific research goals were to: (1) quantify the independent and combined effects of climate change and ACP implementation on walleye, yellow perch, and white perch recruitment; (2) explore whether climate change and ACP implementation might alter western Lake Erie's fish community by differentially affecting native cool-water fish species (walleye and yellow perch) versus nonnative warm-water ones (white perch); and (3) provide insights to Lake Erie management agencies regarding the potential future of their fisheries. We hypothesised that, in general, climate warming would negatively affect walleye and yellow perch recruitment, owing to their seeming dependence on long winters for successful reproductive output and strict thermal requirements during the spring (Busch et al., 1975; Farmer et al., 2015; Hokanson, 1977). However, depending on their magnitude, reductions in total phosphorus (TP) inputs from ACP implementation could offset or exacerbate anticipated climate-driven declines in yellow perch recruitment. For example, reduced NPS TP loading could offset warming-induced recruitment declines by alleviating the adverse effects of eutrophic conditions (e.g. bottom hypoxia; Caddy, 1993; Roberts et al., 2009; Scavia et al., 2014). By contrast, reduced NPS inputs of phosphorus (and associated sediments) could exacerbate declines in recruitment by reducing the extent and productivity of turbid Maumee River plumes during the spring, which appear to offer protection to larval yellow perch from predators such as invasive white

**FIGURE 1** Map of the western Lake Erie basin catchment (MI, IN, OH, U.S.A.) and the west basin of Lake Erie (U.S.A.–Canada). Trawling stations are denoted by solid black circles, weather stations by black triangles, and the Maumee River gauge station used to validate the Soil and Water Assessment Tool model by a gold star





**FIGURE 2** Conceptual modelling framework for forecasting Lake Erie walleye, yellow perch, and white perch recruitment under two greenhouse gas emission scenarios (RCP4.5 and RCP8.5) crossed by four levels of agricultural conservation practice (ACP) implementation in the western Lake Erie basin (WLEB) catchment. Predictive models of fish recruitment were built using generalised additive models (GAMs). Predictor variables included winter severity, spring warming rate, and Maumee River total phosphorus (TP) from Heidelberg University's National Center for Water Quality Research (NCWQR). Age-0 (juvenile) abundance data from bottom trawl surveys by the Ohio Department of Natural Resources—Division of Wildlife (ODNR-DOW) and the Ontario Ministry of Natural Resources and Forestry (OMNRF, 1987–2015) was our recruitment proxy. Future recruitment was projected using ensemble climate forecasts and linked Soil and Water Assessment Tool (SWAT) and Agricultural Policy/Environmental eXtender (APEX) models

perch (Carreon-Martinez et al., 2014; Ludsin et al., 2011) and may also enhance foraging through bottom-up effects (Barbiero, Balcer, Rockwell, & Tuchman, 2009; Grimes & Finucane, 1991). In this way, the relationship between yellow perch recruitment and TP inputs from the Maumee River could be expected to be dome-shaped (unimodal), a notion supported by previous studies that have quantified the relationship between ecosystem productivity metrics and fish(eries) yield (e.g. Caddy, 1993, 2000; Oglesby, Leach, & Forney, 1987). By contrast, we hypothesised that white perch recruitment would be positively affected by climate warming and negatively affected by increased ACP implementation because of this species' higher thermal optimum compared to walleye and yellow perch (Johnson & Evans, 1990) and its tolerance of eutrophic conditions (Briland, 2018).

## 2 | METHODS

### 2.1 | Study system

#### 2.1.1 | West basin of Lake Erie

Lake Erie is the smallest of the Laurentian Great Lakes (by volume), but is the most biologically productive, supporting numerous commercial and recreational fisheries (Bunnell et al., 2013; Ludsin et al., 2014). The lake has three distinct basins (west, central, and east), each having unique chemical and physical properties. The focal area of this study, the west basin (Figure 1), is the warmest, shallowest, and most biologically productive of the three (Bolsenga & Herdendorf, 1993; Leach & Nepszy, 1976; Ludsin et al., 2001). Owing to these properties, the west basin has historically provided spawning and nursery habitat for a diversity of fishes including walleye, yellow perch, and white perch (DuFour et al., 2015; Farmer et al., 2015; Jones et al., 2003; Ludsin et al., 2001, 2011; Mion et al., 1998; ODW, 2017). A major driver of the biologically productive west

basin is nutrient inputs from the WLEB catchment and specifically, the Maumee River, which drains the largest catchment in the entire Great Lakes basin (Bolsenga & Herdendorf, 1993). The Maumee River catchment is composed of primarily agricultural land (>70%, USDA NRCS, 2011) and delivers substantial nutrient and sediment inputs to the west basin (Baker & Richards, 2002; Keitzer et al., 2016; Scavia et al., 2014). Excessive phosphorus loading from agricultural runoff in the Maumee River catchment has been identified as the primary driver of Lake Erie's recent re-eutrophication (Scavia et al., 2014; Watson et al., 2016), resulting in efforts to reduce loading via the implementation of ACPs (Ohio EPA, 2013). Given that the Maumee River contributes a substantial portion of the TP load from the WLEB into the west basin of Lake Erie (Maccoux, Dove, Backus, & Dolan, 2016; Scavia et al., 2014), the need exists to understand how ACP implementation in this catchment will impact the resident fish community, especially amidst a changing climate (Keitzer et al., 2016).

#### 2.1.2 | Study species

The three focal species in this study are: (1) walleye, which supports Lake Erie's largest recreational fishery and second largest commercial fishery (Kayle, Oldenburg, Murray, Francis, & Markham, 2015; Markham & Knight, 2017; ODW, 2017, 2018); (2) yellow perch, which supports Lake Erie's largest commercial fishery and second largest recreational fishery (Belore et al., 2014; ODW, 2018); and (3) white perch, an invasive species that is of minor commercial importance but has become the most abundant prey-fish in Lake Erie (FTG, 2013; ODW, 2017) and is a known predator of walleye and yellow perch during their early life stages (Carreon-Martinez et al., 2014; Ludsin et al., 2011; Schaeffer & Margraf, 1987). In addition to their economic and ecological roles in Lake Erie, walleye, yellow perch, and white perch are common and widespread across North America, and support recreational fisheries across their ranges. These three species also span a gradient of thermal

guilds. Although walleye and yellow perch are both considered cool-water species, walleye has a lower optimal temperature range for both spawning and embryo hatching compared to yellow perch (Hokanson, 1977). In Lake Erie, walleye typically spawn during March–mid-May at temperatures of 3–12°C (May, 2015; Roseman et al., 1996) and yellow perch typically spawn during mid-April to May at temperatures of 8–14°C (Belore et al., 2014; Collingsworth & Marschall, 2011; Farmer et al., 2015). Both walleye and yellow perch age-0 (juvenile) abundance indices during August (c. 3–4 months post-hatch) are excellent predictors of age-2 abundance when recruitment to the fishery occurs (Belore et al., 2014; Farmer et al., 2015; Kayle et al., 2015), highlighting the importance of early life processes in determining fishery production. Because white perch prefer warmer temperatures compared to walleye and yellow perch, the west basin of Lake Erie is a favorable recruitment environment for this species. White perch spawn in its tributaries (e.g. Maumee River) and shallow (<1.5 m) waters during spring at temperatures of 11–15°C (Boileau, 1985; Hartman, 1972).

## 2.2 | Modelling overview

Our modelling approach involved two primary steps (Figure 2). First, we built species-specific predictive recruitment models using historical age-0 (juvenile) abundance data and indices of winter severity, spring warming rate, and Maumee River TP loads. Second, we projected future (2020–2065) recruitment under different combinations of anticipated climate change and four levels of ACP implementation in the WLEB catchment, using our predictive models and forecasted values of winter severity, spring warming rate, and Maumee River TP loads that were generated from linked climate, catchment-hydrology, and agricultural-practice-simulation models.

## 2.3 | Predictive fish recruitment models

### 2.3.1 | Fish recruitment indices

We used annual indices of age-0 abundance generated from bottom trawl surveys (typically 10 min duration) conducted by the Ohio Department of Natural Resources–Ohio Division of Wildlife (ODNR–DOW) and the Ontario Ministry of Natural Resources and Forestry (OMNRF) during 1987–2015 (walleye and yellow perch) and 1992–2015 (white perch). The white perch time-series was truncated to avoid the confounding effects of early establishment dynamics (i.e. large boom–bust cycles) during which environmental drivers were probably not the main drivers of population dynamics (Simberloff & Gibbons, 2004; Williamson, 1996). Surveys were conducted during the last 2 weeks of August, sometimes extending into early September. The agencies used a stratified-random design to sample 56–70 stations annually across the west basin of Lake Erie. To correct for catchability differences, vessel-specific and species-specific fishing power corrections were applied to standardise trawl catches (Tyson, Johnson,

Knight, & Bur, 2006). Catches were averaged within each year to generate a basin-wide mean. Herein, we report annual catch per unit effort (CPUE) as the number of individuals per minute of trawling.

### 2.3.2 | Abiotic predictors

We assessed winter severity, spring warming rate, and total spring-time (March–May) Maumee River TP loads as potential environmental predictors of walleye, yellow perch, and white perch recruitment. We chose these metrics based on previous research indicating their influence on recruitment for at least one of the three species (Busch et al., 1975; Carreon-Martinez et al., 2014; Clady, 1976; Farmer et al., 2015; Hokanson, 1977; Johnson & Evans, 1990; Jones et al., 2006; Ludsin et al., 2011; Mion et al., 1998; Reichert et al., 2010). We calculated historical winter severity and spring warming rate from observed maximum daily air temperatures during 1987–2015 from stations ( $n = 29$ ) located throughout the WLEB catchment (National Oceanic and Atmospheric Administration's Daily Global Historical Climatology Network, Menne, Durre, Vose, Gleason, & Houston, 2012). Our use of air temperature is justified, as it has often been used as a proxy for water-related thermal metrics (Sharma, Jackson, Minns, & Shuter, 2007; Van Zuiden et al., 2016) and has been used to successfully predict the effects of climate change on fisheries (Van Zuiden et al., 2016). Furthermore, previous research has shown that local air temperature is correlated to Lake Erie water temperature in western Lake Erie (Farmer, 2013). We defined winter severity as the total number of days that the mean daily maximum temperature across the WLEB catchment was  $\leq 6^\circ\text{C}$  during January–April of each year. Our inclusion of winter severity as a recruitment predictor was based on previous research identifying optimal spawning conditions for percids, which showed that at colder water temperatures, maturation is more likely to result in a spawning event as compared to warmer water temperatures (Hokanson, 1977). Our winter index is also strongly correlated with ice cover indices used in previous studies (e.g. Farmer et al., 2015) that have been shown to explain variation in Lake Erie recruitment success, and it is easily projected using existing climate change models. To calculate spring warming rate ( $^\circ\text{C}/\text{day}$ ), we fit a linear regression model to the basin-wide mean daily maximum temperature during April–May (the approximate larval production period for all three species) for each year and defined the annual spring warming rate ( $^\circ\text{C}/\text{day}$ ) as the slope of the least-squares regression line (Busch et al., 1975). Finally, we calculated total annual springtime TP loading (metric tons) as the sum of the recorded daily (March–May) Maumee River TP loads obtained from the National Center for Water Quality Research housed by Heidelberg University (<https://ncwqr.org/monitoring/>).

### 2.3.3 | Predictive models of fish recruitment

Because environmental driver–biological response relationships are often nonlinear (Hunsicker et al., 2016), we used generalised additive

models (GAMs, Hastie & Tibshirani, 1987) to examine the relationship between fish recruitment and winter severity, spring warming rate, and Maumee River TP loads. Generalised additive models are an ideal tool because of their flexibility in fitting nonlinear relationships that need not be defined a priori, and they have previously been used to model fish recruitment (Cardinale & Arrhenius, 2000; Daskalov, 1999). We built species-specific GAMs using thin-plate regression splines (Adams, Leaf, Wu, & Hernandez, 2018) and a  $\gamma$ -distribution with a log-link function. The  $\gamma$ -distribution is a flexible, continuous distribution, appropriate for skewed data, which has commonly been used in fisheries applications (Maunder & Punt, 2004). Smoothness parameters were estimated with generalised cross validation. Because fewer years of data were available for white perch, as compared to walleye and yellow perch, we restricted the basis dimension,  $k$  (controls the degree of smoothness in the model), to 6 in all white perch models to avoid overfitting (Decker et al., 2013; Quiñones et al., 2015). To avoid the confounding effects of multicollinearity, prior to model construction, we used pairwise correlations to confirm that no substantial ( $r > 0.6$ , Zuur, Ieno, Walker, Saveliev, & Smith, 2009) multicollinearity between predictor variables was present.

Once we determined that the predictor variables were not strongly correlated, a global model with the form:

$$\text{CPUE} \sim s(\text{TP}) + s(\text{spring warming rate}) + s(\text{winter severity})$$

was constructed and fit for each species where  $s$  represents the smoothing function. Model fit and temporal autocorrelation were assessed using standard diagnostics (Anderson & Burnham, 2002). To determine the most supported predictive model for each species, we constructed model formulations with all possible combinations of predictor variables (Burnham & Anderson, 2003) and considered the most supported model for each species as the one with the lowest sample size-corrected Akaike information criteria (AICc) value. If models were equally supported ( $\Delta\text{AICc} < 2$ ), we chose the model with the greatest predictive ability. All GAM analyses were conducted using the *mgcv* package in R 3.3.0 (Wood & Wood, 2015; R Core Team, 2019).

We used a resampling technique to visualise the partial effects of each predictor variable on the response variable (recruitment). First, we generated a separate, simulated uniform sequence ( $n = 250$ ) of each predictor variable using its observed range as bounds. Next, using the original data, we resampled the other two predictor variables (with replacement) to generate a new resampled dataset. We repeated this process with each predictor to generate three new resampled datasets, each with a simulated sequence of one variable and a resampled sequence for the other(s). Finally, we predicted recruitment values using the most supported candidate model for each species for each new dataset. We then plotted the predicted recruitment values as a function of the simulated predictor sequence for each of the predictors included in the most supported model (maximum of three possible predictors).

