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

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33 **RUNNING HEADER:** Forecasting fish recruitment under climate and land-use scenarios

34 **KEYWORDS:** percid; eutrophication; fisheries management; climate warming; multiple
35 stressors

36 **SUMMARY**

- 37 1. Many aquatic ecosystems are experiencing multiple anthropogenic stressors that threaten
38 their ability to support ecologically and economically important fish species. Two of the
39 most ubiquitous stressors are climate change and non-point source nutrient pollution.
- 40 2. Agricultural conservation practices (ACPs, i.e., farming practices that reduce runoff,
41 prevent erosion, and curb excessive nutrient loading) offer a potential means to mitigate
42 the negative effects of non-point source pollution on fish populations. However, our
43 understanding of how ACP implementation amidst a changing climate will affect fish
44 production in large ecosystems that receive substantial upstream sediment and nutrient
45 inputs remains incomplete.
- 46 3. Towards this end, we explored how anticipated climate change and the implementation of
47 realistic ACPs might alter the recruitment dynamics of three fish populations (native
48 walleye *Sander vitreus* and yellow perch *Perca flavescens* and invasive white perch
49 *Morone americana*) in the highly productive, dynamic west basin of Lake Erie. We
50 projected future (2020-2065) recruitment under different combinations of anticipated
51 climate change (N = 2 levels) and ACP implementation (N = 4 levels) in the western
52 Lake Erie watershed using predictive biological models driven by forecasted winter
53 severity, spring warming rate, and Maumee River total phosphorus loads that were

54 generated from linked climate, watershed-hydrology, and agricultural practice-simulation
55 models.

56 4. In general, our models projected reduced walleye and yellow perch recruitment whereas
57 invasive white perch recruitment was projected to remain stable or increase relative to the
58 recent past. Our modeling also suggests the potential for tradeoffs, as ACP
59 implementation was projected to reduce yellow perch recruitment with anticipated
60 climate change.

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

66

67 INTRODUCTION

68 Many aquatic ecosystems are experiencing multiple anthropogenic stressors that threaten
69 their ability to support fish populations. One of the most ubiquitous stressors is climate change,
70 which has caused distributional shifts (Comte, Buisson, Daufresne, & Grenouillet, 2013; Filipe et
71 al., 2013; Van Zuiden, Chen, Stefanoff, Lopez, & Sharma, 2016; Hansen, Read, Hansen,
72 & Winslow, 2017), increased the spread of invasive fish species (Rahel & Olden, 2008; Van
73 Zuiden et al., 2016), altered fish community composition (Alofs, Jackson, & Lester, 2014),
74 affected reproductive dynamics (Farmer, Marschall, Dabrowski, & Ludsin, 2015; Krabbenhoft,
75 Platania, & Turner, 2014; Hansen et al., 2017), and changed fish production (Blanchard et al.,
76 2012). Seemingly as pervasive has been non-point source (NPS) nutrient and sediment pollution,
77 which can negatively affect fish populations by causing bottom hypoxia, harmful algal blooms,
78 reduced water clarity, and altered food-web interactions (Caddy 2000; Ludsin, Kershner,
79 Blocksom, Knight, & Stein, 2001; Diaz & Rosenberg, 2008; Breitburg, Hondrop, Davias, &
80 Diaz, 2009; Scavia et al., 2014). Although the observed and projected individual effects of
81 climate change (e.g., Comte et al., 2013; Lynch et al., 2016) and NPS pollution (e.g., Leach &
82 Nepszy 1976; Ludsin et al., 2001) are well-documented and can be substantial, many fish
83 populations are experiencing climate change and NPS pollution simultaneously, which could
84 magnify or mitigate their independent effects. However, the effects of climate change combined

85 with NPS pollution on fish populations remain largely unstudied, especially in lake ecosystems.
86 Understanding the combined effects of multiple stressors is especially critical in ecosystems that
87 support economically and ecologically important fisheries as it can help guide management and
88 conservation strategies (DeVanna Fussell et al., 2016; Lynch et al., 2016; Paukert et al., 2016;
89 Collingsworth et al., 2017).