## 2.4 | Future projections

### 2.4.1 | Climate change scenarios: thermal metrics

We projected future (2020–2065) winter severity and spring warming rate using daily maximum air temperature values from global circulation models (GCMs) used in the IPCC's Fifth Assessment Report (IPCC, 2014). We included two greenhouse gas emission (representative concentration pathway, RCP) scenarios: a moderate-reductions scenario (RCP4.5, 18 GCMs) and a *business-as-usual* scenario (i.e. status quo, RCP8.5, 17 GCMs). For each GCM, multiple ensembles (slightly different versions of a GCM model) were run to generate a range of future climate conditions. (RCP4.5,  $n = 38$ ; RCP8.5,  $n = 37$ , Table S1; Ohio Supercomputer Center, 1987). The use of multiple GCMs and ensembles is a common way to incorporate uncertainty in future climate conditions and to better reflect the range of possible future outcomes (Sharma, Vander Zanden, Magnuson, & Lyons, 2011; Van Zuiden et al., 2016). The GCM data spatially overlapped the 29 stations that were used to calculate historical winter severity and spring warming rate.

Although the GCM outputs were bias-corrected and downscaled (both temporally and spatially) using standard approaches (Bureau of Reclamation, 2013; Maurer, Brekke, Pruitt, & Duffy, 2007), we further adjusted the forecasted data to account for any remaining bias, given that the climate data were generated at different temporal and spatial scales than those used in this study. For our winter severity and spring warming metrics, we employed a multi-step approach. First, we built scenario-specific linear models between hindcasted (1987–2015) temperature data from each climate scenario and historical observed temperature data during the same period. We then applied the linear coefficients to future forecasted temperature data. Next, we used the bias-corrected temperature data to calculate winter severity and spring warming rate with the same methods described above. We then calculated the magnitude of change between the forecasted value and hindcasted (1987–2015) median value for that specific scenario. Finally, we added this difference to the historical median. We used the resulting forecasted values to predict recruitment, which mitigated potential bias in our modelling efforts. We removed a small subset ( $n = 11$ ) of scenarios in which the projected spring warming rate was  $\leq 0$  for the remainder of our analyses. These scenarios only represented c. 0.3% of our total projections.

### 2.4.2 | Agricultural conservation practice scenarios

To generate future TP loads that resulted from different levels of implementation of nutrient and sediment reduction strategies in the catchment, we applied a set of previously developed catchment-hydrology and agricultural-simulation models (Arnold, Srinivasan, Muttiah, & Williams, 1998; Gassman et al., 2009; USDA NRCS, 2011; Wang et al., 2011; Daggupati et al., 2015; Yen et al., 2016). Briefly, we used conservation scenarios developed by U.S. Department of Agriculture (USDA) Conservation Effects Assessment Program (CEAP, USDA NRCS, 2011), which represent

different levels of ACP implementation in the WLEB catchment. Each scenario consists of implementing ACPs on varying numbers of farm acres, depending on their perceived level of need (USDA NRCS, 2011). A farm acre's level of need was based on its vulnerability to sediment and nutrient loss and its current level of ACP treatment (USDA NRCS, 2011). The four levels of ACP implementation in this study were: (1) a *baseline* scenario, where historical (1990–2015) levels of nutrient and erosion control practices in the WLEB were carried into the future; (2) a scenario where only WLEB farm acres deemed in critical need were treated (ENMC, 8% of the catchment, 384,160 acres); (3) a scenario where WLEB farm acres deemed in critical or moderate need were treated (ENMA, 48% of the catchment, 2,304,960 acres); and (4) a scenario where all farm acres were treated, regardless of their level of need (ENM) (USDA NRCS, 2011). The implementation of ACPs was simulated using the Agricultural Policy/Environmental eXtender (APEX) model (Gassman et al., 2009; Wang et al., 2011; Williams, Izaurrealde, & Steglich, 2008) and the output from this model was ultimately used as input into a previously developed, calibrated, and validated Soil and Water Assessment Tool (SWAT) model (1:100,000 resolution), which reliably simulates TP input into the west basin of Lake Erie via the Maumee River (Daggupati et al., 2015; Yen et al., 2016).

The SWAT is a commonly used catchment-hydrology model and has been used in multiple WLEB studies to explore the impact of climate change and ACP implementation on river flow and agricultural runoff (e.g. Bosch et al., 2013; Keitzer et al., 2016). In our study, SWAT inputs were nutrient loads from cultivated fields simulated by APEX (under each level of ACP implementation) and meteorological data from each climate change model. We used an approach similar to that used for our thermal metrics to bias-correct the TP forecasts from the SWAT, with some notable differences. In this case, we built scenario-specific and month-specific (March–May) linear models because the observed biases were month-specific. After forecasting springtime TP loads, we calculated the proportional change between the forecasted value and the hindcasted (1987–2015) median value for that specific scenario. Regardless of the level of ACP implementation, we used the baseline ACP median in each emission scenario, which simulated historical nutrient and erosion control practices. Finally, we multiplied the proportional change by the historical median to obtain the forecasts that were used to predict recruitment. We chose to use proportional change for TP to account for precipitation-driven changes in TP loading in the climate models, as simply adding or subtracting load differences would not make sense. The results of this modelling effort were projections of Maumee River TP loads for each combination of climate change and ACP implementation scenario, analogous to the historical Maumee River TP loads in regards to timing (spring) and spatial scale.

### 2.4.3 | Forecasting fish recruitment

We used our predictive recruitment models to forecast walleye, yellow perch, and white perch recruitment under both RCP scenarios

and the four ACP implementation scenarios. Under each combination of climate and ACP implementation scenario (total  $n = 8$ ), species-specific recruitment values were projected from winter severity, spring warming rate, and/or Maumee River TP loads annually and subsequently summarised by decade.

We evaluated the effects of future climate change and ACP implementation on fish recruitment at the decadal scale using two approaches. First, we compared the median decadal recruitment trends, relative to the past (1987–2015). Second, because walleye and yellow perch fisheries in Lake Erie are supported by sporadic strong recruitment events (i.e. year-classes; Farmer et al., 2015; Vandergoot, Cook, Thomas, Einhouse, & Murray, 2010), we calculated the frequency of annual forecasts in a decade that would constitute a strong recruitment event, defined as greater than or equal to the historical 75th percentile. The 75th percentile has commonly been used as a metric to define a *strong* recruitment event in Lake Erie (Vandergoot et al., 2010). We calculated the median proportion of strong recruitment events in each decade under each climate and ACP implementation scenario. If no differences in the frequency of strong recruitment events in the future existed relative to the past, we would expect the proportion of strong recruitment events within a decade to be centered on 25%, indicating that strong recruitment events occurred at the same frequency compared to the past.

## 3 | RESULTS

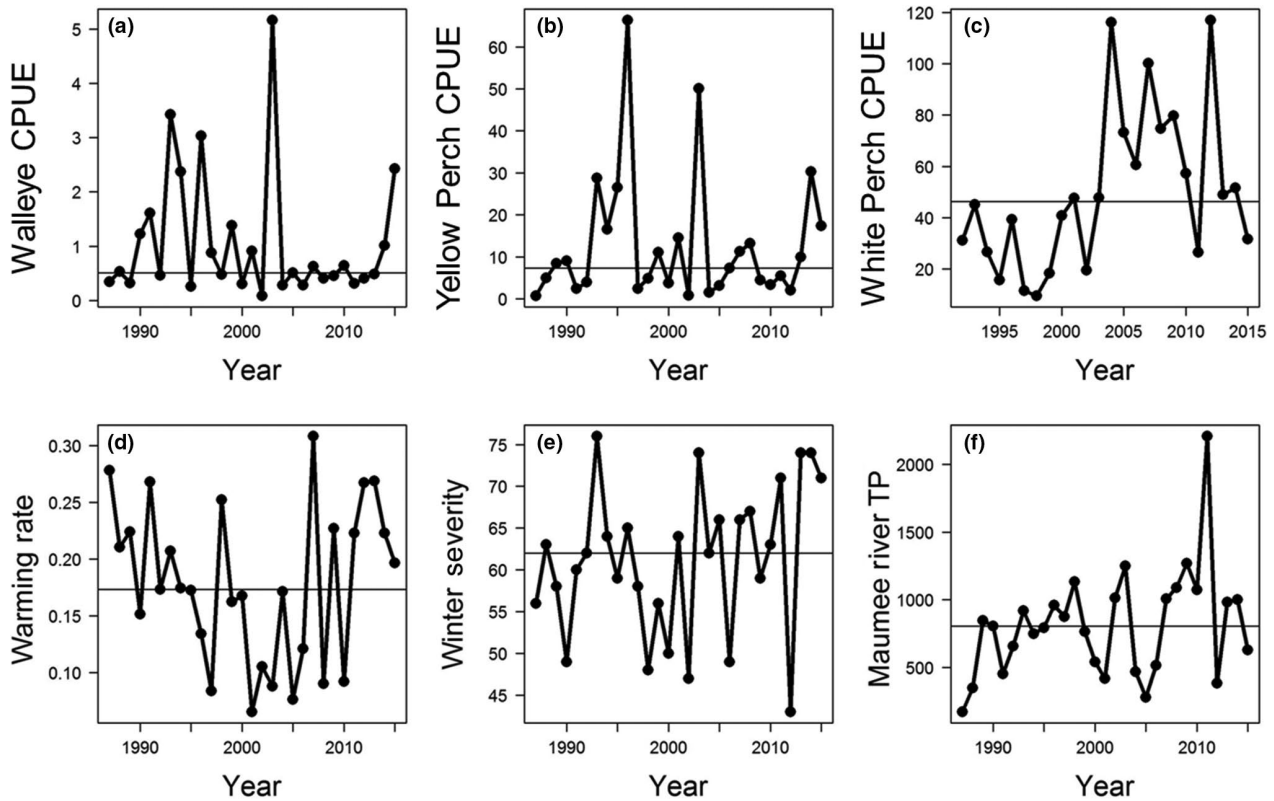
### 3.1 | Predictive models of fish recruitment

#### 3.1.1 | Fish recruitment indices

Lake Erie walleye, yellow perch, and white perch recruitment, as indexed by age-0 abundance (i.e. year-class strength), varied by up to an order of magnitude during the historical time period (Figure 3a–c). Annual age-0 walleye trawl CPUE ranged from 0.09 to 5.2 individuals/min, with a median CPUE of 0.5. The strongest walleye recruitment events occurred in 1993, 1996, 2003, and 2015 (Figure 3a). Age-0 yellow perch CPUEs ranged from 0.7 to 66.4 individuals/min, with a median value of 7.4 individuals/min (Figure 3b). The three strongest recruitment events occurred during years similar to walleye (1996, 2003, and 2015; Figure 3b). Age-0 white perch CPUE also varied by an order of magnitude with annual CPUEs ranging from 9.5 to 117.0 individuals/min, with a median value of 46.3 individuals/min. White perch recruitment was highest during the 2000s with the strongest recruitment events occurring in 2004 and 2012 (Figure 3c).

#### 3.1.2 | Abiotic predictors

Winter severity, spring warming rate, and Maumee River TP loads also varied throughout the historical period (Figure 3d–f). Winter severity (number of days with a maximum temperature  $\leq 6^{\circ}\text{C}$ )



**FIGURE 3** Indices of historical (1987–2015) age-0 (juvenile) (a) walleye, (b) yellow perch, and (c) white perch trawl catch per unit effort (CPUE, individuals/min) in western Lake Erie and (d) spring warming rate ( $^{\circ}\text{C}/\text{day}$ , during April–May), (e) winter severity (number of days with a maximum temperature  $\geq 6^{\circ}\text{C}$  during January–May), and (f) Maumee River total phosphorus load (TP, metric tons, March–May). Age-0 recruitment indices were generated from annual trawl surveys conducted by the Ohio Department of Natural Resources–Ohio Division of Wildlife and that Ontario Department of Natural Resources and Forestry during August. Horizontal lines indicate the historical median

**TABLE 1** Summary of final generalised additive models used to predict walleye, yellow perch, and white perch recruitment in western Lake Erie. Possible predictors included winter severity (the total number of days that the mean daily maximum temperature across the western Lake Erie catchment was  $\leq 6^{\circ}\text{C}$  during January–May of each year), spring warming rate ( $^{\circ}\text{C}/\text{day}$ ), and Maumee River total phosphorus (TP) load (metric tons). Reported are the effective degrees of freedom (EDF) for each smooth term. NA indicates that the predictor variable was not included in the final species-specific model based on  $\text{AIC}_c$  model selection. All included smooth terms have  $p < 0.05$

Species	EDF			Overall deviance explained (%)
	Winter severity	Spring warming rate	Maumee River TP	
Walleye	1.00	NA	NA	31.3
Yellow Perch	1.00	NA	2.587	51.1
White Perch	NA	1.00	4.523	55.4

ranged from 43 to 76 days, with a median winter severity of 62 days (Figure 3e). Extremely mild winters occurred in 2002 and 2012, whereas severe winters occurred in 1993, 2003, and during 2013–2015. Spring warming rate varied throughout the period, ranging from 0.06 to 0.31 $^{\circ}\text{C}/\text{day}$  (Figure 3d). Generally, warming rates were lower in the middle of the time-series (1996–2006) compared to the early and late periods (Figure 3d). The median springtime Maumee River TP load was 807.0 MT and ranged from 172.1 to 2,208.8 MT (Figure 3f). Notably, the 2011 TP load was very high, approximately double the next highest load. Because no substantial collinearity

between these environmental variables existed ( $r < 0.4$ ), all were included as potential predictors of recruitment in our species-specific models.

### 3.1.3 | Predictive models of fish recruitment

Based on standard, qualitative diagnostics (Anderson & Burnham, 2002) all three final models of fish recruitment displayed good fit with no obvious patterns in the residuals (Figure S1) and no

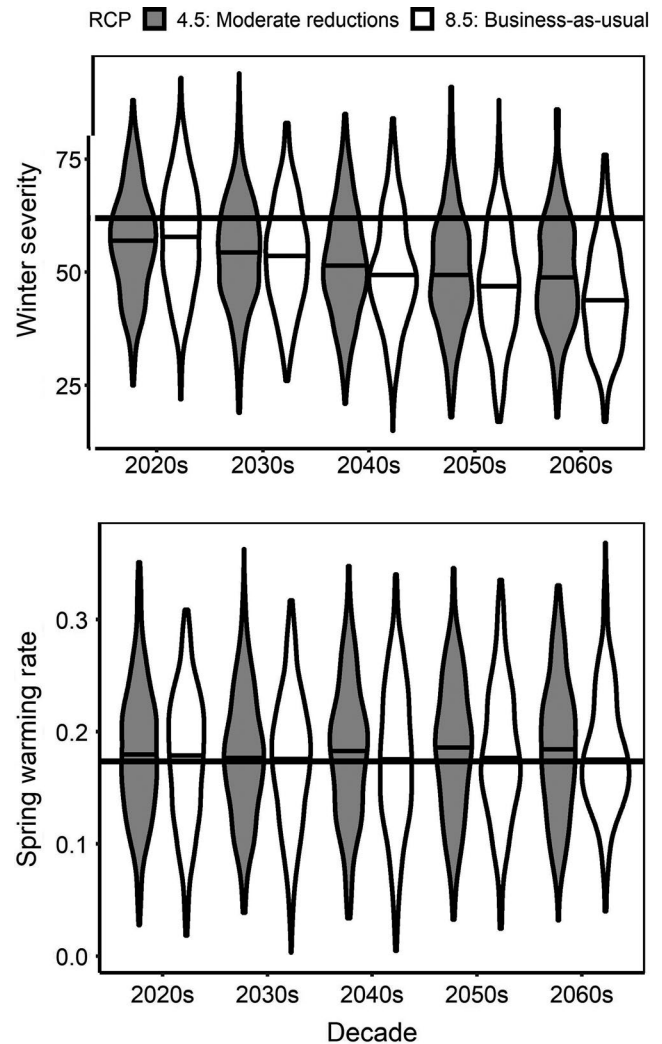


significant temporal autocorrelation based on autocorrelation function plots (Figure S2, Zuur et al., 2009). Based on our defined AICc and predictive ability criteria, the most supported predictive model of walleye recruitment included only winter severity (Table S2). Our resampling analysis revealed that, as winter severity increased, so did walleye recruitment, with exponentially higher walleye recruitment occurring after severe winters (Figure S3). The final walleye model explained 31.3% overall deviance in walleye recruitment (Table 1). The most supported predictive model of yellow perch recruitment included winter severity and Maumee River TP as predictors (Table S2). The partial response of yellow perch recruitment to winter severity was similar to the walleye partial response; as winter severity increased, so did yellow perch recruitment (Figure S4). The partial response of yellow perch recruitment to TP was dome-shaped (unimodal) with the greatest positive effect occurring at intermediate TP loads (Figure S4). The final yellow perch predictive model explained 51.1% of the overall deviance in yellow perch recruitment (Table 1). The most supported predictive model of white perch recruitment included spring warming rate and Maumee River TP as predictor variables (Table S2). In general, white perch recruitment increased with increasing spring warming rate (Figure S5). Although the partial response of white perch recruitment to Maumee River TP was nonlinear, as TP increased white perch recruitment generally decreased (Figure S5), a finding that ran counter to our expectations. The final white perch recruitment model explained 55.4% of the variation in observed recruitment (Table 1).

### 3.2 | Future projections

#### 3.2.1 | Forecasts of winter severity and spring warming rate

As expected, winter severity decreased through time in both the RCP4.5 and RCP8.5 emission scenarios, although the declines varied in their magnitude, especially during later decades (Figure 4a). Median winter severity decreased by 5 days during the 2020s and 7 days during the 2030s relative to the median historical winter severity (62 days) in the RCP4.5 emission scenario. Similarly, it decreased 4 days during the 2020s and 8 days during the 2030s relative to the median historical winter severity (62 days) in the RCP8.5 emission scenario. After the 2030s, however, the two emission scenarios diverged, with winter severity decreasing more in the RCP8.5 scenario compared to the RCP4.5 emission scenario (Figure 4a). By the 2060s, projected median winter severity decreased by 13 days in the RCP4.5 emission scenario and 18 days in the RCP8.5 emission scenario, representing a 21% and 29% reduction, respectively, relative to the historical period. In contrast to winter severity, no obvious temporal trends in projected spring warming rate were apparent, with differences between emission scenarios also being negligible (Figure 4b). Median spring warming



**FIGURE 4** Violin plots of projected (2020–2065) (a) winter severity and (b) spring warming rate in the western Lake Erie basin under the RCP4.5 (moderate reductions, grey), and RCP8.5 (business-as-usual, white) greenhouse gas emission scenarios by decade. The violin plot shows the distribution of the unsummarized (all years, all ensembles) data with the black lines in each plot representing the projected median winter severity (number of days with a maximum temperature  $\geq 6^{\circ}\text{C}$  during January–May) or median spring warming rate ( $^{\circ}\text{C}/\text{day}$ , during April–May). The horizontal line represents the historical (1987–2015) median

rates under the RCP4.5 emission scenario were slightly higher than the historical median, although the projected rates were variable (Figure 4b).

#### 3.2.2 | Forecasts of TP loading

Three general patterns emerged from our projected Maumee River TP loads (Figure 5). First, as expected, increased levels of ACP implementation (i.e. more farm acres treated with nutrient and erosion control practices) resulted in lower TP loads. For example, implementing ACPs in all farm acres (ENM) resulted in a 45.4% reduction in TP loading during the 2020s under the RCP4.5 emission scenario and a reduction

of 39.2% under the RCP8.5 emission scenario, relative to the historical period. Second, TP loads increased through time, within each level of ACP implementation, indicating that anticipated climate change can be expected to reduce the effect of ACP implementation during later decades. Finally, during most decades and ACP implementation scenarios, the RCP8.5 emission scenario had greater median expected TP loads compared to the corresponding RCP4.5 emission scenario, probably because of greater projected increases in springtime precipitation, and subsequent TP loading, under the RCP8.5 emission scenario (N. Aloysius, unpublished data). However, the differences in median forecasted TP loads between emissions scenarios were modest, especially when compared to the differences that we observed among ACP implementation scenarios. The implementation of ACPs influenced TP loading more than the projected changes in climate in the two highest levels of ACP implementation (ENMA and ENM). For example, substantial reductions (e.g. 27.6% during the 2060s, RCP4.5, ENM scenario) in TP loading could still be achieved in the far term, despite the overall upward trends in climate-driven TP loading through time (Figure 5). However, in the ACP implementation scenarios where current levels of implementation were carried into the future or only acres in critical need were treated, TP loads were forecast to increase above the historical median levels (Figure 5).

### 3.2.3 | Forecasts of fish recruitment

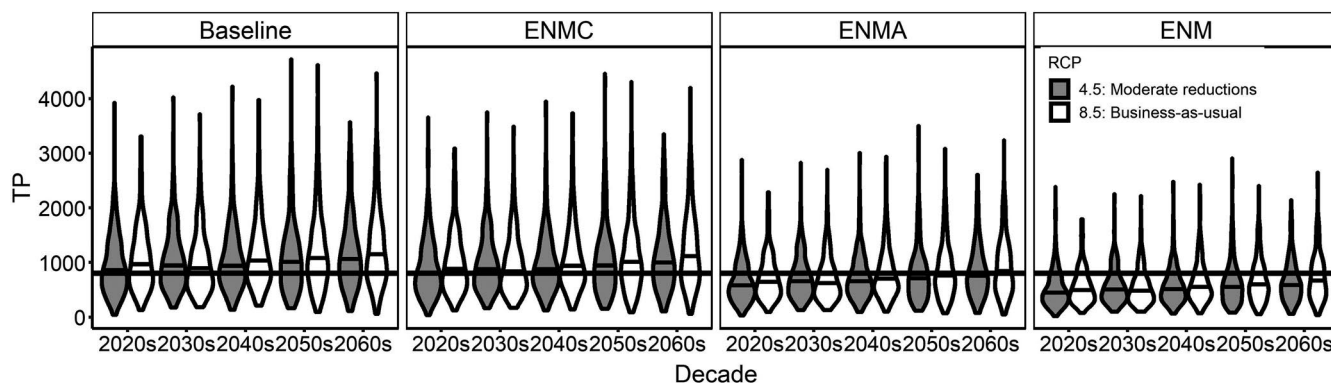
#### Walleye

The final walleye recruitment model only included winter severity as a predictor. Thus, walleye recruitment was not projected under different levels of ACP implementation, only under different greenhouse gas emission (RCP) scenarios. In general, median annual projections of recruitment decreased through time in both the moderate reductions (RCP4.5) and business-as-usual (RCP8.5) scenarios (Figure 6). Interestingly, the projected median annual recruitment

values during earlier decades (2020s–2040s for RCP4.5, 2020s and 2030s for RCP8.5) were 3–5% higher than the historical median, owing to more variable forecasts that resulted in projected severe winters during earlier decades. However, during subsequent decades (2040s–2060s), both emission scenarios had projected median annual recruitment values lower than the historical median (Figure 6). During the 2060s under the RCP8.5 emission scenario, which represents the *worst-case scenario* in our projections, median annual recruitment decreased by 38% relative to the historical median. By contrast, the frequency of a projected strong ( $\geq$  historical 75th percentile) annual walleye recruitment event (year-class) during a decade was lower than 25% (the expected frequency) during all decades, under both emission scenarios (Figure 7), except under the RCP8.5 emission scenario during the 2020s. Under the RCP4.5 emission scenario, the median frequency of a projected annual strong recruitment event decreased from 18% during the 2020s to 5% during the 2060s. The decline was more severe under the RCP8.5 emission scenario during which the median value was only 5 and 4% in the 2050s and 2060s, respectively. The median frequency of strong recruitment events was slightly higher early in the projected period under the RCP8.5 emission scenario compared to the RCP4.5 one, owing to a slightly higher occurrence of projected severe winters during early decades. Overall, under both future greenhouse gas emission scenarios, the projected frequency of strong walleye recruitment events decreased substantially compared to the past.

#### Yellow perch

Our analysis of yellow perch recruitment yielded four major findings. First, median annual recruitment was projected to be lower than the historical median across all decades under all climate change  $\times$  ACP implementation scenarios, except for one (RCP8.5, ENMC, 2020s; Figure 8). These reductions ranged from 3.3% (RCP8.5, Baseline, 2020s) to 61% (RCP8.5, ENM, 2060s) relative to the historical median. Second, projected median annual yellow perch recruitment declined



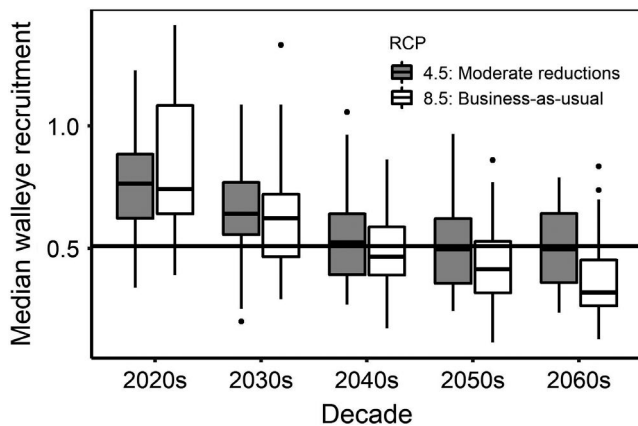
**FIGURE 5** Violin plot of projected (2020–2065) Maume River total phosphorus (TP) load under the RCP4.5 (moderate reductions, grey), and RCP8.5 (business-as-usual, white) emission scenarios by decade and agricultural conservation practice implementation scenario. The number of acres treated with nutrient and erosion control practices increases from left to right: (1) *baseline* scenario, where current (1990–2010) levels of nutrient and erosion control practices were carried into the future; (2) a scenario where only farm acres in critical need were treated (ENMC); (3) a scenario where farm acres in critical and moderate need were treated (ENMA); and (4) a scenario where all farm acres were treated (ENM). The violin plot shows the distribution of the unsummarised (all years, all ensembles) data with the black lines representing the median springtime TP load (total March–May TP load, MT)

through time in all future climate and ACP implementation scenarios (Figure 8). Generally, the reductions were greater under the RCP8.5 emission scenario during any decade at any level of ACP implementation relative to the RCP4.5 emission scenario; however, some exceptions to this pattern existed (e.g. ENMC, 2020s). The greatest reductions in median annual yellow perch recruitment (56.5–60%) occurred during the 2060s under the RCP8.5 emissions scenario. Third, increasing the level of ACP implementation (i.e. reducing TP loads) exacerbated the climate-driven decline in median annual yellow perch recruitment. For example, during the 2020s, we documented a 4.6% decline in median annual yellow perch recruitment under the RCP4.5-Baseline scenario. By contrast, we observed a 27.3% reduction in median annual yellow perch recruitment in the 2020s under the RCP4.5-ENM (all acres treated) scenario. This trend was similar across all decades and combinations of climate and ACP implementation scenarios (Figure 8). Fourth, similar trends emerged for the projected frequency of strong ( $\geq$  historical 75th percentile) yellow perch

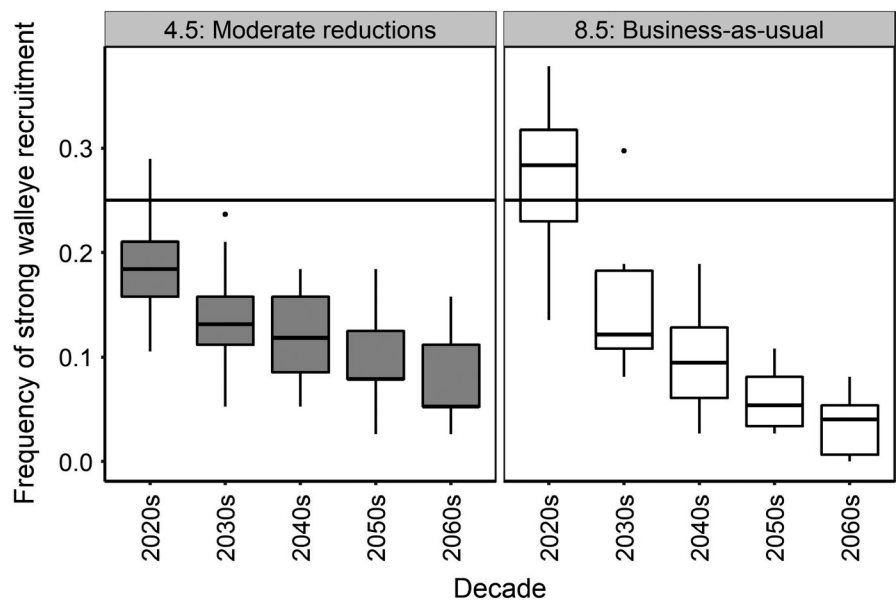
recruitment events (Figure 9). Projected strong yellow perch recruitment events decreased through time, decreased with increasing levels of ACP implementation, and were lower than expected (a frequency of 25%, based on the historical frequency) across all decades during all future scenarios (Figure 9). In contrast to the projected median levels of yellow perch recruitment, the highest projected frequency of strong recruitment events (23%) occurred under the RCP8.5-ENMC scenario, in part, owing to a greater proportion of projected severe winters relative to the RCP4.5 emissions scenario (Figure 9).