90 Highly productive coastal and large-lake ecosystems that receive substantial river-
91 transported runoff from agricultural watersheds are typically negatively affected by the
92 combined impacts of climate change and NPS pollution (Buchheister, Bonzek, Gartland, &
93 Latour, 2013). Because these ecosystems (e.g., Chesapeake Bay: Breitburg, 2002; Kemp et al.,
94 2005; Buchheister et al., 2013; northern Gulf of Mexico: de Mutsert et al., 2016; Lake Erie:
95 Ludsin et al., 2001) often support valuable commercial and recreational fisheries, which can be
96 adversely affected by eutrophication, regulatory agencies and policy-makers have typically
97 sought to improve habitat conditions (e.g., water quality) by altering farming practices in the
98 watershed (Hagy, Boyton, Keefe, & Wood, 2004; Ohio EPA, 2013; Scavia et al., 2014; Keitzer
99 et al., 2016; Wilson et al., 2019). Agricultural conservation practices (ACPs), which are farming
100 practices that reduce runoff, prevent erosion, curb excessive nutrient loading, and mitigate
101 ecosystem degradation, offer one potential means to reduce the negative effects of NPS pollution
102 on fish production while, ideally, not compromising agricultural production (USDA NRCS,
103 2011; Keitzer et al., 2016). The benefits of such practices are well-documented and have been
104 shown to limit in-stream nutrient and sediment loading, improve water quality, promote diverse
105 stream-fish assemblages, and even reduce nutrient inputs into downstream recipient water bodies
106 (Richards, Baker & Crumrine, 2009; Bosch, Allan, Selegan, & Scavia, 2013; Keitzer et al.,
107 2016). Even so, how ACP implementation amidst a changing climate would affect fish
108 production in large ecosystems that receive substantial upstream nutrient and sediment loads
109 remains a conspicuous information gap. Such information could help managers design more
110 resilient and adaptive management strategies (Lynch et al., 2016; Paukert et al., 2016; Hansen et
111 al., 2017).

112 Climate change and nutrient loading can directly and indirectly drive fishery dynamics by
113 affecting the recruitment of individuals to the fishable population (Farmer et al., 2015; Hansen et
114 al., 2017). Recruitment (herein, defined as the contribution of individuals to older ages that can
115 be targeted by a fishery) responses can be complex – positive or negative, species-specific,

116 variable across spatial and temporal scales, and life-stage dependent (Drinkwater et al., 2010;
117 Ludsin, DeVanna, & Smith, 2014; Radinger et al., 2016). For example, climate change and NPS
118 pollution can alter key habitat characteristics that affect early life growth and survival (Brunel &
119 Boucher et al., 2007; Lindegren et al., 2010; Mueter, Bond, Ianelli, & Hollowed, 2011; Brochier
120 et al., 2013). In many cases, the magnitude and direction of response to increasing temperature is
121 linked to a species' thermal guild, with cool- and cold-water species showing negative responses
122 to warming and warm-water species showing positive ones (Comte et al., 2013; Lynch et al.,
123 2016; Hansen et al., 2017). Similarly, a species' tolerance, or lack thereof, of eutrophic, nutrient-
124 rich waters can affect recruitment positively or negatively through top-down or bottom-up
125 processes (Ludsin et al., 2001; Briland, 2018). Thus, understanding the response of fish
126 recruitment, and ultimately fishery production, to climate change and the implementation of
127 ACPs is a key component to future management and conservation (Pritt, Roseman, & O'Brien,
128 2014).