#### White perch

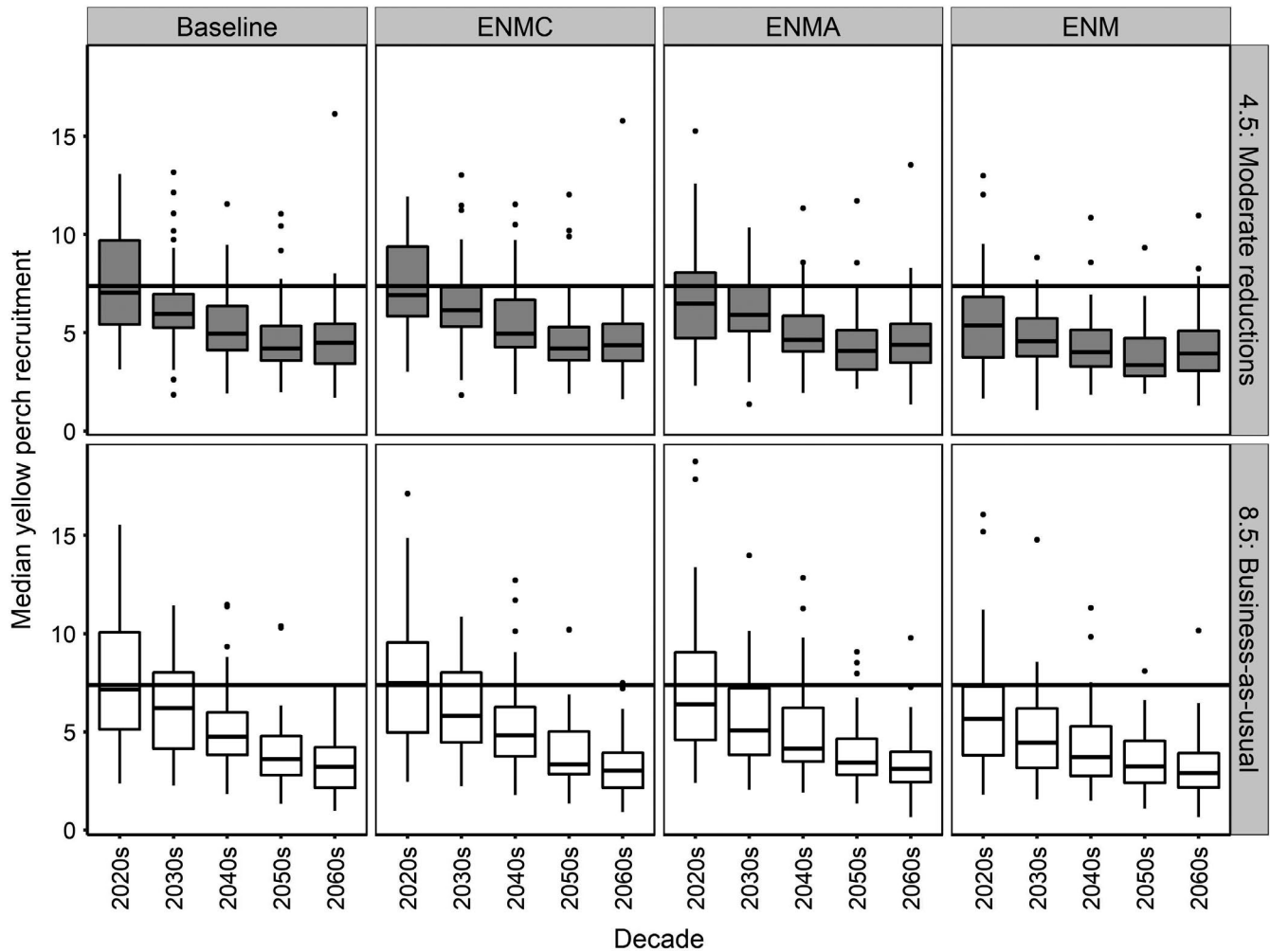
Unlike walleye and yellow perch, recruitment of invasive white perch was projected to be near or above the historical median across all climate and ACP implementation scenarios (Figure 10). The projected increases in the median annual recruitment values were typically greatest during the near-term (2020s and 2030s) at the two highest levels of ACP implementation (ENMA and ENM; Figure 10). Although temporal trends in median white perch recruitment were less apparent relative to yellow perch and walleye, white perch recruitment was projected to be slightly higher during the 2020s relative to the 2060s under any given climate and ACP implementation scenario (Figure 10). Even so, during all decades, under all future scenarios, annual median recruitment was projected to be greater than the historical median at the two highest levels of ACP implementation. Unlike yellow perch, median white perch recruitment was projected to increase with increasing levels of ACP implementation under both emission scenarios, a finding that ran counter to our expectations. However, the projected trends in the frequency of strong ( $\geq$  historical 75th percentile) annual recruitment events differed from the trends in median recruitment. At the two lowest levels of ACP implementation, the proportion of strong recruitment events was lower than the expected frequency across all decades. However, during all decades under both emission scenarios, at the highest level of ACP



**FIGURE 6** Boxplot of projected (2020–2065) median annual walleye recruitment (year-class strength, CPUE, individuals/min) in western Lake Erie under the RCP4.5 (grey) and RCP8.5 (white) emission scenarios by decade



**FIGURE 7** Boxplot of the proportion of projected forecasts of annual western Lake Erie walleye recruitment events (year-classes) that were greater than or equal to the historical (1987–2015) 75th percentile by decade, under the RCP4.5 (grey) and RCP8.5 (white) emission scenarios by decade. The horizontal line represents the *expected* proportion of strong recruitment events, if the frequency were not to change in the future relative to the past



**FIGURE 8** Boxplot of projected (2020–2065) median annual yellow perch recruitment (year-class strength, catch per unit effort, individuals/min) in western Lake Erie under the RCP4.5 (grey) and RCP8.5 (white) emission scenarios by decade and agricultural conservation practice implementation scenario. See Figure 5 legend for a description of each agricultural conservation practice scenario

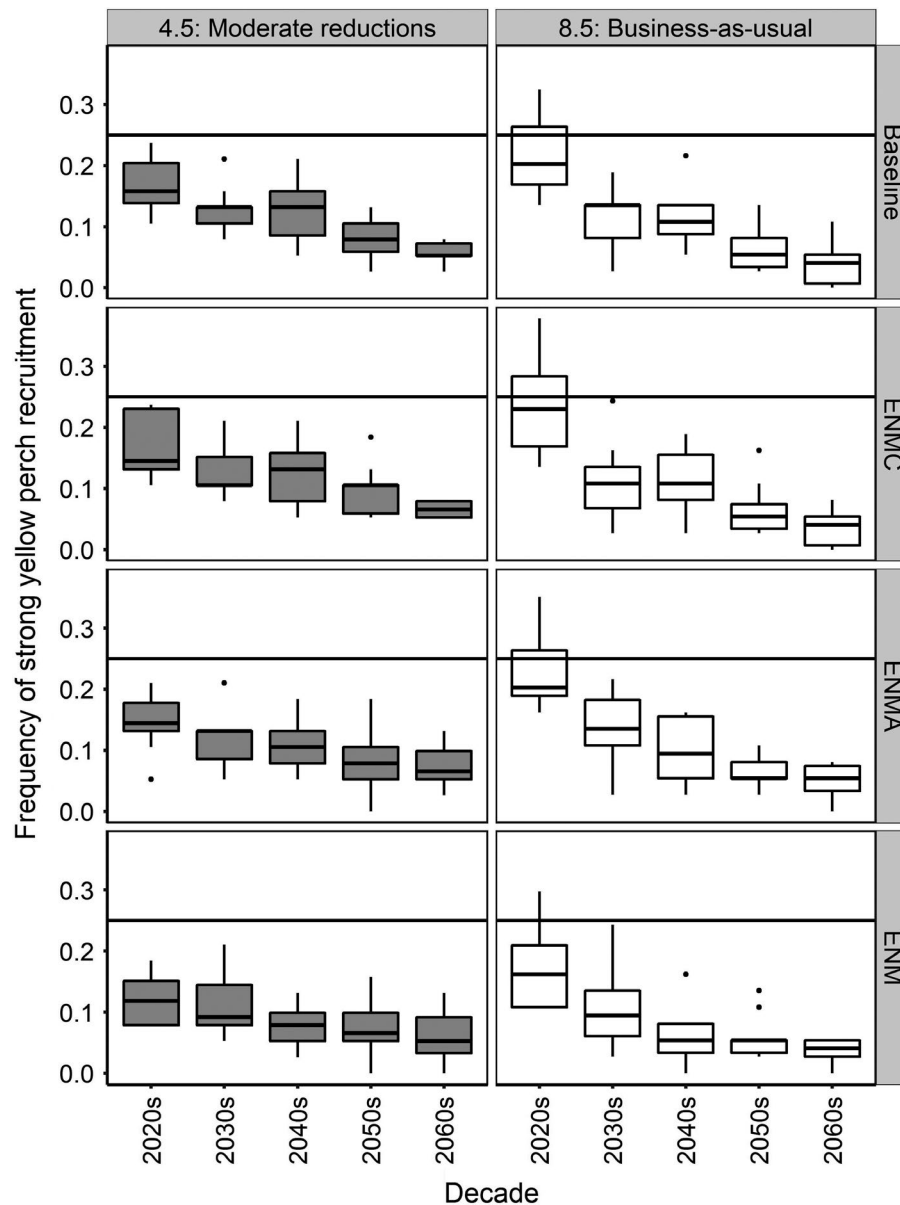
implementation, the frequency of strong white perch recruitment events was projected to be above the expected frequency (25% based on the historical occurrence of strong recruitment events), ranging from 27 to 54% (Figure 11).

## 4 | DISCUSSION

Predicting the effects of anthropogenic stressors such as climate change and agricultural-derived NPS pollution has been identified as a critical research need that could benefit fisheries management in the face of future ecosystem change (Arvai et al., 2006; DeVanna Fussell et al., 2016; Pritt et al., 2014). The Great Lakes, and specifically Lake Erie, is an ideal study system for such work because it has experienced these anthropogenic stressors, supports valuable fisheries, and is data-rich (Farmer et al., 2015; Ludsin et al., 2014; Pritt et al., 2014; Scavia et al., 2014). In this study, we forecasted how the recruitment of three ecologically and/or economically important western Lake Erie fish populations, which span a gradient of thermal preferences, might vary under future scenarios of climate change and ACP implementation in the

WLEB catchment. Our modelling showed that, in general, walleye and yellow perch recruitment can be expected to decrease and that white perch recruitment can be expected to remain stable or increase during the next several decades, relative to the recent past. Interestingly, our modelling also revealed offsetting effects between climate change and ACP implementation, highlighting the potential for trade-offs between improving water quality, maintaining fisheries production, and controlling invasive species in the face of potential climate change. Although attaining a complete understanding of future recruitment dynamics is impossible (Schindler & Hilborn, 2015), and more research is encouraged to verify some of our suggested mechanistic linkages and recruitment projections, our study presents a useful modelling framework to forecast fish population dynamics, specifically recruitment, and provides a range of potential outcomes for resource management agencies and policy-makers that can help them develop adaptive and resilient management strategies in the face of continued ecosystem change (Heller & Zavaleta, 2009; Lynch et al., 2016; Paukert et al., 2016).

Our results support previous studies, which have predicted that climate warming will differentially affect species with varying thermal preferences. Similar to other studies (Chu, Mandrak, & Minns, 2005;



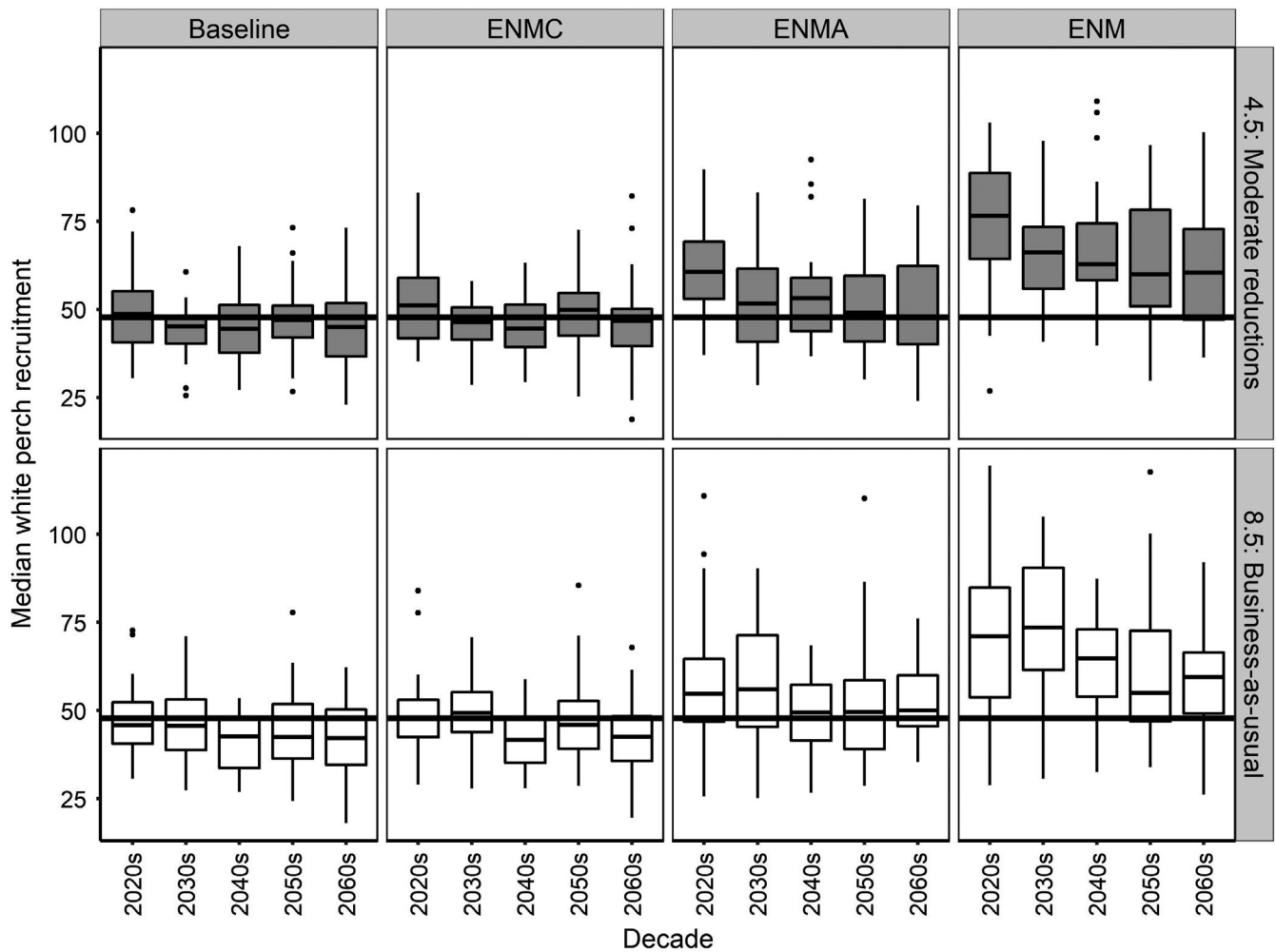
**FIGURE 9** Boxplot of the proportion of projected (2020–2065) forecasts of annual western Lake Erie yellow perch recruitment events (year-classes) that were greater than or equal to the historical (1987–2015) 75th percentile by decade and agricultural conservation practice implementation scenario. Projections were made for two greenhouse gas emission scenarios: RCP4.5 (grey) and RCP8.5 (white). The horizontal line represents the *expected* proportion of strong recruitment events, if the frequency were not to change in the future relative to the past. See the Figure 5 legend for a description of each agricultural conservation practice scenario

Farmer, 2013; Hansen et al., 2017; Van Zuiden et al., 2016), we projected declines in recruitment for walleye and yellow perch, which are considered cool-water species, and increased or stable recruitment in white perch, an invasive warm-water species. Although previous research has suggested that habitat conditions for *adult*, cool-water fishes, such as walleye, would increase with continued warming, especially in northern latitudes (e.g. Chu et al., 2005; Wiley et al., 2010), our research demonstrates the importance of considering other life stages (e.g. juvenile) and specific biological processes (e.g. reproduction and ovary development) that require cold temperatures, and therefore, are more likely to be affected by warming. Understanding the influence of warming is especially critical for populations such

as Lake Erie walleye and yellow perch, the recruitment dynamics of which have been shown to be influenced by temperature, which in turn drives variability in the fishery (Farmer et al., 2015; Shuter & Koonce, 1977; WTG, 2017). In fact, species that are sensitive to winter conditions (such as walleye and yellow perch) may be the first to be affected by climate change (Shuter, Minns, & Lester, 2002).

#### 4.1 | Walleye recruitment

Based on our findings, western Lake Erie walleye recruitment, especially episodically strong recruitment events that keep the



**FIGURE 10** Boxplot of projected (2020–2065) median annual western Lake Erie white perch recruitment (year-class strength, CPUE, individuals/min) under the RCP4.5 (grey) and RCP8.5 (white) emission scenarios by decade and agricultural conservation practice implementation scenario. See the Figure 5 legend for a description of each agricultural conservation practice scenario

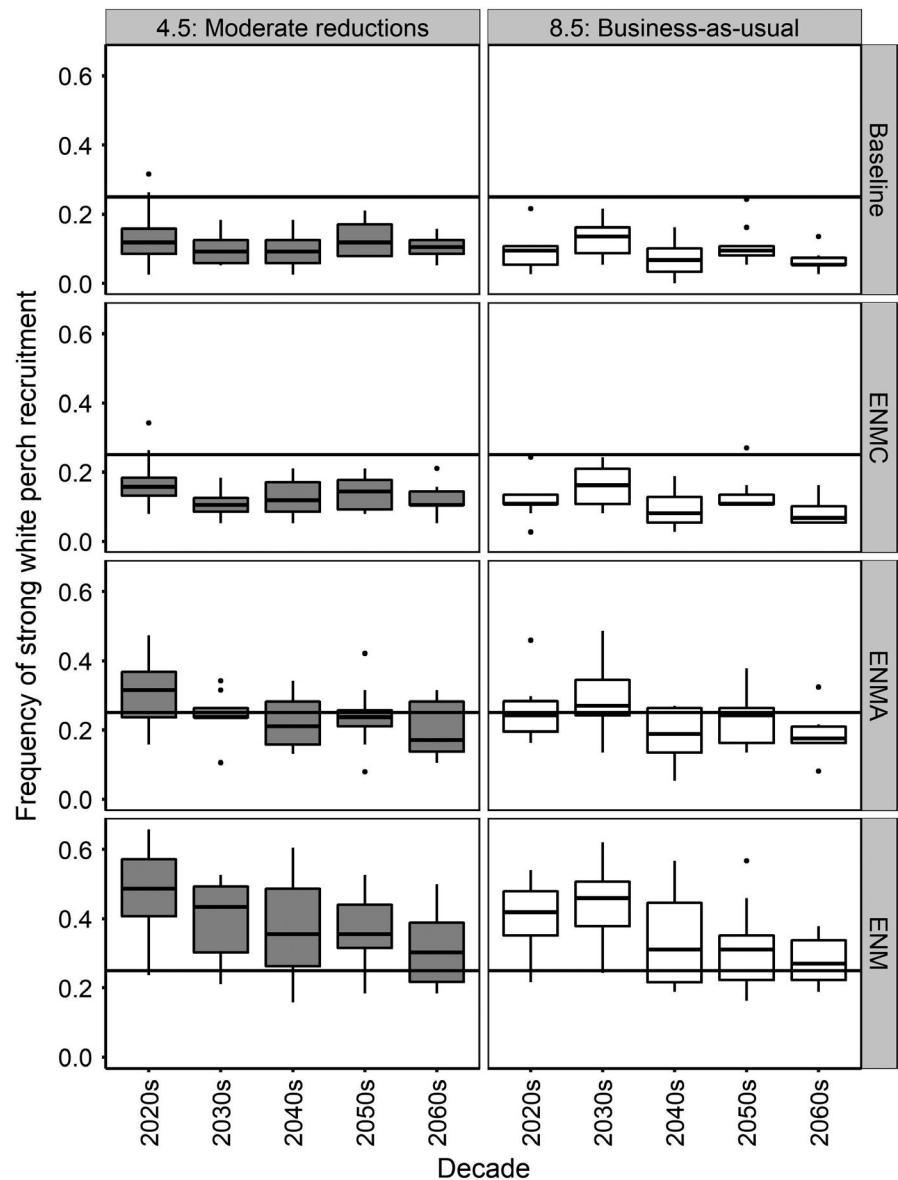
recreational and commercial fisheries viable (Vandergoot et al., 2010), were predicted to decline, owing to a projected reduction in winter severity. Recruitment declines were greatest further into the 21st century and in the *business-as-usual* greenhouse gas emission scenario (RCP8.5), relative to the moderate-reduction (RCP4.5) scenario. Although we documented an overall downward trend in projected walleye recruitment in the future, median walleye recruitment was generally projected to be at or above the historical median during the 2020s–2040s. Even so, the projected frequency of strong walleye recruitment events was below the *expected* proportion (25%) during these and subsequent decades, under both greenhouse gas emission scenarios.

Our modelling results are consistent with other modelling studies that have forecasted walleye recruitment under a changing climate. For example, Hansen et al. (2017) showed that the projected number of Wisconsin (U.S.A.) lakes likely to support walleye recruitment decreased in the future, owing to increases in the number of annual degree days under future warming scenarios. Likewise, Van Zuiden et al. (2016) concluded that projected warming should lead to an increase in unsuitable habitat at the southern range of walleye,

resulting in a general northward shift in their distribution. While we fully expect western Lake Erie to continue to support walleye fisheries, our modelling suggests that the strong recruitment events (year-classes) that drive order of magnitude differences in the fishable population (Vandergoot et al., 2010) may decline with continued climate warming.

Our predictive model explained 31.3% of the variation in walleye recruitment, which is similar to or better than studies that have correlated walleye recruitment to abiotic and/or biotic factors (e.g. Madenjian, Tyson, Knight, Kershner, & Hansen, 1996; Shaw, Sass, & VanDeHey, 2018; Shuter & Koonce, 1977; Zhao, Kocovsky, & Madenjian, 2013). Historically, explaining walleye recruitment variability using various measures of spawning-stock biomass has yielded poor results (Madenjian et al., 1996; Shaw et al., 2018), and considering environmental drivers of recruitment has consistently yielded better results (Busch et al., 1975; Madenjian et al., 1996; Roseman et al., 1999; Shuter & Koonce, 1977; Zhao et al., 2009). Much work on Lake Erie walleye recruitment has suggested the rate of spring warming is significantly and positively related to walleye recruitment (Busch et al., 1975; Madenjian et al., 1996; Roseman

**FIGURE 11** Boxplot of the proportion of projected (2020–2065) forecasts of annual western Lake Erie white perch recruitment events (year-classes) that were greater than or equal to the historical (1992–2015) 75th percentile by decade and agricultural conservation practice implementation scenario. Projections were made for two greenhouse gas emission scenarios: RCP4.5 (grey) and RCP8.5 (white). The horizontal line represents the expected proportion of strong recruitment events, if the frequency were not to change in the future relative to the past. See the Figure 5 legend for a description of each agricultural conservation practice scenario



et al., 1999; Zhao et al., 2013). Although we considered spring warming rate, it was not included in our final predictive model of walleye recruitment. The lack of inclusion of spring warming rate as a recruitment driver is not, however, inconsistent with all previous Lake Erie walleye recruitment work. For example, Zhao et al. (2009) used a three-dimensional hydrodynamic model to demonstrate that walleye recruitment was more strongly associated with wind speed and direction than it was with spring warming rate. Data such as wind speed, however, are not available from climate models and were therefore not considered in this study.

In addition to abiotic factors, biotic factors are also likely to affect walleye recruitment, which we did not consider. For example, prey abundance, specifically, age-0 gizzard shad (*Dorosoma cepedianum*) abundance has been correlated to Lake Erie walleye recruitment (Madenjian et al., 1996), but not with consistent, replicable results (Zhao et al., 2013). It is also possible that climate change could have indirect effects on walleye recruitment that is mediated by biotic factors such as zooplankton prey availability to larvae (Ludsin et al.,

2014). Ultimately, our understanding of walleye recruitment in Lake Erie remains largely speculative and is based primarily on correlative work. While the use of winter severity to predict walleye recruitment is partially supported by mechanistic evidence, as walleye prefer cooler incubation and fertilisation temperatures (Koest & Smith, 1976), exactly why the relationship between winter severity and walleye recruitment exists remains unknown (Fedor, 2008). More research into this linkage is warranted, as well as into how climate change might affect walleye through other direct and indirect pathways.

## 4.2 | Yellow perch recruitment

Similar to walleye, our modelling projected that Lake Erie yellow perch recruitment will decline under future climate warming scenarios. Furthermore, it suggests that this decline would be exacerbated by efforts to reduce nutrient inputs (i.e. TP) into Lake Erie via

the implementation of ACPs in the WLEB catchment. The prominent driver of the projected yellow perch recruitment decline was reduced winter severity, with the level of ACP implementation having a secondary negative effect. Although yellow perch recruitment displayed a unimodal, dome-shaped response to Maumee River TP inputs, future anticipated ACP implementation led to TP loads that were lower than the optimum for strong recruitment events to occur. Previous studies of yellow perch recruitment have suggested that rapid warming during the spring can positively (Eshenroder, 1977) and negatively (Zhang, Reid, & Nudds, 2016) influence yellow perch recruitment, whereas it was not identified as a useful predictor in our final model.

Median annual yellow perch recruitment was projected to be less than the historical median during all decades considered, under all climate and ACP implementation scenarios. Similarly, the projected frequency of a strong annual recruitment event occurring was lower than the expected 25% across all scenarios and decades with the lowest projected frequency occurring at the highest level of ACP implementation, during the 2050s–2060s under the *business-as-usual* emission scenario (RCP8.5). These results are generally consistent with other studies, which have demonstrated that short, warm winters can reduce yellow perch recruitment (Farmer et al., 2015; Hokanson, 1977). Additionally, our modelling suggests that ACP implementation efforts designed to improve water quality by reducing NPS nutrient loading could inadvertently reduce fisheries production, a notion that was espoused earlier when Lake Erie was undergoing oligotrophication (Ludsin, 2000; Ludsin et al., 2001). In this way, ACP implementation could potentially magnify the anticipated negative effects of climate warming on yellow perch recruitment. The need to consider these kinds of trade-offs is paramount as they could help fishery managers and policy-makers identify nutrient mitigation strategies that improve water quality without compromising fisheries production.

Our yellow perch model explained 51.1% of the variation in recruitment and included both winter severity and Maumee River TP as environmental predictors. Similar to walleye, various measures of spawning-stock size have not consistently explained yellow perch recruitment variation (Henderson, 1985; Henderson & Nepszy, 1988; Zhang et al., 2016) and yellow perch recruitment synchrony throughout the Great Lakes region indicate that regional-scale environmental factors, such as those included in this study, are more likely than stock size to drive recruitment (Honsey et al., 2016). The two environmental drivers of yellow perch recruitment that we identified are consistent with findings from previous correlative and mechanistic studies (Carreon-Martinez et al., 2014; Farmer et al., 2015; Hall & Rudstam, 1999; Hokanson, 1977; Ludsin et al., 2011; Reichert et al., 2010). For example, a greater percentage of yellow perch successfully spawn at colder water temperatures and after long chill durations (Hokanson, 1977) compared to warmer temperatures, indicating a benefit of long, cold winters for yellow perch. This finding is supported by experimental research, which has demonstrated that short warm winters cause reduced egg hatching success and reduced egg and larvae

size and quality (Farmer et al., 2015). Declines in yellow perch abundance have also previously been correlated with reduced TP availability (Hall & Rudstam, 1999).

The possibility exists, however, that Maumee River TP is only a proxy for a more complex suite of ecological responses associated with Maumee River discharge and nutrient and sediment loading, all of which are highly correlated (D.A.D., unpublished data). Turbid, nutrient-rich river plumes, which are created by Maumee River inflow during the spring, have been shown to lead to greater yellow perch recruitment in western Lake Erie (Carreon-Martinez et al., 2014; Ludsin et al., 2011; Reichert et al., 2010). Survival of larvae inside the Maumee River plume has been shown to be greater than larval survival outside the plume (Carreon-Martinez et al., 2014; Reichert et al., 2010), and this difference appears due to reduced predation inside the plume (Carreon-Martinez et al., 2014; Ludsin et al., 2011; Reichert et al., 2010). Although the exact causal mechanism(s) remain incomplete, sediment and/or nutrient loading from the Maumee River seem(s) to have a positive effect on yellow perch survival to the age-0 stage. Thus, reduced nutrient loading in the future via ACP implementation could have negative effects on yellow perch recruitment. Given the high degree of covariation among TP loading, sediment loading, and Maumee River inflows, as well as a possible trade-off between water quality and yellow perch production with ACP implementation under a changing climate, we advocate for more research aimed at identifying the mechanism(s) underlying the unimodal relationship that we found between Maumee River TP loading and yellow perch recruitment.

### 4.3 | White perch recruitment

White perch recruitment (both median levels and the frequency of strong recruitment events) was forecasted to be close to or greater than the historical median across all scenarios during all decades, and increased levels of ACP implementation (i.e. reduced TP loading) resulted in generally higher white perch recruitment. Substantially less information exists on the drivers of white perch recruitment relative to walleye or yellow perch, especially in ecosystems where this species is invasive (e.g. Lake Erie). However, our finding that climate warming may lead to higher white perch recruitment is generally consistent with the literature that does exist. For example, Johnson and Evans (1990) speculated that climate warming would cause higher recruitment and ultimately expansion of white perch in the Great Lakes by reducing overwinter mortality. Although winter severity was not included in the final predictive model of white perch recruitment, climate warming could possibly result in a longer growing season and improve overwinter survival (Johnson & Evans, 1990). The generally negative (although nonlinear) relationship between Maumee River TP and white perch recruitment was the opposite of our expectation, as white perch generally prefer eutrophic over oligotrophic waters (Boileau, 1985). Adult white perch abundance has also previously been shown to be positively associated with high turbidity and eutrophic conditions in



other ecosystems (Hawes & Parrish, 2003), indicating a need for more research to understand our observed association.

Similar to yellow perch, the possibility exists that our TP metric is only a proxy for another correlated abiotic factor, such as river discharge, which could actually be the driver of our observed association. For example, because white perch spawn in west basin tributaries (Boileau, 1985; Schaeffer & Margraf, 1986, 1987), high river discharge events (strongly correlated with TP loading) could potentially dislodge or flush white perch eggs out of the Maumee River prematurely, thus reducing their survival potential. This hypothesis is consistent with previous research that found significant negative correlations between Maumee River discharge and age-0 white perch abundance in the west basin of Lake Erie (Briland, 2018). Maumee River TP could also be a proxy for a complex biotic mechanism. For example, another plausible hypothesis is that high levels of TP, which results in high yellow perch recruitment, could reduce white perch recruitment through interspecific competition. Such interactions between age-0 white perch and yellow perch have been observed in other ecosystems (Prout, Mills, & Forney, 1990). Ultimately, this surprising relationship between Maumee River TP loading and white perch recruitment leads to more questions than it provides answers, pointing to the need for additional research.

Regardless of the ultimate mechanism, increases in white perch recruitment could have serious ecological effects that warrant further study. For example, white perch are known predators of walleye eggs (Schaeffer & Margraf, 1987), and increased white perch abundance could potentially negatively affect walleye recruitment. Also, yearling and adult white perch are known predators of yellow perch larvae (Carreon-Martinez et al., 2014; Ludsins et al., 2011), and increased predation from an even more abundant white perch population in the future could further exacerbate the projected negative effects of climate warming and ACP implementation on western Lake Erie's yellow perch population. Although we did not account for biotic interactions in our study, collectively, our results highlight the need to understand how warm-water invasive species, such as white perch, which are likely to thrive in a warmer future climate, might impact native cool-water fishes in temperate ecosystems such as Lake Erie.

#### 4.4 | Study limitations

As with all forecasting studies, our approach has several limitations. Although the proportions of variance in recruitment that our predictive models explained were similar to or better than those reported in the literature (see species-specific examples above), they certainly did not explain all, or in some cases the majority of recruitment variation. Still, such models can be useful in assessing the impacts of climate change (Guisan & Thuiller, 2005), although we strongly encourage managers to consider the breadth of information available when making future management and conservation decisions. Furthermore, care should be taken when extrapolating recruitment responses to environmental conditions outside the range of

observed historical conditions, as species-environment relationships may not be stationary (Schindler & Hilborn, 2015; Zhang, Reid, & Nudds, 2018). We also caution against interpreting the exact magnitude of our future recruitment values in a *predict and prescribe* approach (Schindler & Hilborn, 2015), given mechanistic uncertainties associated with our predictive models. Even so, we feel comfortable interpreting the general trends and drivers apparent in our results and their use as guidance for future management.

Forecasting future population dynamics will always be incomplete, uncertain, and a simplification of reality, regardless of the ecosystem. However, studies like ours provide a range of possible outcomes that can be used as tools for resource managers (Schindler & Hilborn, 2015). While we do not know the true magnitude or extent of future warming, by modelling multiple greenhouse gas emission scenarios, using a suite of climate ensembles, we could propagate some of that future uncertainty into our recruitment forecasts (Hansen et al., 2017). This *ensemble approach* to forecasting future dynamics is ubiquitous and is an accepted way of acknowledging the uncertainty in future predictions (Bartolino et al., 2014; Hollowed et al., 2009; Lindegren et al., 2010), although we recognise this approach does not account for all of the uncertainty associated with forecasting future recruitment.

Another limitation to our study is that our methods were correlative and did not verify the underlying mechanisms by which winter severity, spring warming rate, and TP loads can alter recruitment dynamics. Thus, while we provided mechanistic support for their inclusion in our predictive models, which strengthens the confidence in our results (Hilborn, 2016), the possibility exists that the metrics included in this study encompass several underlying mechanisms (Hansen et al., 2017) or are actually proxies for other correlated environmental drivers. For example, because Maumee River TP loads into Lake Erie are highly correlated with Maumee River inflows and total suspended sediment loads, TP itself may not be the exact mechanistic driver of yellow perch or white perch recruitment. Owing to the difficulty in implementing and designing rigorous, experimental approaches to determine causal relationships over large spatial and temporal extents (Hilborn, 2016), correlative studies such as ours remain the most reasonable approach to forecasting recruitment on large spatial and temporal scales (Guisan & Thuiller, 2005; Hansen et al., 2017).

Because of the inherent difficulty in forecasting future biotic conditions, we restricted our analysis to include only abiotic predictors. However, biotic factors such as competition and predation probably also contribute to current recruitment dynamics of these species, and will probably affect future recruitment dynamics (Forsythe, Doll, & Lauer, 2012; Guisan & Thuiller, 2005; Hall & Rudstam, 1999; Hartman & Margraf, 1993). Thus, we encourage continued investigations into the drivers of recruitment for all three species, especially those that consider other factors, use alternative modelling approaches, and occur at different spatiotemporal scales (Hilborn, 2016). This need is especially critical because the mechanisms underlying our observed correlations are unlikely to remain stationary in the future (Schindler & Hilborn, 2015).

## 5 | CONCLUSIONS

Our modelling allowed us to explore how anticipated climate change and ACP implementation designed to reduce NPS nutrient loading might interact to affect the recruitment dynamics of ecologically and economically important fish populations in Lake Erie. By including two emission scenarios, four levels of ACP implementation, and numerous GCMs and ensembles, we forecasted a range of future outcomes to better equip resource managers to make decisions that can promote sustainable and resilient fisheries in the future (Lynch et al., 2016; Paukert et al., 2016). Our findings highlight the importance of climate as a driver of fish recruitment dynamics and indicate that, in the future, native cool-water species such as walleye and yellow perch may be detrimentally affected by climate change, whereas nonnative warm-water species such as white perch might benefit. Our modelling also suggests that reducing nutrient inputs to improve water quality (though ACP implementation) may lead to inadvertent trade-offs that could negatively affect the production of valued fisheries (Kao, Rogers, & Bunnell, 2018; Ludsins, 2000; Ludsins et al., 2001; Ney, 1996). For example, our modelling provided evidence to suggest that reduced nutrient (or possibly sediment) runoff from the WLEB catchment—resultant of ACP implementation—could exacerbate anticipated climate-driven reductions in western Lake Erie yellow perch recruitment. Simultaneously, these same conditions were projected to promote invasive white perch, which is a known predator on walleye and yellow perch early life stages (Carreon-Martinez et al., 2014; Ludsins et al., 2011; Schaeffer & Margraf, 1987).

In addition to identifying a need for more research into the mechanistic relationships among climate, catchment runoff, and yellow perch and white perch recruitment, we recommend that future studies seeking to quantify the independent and combined effects of human-driven perturbations (e.g. climate change, altered nutrient inputs) assess both the costs and benefits associated with changing conditions, in both upstream and downstream ecosystem services. Such information would allow for the development of improved forecasting models, as well as allow resource management agencies and policy-makers to better anticipate trade-offs and avoid ecological surprises. For example, decision-makers could learn whether any likely combination of climate and land use conditions provide a *win-win* scenario (sensu Keitzer et al., 2016) for upstream (catchment) fish production, downstream (recipient ecosystem) water quality (e.g. reduced bottom hypoxia and harmful algal blooms), and downstream fisheries production. Armed with this knowledge, informed decisions can be made to keep fisheries productive and sustainable in the face of continued ecosystem change.

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### CONFLICT OF INTEREST

The authors report no conflicts of interest.

### DATA AVAILABILITY STATEMENT

Data used to build the recruitment models are available as a separate file. The climate data are available at [https://gdo-dcp.ucllnl.org/downscaled\\_cmip\\_projections/dcpInterface.html](https://gdo-dcp.ucllnl.org/downscaled_cmip_projections/dcpInterface.html).

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### REFERENCES

- Adams, G. D., Leaf, R. T., Wu, W., & Hernandez, F. J. (2018). Environmentally driven fluctuations in condition factor of adult Gulf menhaden (*Brevoortia patronus*) in the northern Gulf of Mexico. *ICES Journal of Marine Science*, 75(4), 1269–1279.
- Alofs, K. M., Jackson, D. A., & Lester, N. P. (2014). Ontario freshwater fishes demonstrate differing range-boundary shifts in a warming climate. *Diversity and Distributions*, 20(2), 123–136.
- Anderson, D. R., & Burnham, K. P. (2002). Avoiding pitfalls when using information-theoretic methods. *The Journal of Wildlife Management*, 66(3), 912–918. <https://doi.org/10.2307/3803155>.
- Arnold, J. G., Srinivasan, R., Muttiah, R. S., & Williams, J. R. (1998). Large area hydrologic modeling and assessment part I: Model development 1. *JAWRA Journal of the American Water Resources Association*, 34(1), 73–89.
- Arvai, J., Bridge, G., Dolsak, N., Franzese, R., Koontz, T., Luginbuhl, A., ... Thompson, A. (2006). Adaptive management of the global climate problem: Bridging the gap between climate research and climate policy. *Climatic Change*, 78(1), 217–225.
- Baker, D. B., & Richards, R. P. (2002). Phosphorus budgets and riverine phosphorus export in northwestern Ohio watersheds. *Journal of Environmental Quality*, 31(1), 96–108.
- Barbiero, R. P., Balcer, M., Rockwell, D. C., & Tuchman, M. L. (2009). Recent shifts in the crustacean zooplankton community of Lake

- Huron. *Canadian Journal of Fisheries and Aquatic Sciences*, 66(5), 816–828.
- Bartolai, A. M., He, L., Hurst, A. E., Mortsch, L., Paehlke, R., & Scavia, D. (2015). Climate change as a driver of change in the Great Lakes St. Lawrence River basin. *Journal of Great Lakes Research*, 41, 45–58.
- Bartolino, V., Margonski, P., Lindegren, M., Linderholm, H. W., Cardinale, M., Rayner, D., ... Casini, M. (2014). Forecasting fish stock dynamics under climate change: Baltic herring (*Clupea harengus*) as a case study. *Fisheries Oceanography*, 23(3), 258–269.
- Belore, M., Cook, A., Hartman, T., Hosack, M., Kayle, K., Knight, C., ...Witzel, L. (2014). Report of the Lake Erie Yellow Perch Task Group. Ann Arbor: Michigan, USA.
- Blanchard, J. L., Jennings, S., Holmes, R., Harle, J., Merino, G., Allen, J. I., ... Barange, M. (2012). Potential consequences of climate change for primary production and fish production in large marine ecosystems. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 367(1605), 2979–2989.
- Boileau, M. G. (1985). The expansion of white perch, *Morone americana*, in the lower Great Lakes. *Fisheries*, 10(1), 6–10.
- Bolsenga, S. J., & C. E. Herdendorf (Eds.) (1993). *Lake Erie and Lake St. Clair Handbook*. Detroit: Wayne State University Press.
- Bosch, N. S., Allan, J. D., Selegean, J. P., & Scavia, D. (2013). Scenario-testing of agricultural best management practices in Lake Erie watersheds. *Journal of Great Lakes Research*, 39(3), 429–436.
- Breitburg, D. (2002). Effects of hypoxia, and the balance between hypoxia and enrichment, on coastal fishes and fisheries. *Estuaries*, 25(4), 767–781.
- Breitburg, D. L., Hondorp, D. W., Davias, L. A., & Diaz, R. J. (2009). Hypoxia, nitrogen, and fisheries: Integrating effects across local and global landscapes. *Annual Review of Marine Science*, 1, 329–349.
- Briland, R. (2018). *Evaluating the causes and consequences of ecosystem change in Lake Erie: From plankton to fish* (Doctoral dissertation. The Ohio: State University).
- Brochier, T., Echevin, V., Tam, J., Chaigneau, A., Goubanova, K., & Bertrand, A. (2013). Climate change scenarios experiments predict a future reduction in small pelagic fish recruitment in the Humboldt Current system. *Global Change Biology*, 19(6), 1841–1853.
- Brunel, T., & Boucher, J. (2007). Long-term trends in fish recruitment in the north-east Atlantic related to climate change. *Fisheries Oceanography*, 16(4), 336–349.
- Buchheister, A., Bonzek, C. F., Gartland, J., & Latour, R. J. (2013). Patterns and drivers of the demersal fish community of Chesapeake Bay. *Marine Ecology Progress Series*, 481, 161–180.
- Bunnell, D. B., Barbiero, R. P., Ludsins, S. A., Madenjian, C. P., Warren, G. J., Dolan, D. M., ... Weidel, B. C. (2013). Changing ecosystem dynamics in the Laurentian Great Lakes: Bottom-up and top-down regulation. *BioScience*, 64(1), 26–39.
- Bureau of Reclamation (2013). *Downscaled CMIP3 and CMIP5 Climate and Hydrology Projections: Release of Downscaled CMIP5 Climate Projections, Comparison with preceding Information, and Summary of User Needs*. (U.S. Department of the Interior, Bureau of Reclamation, Technical Service Center, Denver, Colorado
- Burnham, K. P., & Anderson, D. R. (2003). *Model selection and multimodel inference: A practical information-theoretic approach*. Berlin: Springer Science & Business Media.
- Busch, W. D. N., Scholl, R. L., & Hartman, W. L. (1975). Environmental factors affecting the strength of walleye (*Stizostedion vitreum vitreum*) year-classes in western Lake Erie, 1960–70. *Journal of the Fisheries Board of Canada*, 32(10), 1733–1743.
- Caddy, J. F. (1993). Toward a comparative evaluation of human impacts on fishery ecosystems of enclosed and semi-enclosed seas. *Reviews in Fisheries Science*, 1(1), 57–95.
- Caddy, J. F. (2000). Marine catchment basin effects versus impacts of fisheries on semi-enclosed seas. *ICES Journal of Marine Science*, 57(3), 628–640.
- Cardinale, M., & Arrhenius, F. (2000). The influence of stock structure and environmental conditions on the recruitment process of Baltic cod estimated using a generalized additive model. *Canadian Journal of Fisheries and Aquatic Sciences*, 57(12), 2402–2409.
- Carreon-Martinez, L. B., Wellband, K. W., Johnson, T. B., Ludsins, S. A., & Heath, D. D. (2014). Novel molecular approach demonstrates that turbid river plumes reduce predation mortality on larval fish. *Molecular Ecology*, 23(21), 5366–5377.
- Chu, C., Mandrak, N. E., & Minns, C. K. (2005). Potential impacts of climate change on the distributions of several common and rare freshwater fishes in Canada. *Diversity and Distributions*, 11(4), 299–310.
- Clady, M. D. (1976). Influence of temperature and wind on the survival of early stages of yellow perch, *Perca flavescens*. *Journal of the Fisheries Board of Canada*, 33(9), 1887–1893.
- Collingsworth, P. D., Bunnell, D. B., Murray, M. W., Kao, Y.-C., Feiner, Z. S., Claramunt, R. M., ... Ludsins, S. A. (2017). Climate change as a long-term stressor for the fisheries of the Laurentian Great Lakes of North America. *Reviews in Fish Biology and Fisheries*, 27(2), 363–391.
- Collingsworth, P. D., & Marschall, E. A. (2011). Identifying relationships between catches of spawning condition yellow perch and environmental variables in the western basin of Lake Erie. *Transactions of the American Fisheries Society*, 140(1), 31–36.
- Comte, L., Buisson, L., Daufresne, M., & Grenouillet, G. (2013). Climate-induced changes in the distribution of freshwater fish: Observed and predicted trends. *Freshwater Biology*, 58(4), 625–639.
- Daggupati, P., Yen, H., White, M. J., Srinivasan, R., Arnold, J. G., Keitzer, C. S., & Sowa, S. P. (2015). Impact of model development, calibration and validation decisions on hydrological simulations in West Lake Erie Basin. *Hydrological Processes*, 29(26), 5307–5320.
- Daskalov, G. (1999). Relating fish recruitment to stock biomass and physical environment in the Black Sea using generalized additive models. *Fisheries Research*, 41(1), 1–23.
- de Mutsert, K., Steenbeek, J., Lewis, K., Buszowski, J., Cowan, J. H. Jr, & Christensen, V. (2016). Exploring effects of hypoxia on fish and fisheries in the northern Gulf of Mexico using a dynamic spatially explicit ecosystem model. *Ecological Modelling*, 331, 142–150.
- Decker, M. B., Liu, H., Ciannelli, L., Ladd, C., Cheng, W., & Chan, K. S. (2013). Linking changes in eastern Bering Sea jellyfish populations to environmental factors via nonlinear time series models. *Marine Ecology Progress Series*, 494, 179–189.
- DeVanna Fussell, K. M., Smith, R. E. H., Fraker, M. E., Boegman, L., Frank, K. T., Miller, T. J., ... Ludsins, S. A. (2016). A perspective on needed research, modeling, and management approaches that can enhance Great Lakes fisheries management under changing ecosystem conditions. *Journal of Great Lakes Research*, 42(4), 743–752.
- Diaz, R. J., & Rosenberg, R. (2008). Spreading dead zones and consequences for marine ecosystems. *Science*, 321(5891), 926–929.
- Drinkwater, K. F., Beaugrand, G., Kaeriyama, M., Kim, S., Ottersen, G., Perry, R. I., ... Takasuka, A. (2010). On the processes linking climate to ecosystem changes. *Journal of Marine Systems*, 79(3–4), 374–388.
- DuFour, M. R., May, C. J., Roseman, E. F., Ludsins, S. A., Vandergoot, C. S., Pritt, J. J., ... Mayer, C. M. (2015). Portfolio theory as a management tool to guide conservation and restoration of multi-stock fish populations. *Ecosphere*, 6(12), 1–21.
- Eshenroder, R. L. (1977). Effects of intensified fishing, species changes, and spring water temperatures on yellow perch, *Perca flavescens*, in Saginaw Bay. *Journal of the Fisheries Board of Canada*, 34(10), 1830–1838.
- Farmer, T. M. (2013). *Climate change effects on Lake Erie yellow perch reproduction and recruitment* (Doctoral dissertation. The Ohio: State University).
- Farmer, T. M., Marschall, E. A., Dabrowski, K., & Ludsins, S. A. (2015). Short winters threaten temperate fish populations. *Nature Communications*, 6, 7724.

- Fedor, S. L. (2008). *Synchronous Recruitment of Walleye in the Great Lakes and the Influence [sic] of Climate on Recruitment* (Master's thesis. Ohio State University).
- Filipe, A. F., Markovic, D., Pletterbauer, F., Tisseuil, C., De Wever, A., Schmutz, S., ... Freyhof, J. (2013). Forecasting fish distribution along stream networks: Brown trout (*Salmo trutta*) in Europe. *Diversity and Distributions*, 19(8), 1059–1071.
- Forsythe, P. S., Doll, J. C., & Lauer, T. E. (2012). Abiotic and biotic correlates of yellow perch recruitment to age-2 in southern Lake Michigan, 1984–2007. *Fisheries Management and Ecology*, 19(5), 389–399.
- FTG Forage Task Group (2013). Report of the Lake Erie Forage Task Group, March 2013. Presented to the Standing Technical Committee, Lake Erie Committee of the Great Lakes Fishery Commission, Ann Arbor, MI.
- Gassman, P. W., Williams, J. R., Wang, X., Saleh, A., Osei, E., Hauck, L. M., ... Flowers, J. (2009). The Agricultural Policy Environmental Extender (APEX) model: An emerging tool for landscape and watershed environmental analyses.
- Grimes, C. B., & Finucane, J. H. (1991). Spatial distribution and abundance of larval and juvenile fish, chlorophyll and macrozooplankton around the Mississippi River discharge plume, and the role of the plume in fish recruitment. *Marine Ecology Progress Series*, 75(2), 109–119.
- Guisan, A., & Thuiller, W. (2005). Predicting species distribution: Offering more than simple habitat models. *Ecology Letters*, 8(9), 993–1009.
- Hagy, J. D., Boynton, W. R., Keefe, C. W., & Wood, K. V. (2004). Hypoxia in Chesapeake Bay, 1950–2001: Long-term change in relation to nutrient loading and river flow. *Estuaries*, 27(4), 634–658.
- Hall, S. R., & Rudstam, L. G. (1999). Habitat use and recruitment: A comparison of longterm recruitment patterns among fish species in a shallow eutrophic lake, Oneida, NY, U.S.A. *Hydrobiologia* 408/409, 101–103.
- Hansen, G. J., Read, J. S., Hansen, J. F., & Winslow, L. A. (2017). Projected shifts in fish species dominance in Wisconsin lakes under climate change. *Global Change Biology*, 23(4), 1463–1476.
- Hartman, K. J., & Margraf, F. J. (1993). Evidence of predatory control of yellow perch (*Perca flavescens*) recruitment in Lake Erie, USA. *Journal of Fish Biology*, 43(1), 109–119.
- Hartman, W. L. (1972). Lake Erie: Effects of exploitation, environmental changes and new species on the fishery resources. *Journal of the Fisheries Board of Canada*, 29(6), 899–912.
- Hastie, T., & Tibshirani, R. (1987). Generalized additive models: Some applications. *Journal of the American Statistical Association*, 82(398), 371–386.
- Hawes, E. J., & Parrish, D. L. (2003). Using abiotic and biotic factors to predict the range expansion of white perch in Lake Champlain. *Journal of Great Lakes Research*, 29(2), 268–279.
- Hayhoe, K., VanDorn, J., Croley, T. II, Schlegal, N., & Wuebbles, D. (2010). Regional climate change projections for Chicago and the US Great Lakes. *Journal of Great Lakes Research*, 36, 7–21.
- Heller, N. E., & Zavaleta, E. S. (2009). Biodiversity management in the face of climate change: A review of 22 years of recommendations. *Biological Conservation*, 142(1), 14–32.
- Henderson, B. A. (1985). Factors affecting growth and recruitment of yellow perch, *Perca flavescens* Mitchell, in South Bay, Lake Huron. *Journal of Fish Biology*, 26(4), 449–458.
- Henderson, B. A., & Nepszy, S. J. (1988). Recruitment of yellow perch (*Perca flavescens*) affected by stock size and water temperature in Lakes Erie and St. Clair, 1965–85. *Journal of Great Lakes Research*, 14(2), 205–215.
- Hilborn, R. (2016). Correlation and causation in fisheries and watershed management. *Fisheries*, 41(1), 18–25.
- Hokanson, K. E. (1977). Temperature requirements of some percids and adaptations to the seasonal temperature cycle. *Journal of the Fisheries Board of Canada*, 34(10), 1524–1550.
- Hollowed, A. B., Bond, N. A., Wilderbuer, T. K., Stockhausen, W. T., A'mar, Z. T., Beamish, R. J., ... Schirripa, M. J. (2009). A framework for modelling fish and shellfish responses to future climate change. *ICES Journal of Marine Science*, 66(7), 1584–1594.
- Honsey, A. E., Bunnell, D. B., Troy, C. D., Fielder, D. G., Thomas, M. V., Knight, C. T., ... Höök, T. O. (2016). Recruitment synchrony of yellow perch (*Perca flavescens*, Percidae) in the Great Lakes region, 1966–2008. *Fisheries Research*, 181, 214–221.
- Hunsicker, M. E., Kappel, C. V., Selkoe, K. A., Halpern, B. S., Scarborough, C., Mease, L., & Amrhein, A. (2016). Characterizing driver–response relationships in marine pelagic ecosystems for improved ocean management. *Ecological Applications*, 26(3), 651–663.
- IPCC (2014). Summary for policymakers. In: *Climate Change 2014: Impacts Adaptation and Vulnerability. Part A: Global and Sectoral Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. eds Field CB Barros VR Dokken DJ Mach KJ Mastrandrea MD Bilir TE Chatterjee M Ebi KL Estrada YO Genova RC et al (Intergovernmental Panel on Climate Change, Cambridge, UK), pp 1–32.
- Johnson, T. B., & Evans, D. O. (1990). Size-dependent winter mortality of young-of-the-year white perch: Climate warming and invasion of the Laurentian Great Lakes. *Transactions of the American Fisheries Society*, 119(2), 301–313.
- Jones, M. L., Netto, J. K., Stockwell, J. D., & Mion, J. B. (2003). Does the value of newly accessible spawning habitat for walleye (*Stizostedion vitreum*) depend on its location relative to nursery habitats? *Canadian Journal of Fisheries and Aquatic Sciences*, 60(12), 1527–1538.
- Jones, M. L., Shuter, B. J., Zhao, Y., & Stockwell, J. D. (2006). Forecasting effects of climate change on Great Lakes fisheries: Models that link habitat supply to population dynamics can help. *Canadian Journal of Fisheries and Aquatic Sciences*, 63(2), 457–468.
- Kane, D. D., Conroy, J. D., Richards, R. P., Baker, D. B., & Culver, D. A. (2014). Re-eutrophication of Lake Erie: Correlations between tributary nutrient loads and phytoplankton biomass. *Journal of Great Lakes Research*, 40(3), 496–501.
- Kao, Y. C., Rogers, M. W., & Bunnell, D. B. (2018). Evaluating stocking efficacy in an ecosystem undergoing oligotrophication. *Ecosystems*, 21, 1–19.
- Kayle, K., Oldenburg, K., Murray, C., Francis, J., & Markham, J. (2015). Lake Erie walleye management plan 2015–2019. Great Lakes Fishery Commission, Ann Arbor, Michigan. Retrieved from [http://www.glf.org/pubs/lake\\_committees/erie/LEC\\_docs/position\\_statements/walleye\\_managment\\_plan.pdf](http://www.glf.org/pubs/lake_committees/erie/LEC_docs/position_statements/walleye_managment_plan.pdf).
- Keitzer, S. C., Ludsin, S. A., Sowa, S. P., Annis, G., Arnold, J. G., Daggupati, P., ... Rewa, C. A. (2016). Thinking outside of the lake: Can controls on nutrient inputs into Lake Erie benefit stream conservation in its watershed? *Journal of Great Lakes Research*, 42(6), 1322–1331.
- Kemp, W. M., Boynton, W. R., Adolf, J. E., Boesch, D. F., Boicourt, W. C., Brush, G., ... Stevenson, J. C. (2005). Eutrophication of Chesapeake Bay: Historical trends and ecological interactions. *Marine Ecology Progress Series*, 303, 1–29.
- Koenst, W. M., & Smith, L. L. Jr (1976). Thermal requirements of the early life history stages of walleye, *Stizostedion vitreum vitreum*, and sauger, *Stizostedion canadense*. *Journal of the Fisheries Board of Canada*, 33(5), 1130–1138.
- Krabbenhof, T. J., Platania, S. P., & Turner, T. F. (2014). Interannual variation in reproductive phenology in a riverine fish assemblage: Implications for predicting the effects of climate change and altered flow regimes. *Freshwater Biology*, 59(8), 1744–1754.
- Leach, J. H., & Nepszy, S. J. (1976). The fish community in Lake Erie. *Journal of the Fisheries Board of Canada*, 33(3), 622–638.
- Lindegren, M., Möllmann, C., Nielsen, A., Brander, K., MacKenzie, B. R., & Stenseth, N. C. (2010). Ecological forecasting under climate change: The case of Baltic cod. *Proceedings of the Royal Society of London B: Biological Sciences*, 277(1691), 2121–2130.

- Ludsin, S. A. (2000). Exploration of spatiotemporal patterns in recruitment and community organization of Lake Erie fishes: A multi-scale, mechanistic approach (Doctoral dissertation. The Ohio: State University).
- Ludsin, S. A., DeVanna, K. M., & Smith, R. E. (2014). Physical-biological coupling and the challenge of understanding fish recruitment in freshwater lakes. *Canadian Journal of Fisheries and Aquatic Sciences*, 71(5), 775–794.
- Ludsin, S. A., Kershner, M. W., Blocksom, K. A., Knight, R. L., & Stein, R. A. (2001). Life after death in Lake Erie: Nutrient controls drive fish species richness, rehabilitation. *Ecological Applications*, 11(3), 731–746.
- Ludsin, S., Pangle, K., Carreon-Martinez, L., Legler, N., Reichert, J., Heath, D., ... Leshkevich, G. (2011). River discharge as a predictor of Lake Erie yellow perch recruitment. *Final Completion Report, Great Lakes Fishery Commission*. Fisheries Research Program, Ann Arbor, MI. 166 pp.
- Lynch, A. J., Myers, B. J. E., Chu, C., Eby, L. A., Falke, J. A., Kovach, R. P., ... Whitney, J. E. (2016). Climate change effects on North American inland fish populations and assemblages. *Fisheries*, 41(7), 346–361.
- Maccoux, M. J., Dove, A., Backus, S. M., & Dolan, D. M. (2016). Total and soluble reactive phosphorus loadings to Lake Erie: A detailed accounting by year, basin, country, and tributary. *Journal of Great Lakes Research*, 42(6), 1151–1165.
- Madenjian, C. P., Tyson, J. T., Knight, R. L., Kershner, M. W., & Hansen, M. J. (1996). First-year growth, recruitment, and maturity of walleyes in western Lake Erie. *Transactions of the American Fisheries Society*, 125(6), 821–830.
- Maghrebi, M., Nalley, D., Laurent, K. L., & Atkinson, J. F. (2015). Water quantity as a driver of change in the Great Lakes–St. Lawrence River Basin. *Journal of Great Lakes Research*, 41, 84–95.
- Markham, J. L., & Knight, R. L. (2017). The state of Lake Erie 2009. Great Lakes Fishery Commission, Ann Arbor, MI. Special Publication 2017–01. Retrieved from [http://www.glfsc.org/pubs/SpecialPubs/Sp17\\_01.pdf](http://www.glfsc.org/pubs/SpecialPubs/Sp17_01.pdf).
- Maunder, M. N., & Punt, A. E. (2004). Standardizing catch and effort data: A review of recent approaches. *Fisheries Research*, 70(2–3), 141–159.
- Maurer, E. P., Brekke, L., Pruitt, T., & Duffy, P. B. (2007). Fine-resolution climate projections enhance regional climate change impact studies. *Eos, Transactions American Geophysical Union*, 88(47), 504–504.
- May, C. J. (2015). The importance of early life processes to future growth and recruitment in Lake Erie walleye (Doctoral dissertation. The Ohio: State University).
- Menne, M. J., Durre, I., Vose, R. S., Gleason, B. E., & Houston, T. G. (2012). An overview of the global historical climatology network-daily database. *Journal of Atmospheric and Oceanic Technology*, 29(7), 897–910.
- Mion, J. B., Stein, R. A., & Marschall, E. A. (1998). River discharge drives survival of larval walleye. *Ecological Applications*, 8(1), 88–103.
- Mueter, F. J., Bond, N. A., Ianelli, J. N., & Hollowed, A. B. (2011). Expected declines in recruitment of walleye pollock (*Theragra chalcogramma*) in the eastern Bering Sea under future climate change. *ICES Journal of Marine Science*, 68(6), 1284–1296.
- Ney, J. J. (1996). Oligotrophication and its discontents: Effects of reduced nutrient loading on reservoir fisheries. *American Fisheries Society Symposium*, 16, 285–295.
- ODW Ohio Division of Wildlife (2017). Ohio's Lake Erie Fisheries, 2016. Annual status report. Federal Aid in Fish Restoration Project F-69-P. Ohio Department of Natural Resources, Division of Wildlife, Lake Erie Fisheries Units, Fairport and Sandusky. 123 pp.
- ODW Ohio Division of Wildlife (2018). Ohio's Lake Erie Fisheries, 2018. Annual Report. Federal Aid in Fish Restoration Project F-69-P. Ohio Department of Natural Resources, Division of Wildlife, Lake Erie Fisheries Units, Fairport and Sandusky. 123 pp.
- Oglesby, R. T., Leach, J. H., & Forney, J. (1987). Potential *Stizostedion* yield as a function of chlorophyll concentration with special reference to Lake Erie. *Canadian Journal of Fisheries and Aquatic Sciences*, 44(S2), s166–s170.
- Ohio EPA (2013). Ohio Lake Erie phosphorus task force II, final report. Columbus, Ohio: Ohio Environmental Protection Agency.
- Ohio Supercomputer Center (1987). Ohio Supercomputer Center. Columbus, OH. Retrieved from <http://osc.edu/ark:/19495/f5s1ph73>.
- Paukert, C. P., Glazer, B. A., Hansen, G. J. A., Irwin, B. J., Jacobson, P. C., Kershner, J. L., ... Lynch, A. J. (2016). Adapting inland fisheries management to a changing climate. *Fisheries*, 41(7), 374–384.
- Pritt, J. J., Roseman, E. F., & O'Brien, T. P. (2014). Mechanisms driving recruitment variability in fish: Comparisons between the Laurentian Great Lakes and marine systems. *ICES Journal of Marine Science*, 71(8), 2252–2267.
- Prout, M. W., Mills, E. L., & Forney, J. L. (1990). Diet, growth, and potential competitive interactions between age-0 white perch and yellow perch in Oneida Lake, New York. *Transactions of the American Fisheries Society*, 119(6), 966–975.
- Quiñones, J., Mianzan, H., Purca, S., Robinson, K. L., Adams, G. D., & Acha, E. M. (2015). Climate-driven population size fluctuations of jellyfish (*Chrysaora plocamia*) off Peru. *Marine Biology*, 162(12).
- R Core Team (2019). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>.
- Radinger, J., Höfler, F., Horký, P., Slavík, O., Dendoncker, N., & Wolter, C. (2016). Synergistic and antagonistic interactions of future land use and climate change on river fish assemblages. *Global Change Biology*, 22(4), 1505–1522.
- Rahel, F. J., & Olden, J. D. (2008). Assessing the effects of climate change on aquatic invasive species. *Conservation Biology*, 22(3), 521–533.
- Reichert, J. M., Fryer, B. J., Pangle, K. L., Johnson, T. B., Tyson, J. T., Drelich, A. B., & Ludsin, S. A. (2010). River-plume use during the pelagic larval stage benefits recruitment of a lentic fish. *Canadian Journal of Fisheries and Aquatic Sciences*, 67(6), 987–1004.
- Richards, R. P., Baker, D. B., & Crumrine, J. P. (2009). Improved water quality in Ohio tributaries to Lake Erie: A consequence of conservation practices. *Journal of Soil and Water Conservation*, 64(3), 200–211.
- Roberts, J. J., Höök, T. O., Ludsin, S. A., Pothoven, S. A., Vanderploeg, H. A., & Brandt, S. B. (2009). Effects of hypolimnetic hypoxia on foraging and distributions of Lake Erie yellow perch. *Journal of Experimental Marine Biology and Ecology*, 381, S132–S142.
- Roseman, E. F., Taylor, W. W., Hayes, D. B., Haas, R. C., Davies, D. H., & Mackey, S. D. (1999). Influence of physical processes on the early life history stages of walleye (*Stizostedion vitreum*) in western Lake Erie. Ecosystem approaches for fisheries management. University of Alaska Sea.
- Roseman, E. F., Taylor, W. W., Hayes, D. B., Haas, R. C., Knight, R. L., & Paxton, K. O. (1996). Walleye egg deposition and survival on reefs in Western Lake Erie (USA). *Annales Zoologici Fennici* (pp. 341–351). Finnish Zoological and Botanical Publishing Board.
- Scavia, D., David Allan, J., Arend, K. K., Bartell, S., Beletsky, D., Bosch, N. S., ... Zhou, Y. (2014). Assessing and addressing the re-eutrophication of Lake Erie: Central basin hypoxia. *Journal of Great Lakes Research*, 40(2), 226–246.
- Schaeffer, J. S., & Margraf, F. J. (1986). Population characteristics of the invading white perch (*Morone americana*) in western Lake Erie. *Journal of Great Lakes Research*, 12(2), 127–131.
- Schaeffer, J. S., & Margraf, F. J. (1987). Predation on fish eggs by white perch, *Morone americana*, in western Lake Erie. *Environmental Biology of Fishes*, 18(1), 77–80.
- Schindler, D. E., & Hilborn, R. (2015). Prediction, precaution, and policy under global change. *Science*, 347(6225), 953–954.
- Sharma, S., Jackson, D. A., Minns, C. K., & Shuter, B. J. (2007). Will northern fish populations be in hot water because of climate change? *Global Change Biology*, 13(10), 2052–2064.

- Sharma, S., Vander Zanden, M. J., Magnuson, J. J., & Lyons, J. (2011). Comparing climate change and species invasions as drivers of cold-water fish population extirpations. *PLoS ONE*, 6(8), e22906.
- Shaw, S. L., Sass, G. G., & VanDeHey, J. A. (2018). Maternal effects better predict walleye recruitment in Escanaba Lake, Wisconsin, 1957–2015: Implications for regulations. *Canadian Journal of Fisheries and Aquatic Sciences*, 75(12), 2320–2331.
- Shuter, B. J., & Koonce, J. F. (1977). A dynamic model of the western Lake Erie walleye (*Stizostedion vitreum vitreum*) population. *Journal of the Fisheries Board of Canada*, 34(10), 1972–1982.
- Shuter, B. J., Minns, C. K., & Lester, N. (2002). Climate change, freshwater fish, and fisheries: Case studies from Ontario and their use in assessing potential impacts. American Fisheries Society Symposium (pp. 77–88). American Fisheries Society.
- Simberloff, D., & Gibbons, L. (2004). Now you see them, now you don't!—population crashes of established introduced species. *Biological Invasions*, 6(2), 161–172.
- Tyson, J. T., Johnson, T. B., Knight, C. T., & Bur, M. T. (2006). Intercalibration of research survey vessels on Lake Erie. *North American Journal of Fisheries Management*, 26(3), 559–570.
- USDA NRCS (2011). Conservation Effects Assessment Project. Assessment of the Effects of Conservation Practices on Cultivated Cropland in the Great Lakes Region. United States Department of Agricultural Natural Resources Conservation Service (172 pp.).
- Van Zuiden, T. M., Chen, M. M., Stefanoff, S., Lopez, L., & Sharma, S. (2016). Projected impacts of climate change on three freshwater fishes and potential novel competitive interactions. *Diversity and Distributions*, 22(5), 603–614.
- Vandergoot, C. S., Cook, H. A., Thomas, M. V., Einhouse, D. W., & Murray, C. (2010). Status of walleye in western Lake Erie, 1985–2006. In Status of Walleye in the Great Lakes: Proceedings of the 2006 Symposium: Great Lakes Fish. Comm. Tech. Rep (Vol. 69, pp. 123–150).
- Wang, X., Kannan, N., Santhi, C., Potter, S. R., Williams, J. R., & Arnold, J. G. (2011). Integrating APEX output for cultivated cropland with SWAT simulation for regional modeling. *Transactions of the ASABE*, 54(4), 1281–1298.
- Watson, S. B., Miller, C., Arhonditsis, G., Boyer, G. L., Carmichael, W., Charlton, M. N., ... Wilhelm, S. W. (2016). The re-eutrophication of Lake Erie: Harmful algal blooms and hypoxia. *Harmful Algae*, 56, 44–66.
- Wiley, M., Hyndman, D., Pijanowski, B. C., Kendall, A., Riseng, C., Rutherford, E., ... Koches, J. (2010). A multi-modeling approach to evaluate impacts of global change on river ecosystems. *Hydrobiologia*, 657(1), 243–262.
- Williams, J. R., Izaurre, R. C., & Steglich, E. M. (2008). Agricultural policy/environmental extender model. Theoretical Documentation, Version, 604, 2008–2017.
- Williamson, M. (1996). *Biological invasions*, (Vol. 15). Berlin: Springer Science & Business Media.
- Wilson, R. S., Beetstra, M. A., Reutter, J. M., Hesse, G., Fussell, K. M. D. V., Johnson, L. T., ... Winslow, C. (2019). Commentary: Achieving phosphorus reduction targets for Lake Erie. *Journal of Great Lakes Research*, 45(1), 4–11.
- Wood, S., & Wood, M. S. (2015). Package 'mgcv'. *R package version*, 1, 29.
- WTG Walleye Task Group (2017). Report of the Lake Erie Walleye Task Group to the Standing Technical Committee, Lake Erie Committee. Great Lakes Fishery Commission, Ann Arbor, MI, USA.
- Yen, H., White, M. J., Arnold, J. G., Keitzer, S. C., Johnson, M.-V., Atwood, J. D., ... Rewa, C. A. (2016). Western Lake Erie Basin: Soft-data-constrained, NHDPlus resolution watershed modeling and exploration of applicable conservation scenarios. *Science of the Total Environment*, 569, 1265–1281.
- Zhang, F., Reid, K. B., & Nudds, T. D. (2016). Relative effects of biotic and abiotic factors during early life history on recruitment dynamics: A case study. *Canadian Journal of Fisheries and Aquatic Sciences*, 74(7), 1125–1134.
- Zhang, F., Reid, K. B., & Nudds, T. D. (2018). Effects of walleye predation on variation in the stock-recruitment relationship of Lake Erie yellow perch. *Journal of Great Lakes Research*, 44(4), 805–812.
- Zhao, Y., Jones, M. L., Shuter, B. J., & Roseman, E. F. (2009). A biophysical model of Lake Erie walleye (*Sander vitreus*) explains interannual variations in recruitment. *Canadian Journal of Fisheries and Aquatic Sciences*, 66(1), 114–125.
- Zhao, Y., Kocovsky, P. M., & Madenjian, C. P. (2013). Development of a stock-recruitment model and assessment of biological reference points for the Lake Erie Walleye fishery. *North American Journal of Fisheries Management*, 33(5), 956–964.
- Zuur, A., Ieno, E. N., Walker, N., Saveliev, A. A., & Smith, G. M. (2009). *Mixed effects models and extensions in ecology with R*. Berlin: Springer Science & Business Media.

## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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