129 Towards this end, we explored how anticipated climate change and the implementation of
130 realistic ACP scenarios might alter the recruitment dynamics of three ecologically and
131 economically important fish populations (walleye *Sander vitreus*, yellow perch *Perca flavescens*,
132 and white perch *Morone americana*) in the highly productive and dynamic west basin of Lake
133 Erie (Figure 1). The recruitment dynamics of these species have been shown to respond to
134 climate-related factors (e.g., winter and spring temperatures: Busch, Scholl, & Hartman, 1975;
135 Clady, 1976; Hokanson, 1977; Johnson & Evans, 1990; Farmer et al., 2015) and factors
136 associated with NPS inputs from rivers (Mion, Stein, & Marschall, 1998; Jones, Shuter, Zhao, &
137 Stockwell, 2006; Reichert et al., 2010; Ludsin et al., 2011; Carreon-Martinez, Wellband,
138 Johnson, Ludsin, & Heath, 2014). We focused on western Lake Erie for several reasons. First,
139 ACPs designed to reduce phosphorus loading are being proposed and implemented in the
140 surrounding western Lake Erie basin (WLEB) watershed to mitigate Lake Erie's eutrophication
141 problem and its potentially harmful effects (e.g., bottom hypoxia, harmful algal blooms, reduced
142 water clarity; Ohio EPA, 2013; Kane, Conroy, Richards, Baker, & Culver, 2014; Scavia et al.,
143 2014; Watson et al., 2016). Second, projected climate change, which is characterized by short,
144 warm winters (Jones et al., 2006; Farmer et al., 2015) and frequent, high-magnitude precipitation
145 events in temperate ecosystems (Hayhoe, VanDorn, Croley, Schlegal, & Wuebbles, 2010;
146 Bartolai et al., 2015; Maghrebi, Nalley, Laurent, & Atkinson 2015), has occurred in the WLEB

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

153 We forecasted walleye, yellow perch, and white perch age-0 (juvenile) abundance, which
154 has been shown to be a strong predictor of future recruitment to the fishery at age-2 (Farmer et
155 al., 2015; WTG 2017), under different combinations of anticipated (2020-2065) climate change
156 and varying levels of ACP implementation in the WLEB watershed. Our specific research goals
157 were to: 1) quantify the independent and combined effects of climate change and ACP
158 implementation on walleye, yellow perch, and white perch recruitment; 2) explore whether
159 climate change and ACP implementation might alter western Lake Erie's fish community by
160 differentially affecting native cool-water fish species (walleye and yellow perch) versus
161 nonnative warm-water ones (white perch); and 3) provide insights to Lake Erie management
162 agencies regarding the potential future of their fisheries. We hypothesized that, in general,
163 climate warming would negatively affect walleye and yellow perch recruitment, owing to their
164 seeming dependence on long winters for successful reproductive output and strict thermal
165 requirements during the spring (Busch et al., 1975; Hokanson, 1977; Farmer et al., 2015).
166 However, depending on their magnitude, reductions in total phosphorus inputs from ACP
167 implementation could offset or exacerbate anticipated climate-driven declines in yellow perch
168 recruitment. For example, reduced NPS total phosphorus loading could offset warming-induced
169 recruitment declines by alleviating the adverse effects of eutrophic conditions (e.g., bottom
170 hypoxia, HABs; Caddy, 1993; Roberts et al., 2010; Scavia et al., 2014). By contrast, reduced
171 NPS inputs of phosphorus (and associated sediments) could exacerbate declines in recruitment
172 by reducing the extent and productivity of turbid Maumee River plumes during the spring, which
173 appear to offer protection to larval yellow perch from predators such as invasive white perch
174 (Ludsin et al., 2011; Carreon-Martinez et al., 2014) and may also enhance foraging through
175 bottom-up effects (Grimes & Finucane, 1991; Barbiero, Balcer, Rockwell, & Tuchman, 2009). In
176 this way, the relationship between yellow perch recruitment and total phosphorus inputs from the
177 Maumee River could be expected to be dome-shaped (unimodal), a notion supported by previous

178 studies that have quantified the relationship between ecosystem productivity metrics and
179 fish(eries) yield (e.g., Oglesby, Leach, & Forney, 1987; Caddy 1993, 2000). By contrast, we
180 hypothesized that white perch recruitment would be positively affected by climate warming and
181 negatively affected by increased ACP implementation because of this species' higher thermal
182 optimum compared to walleye and yellow perch (Johnson & Evans, 1990) and its tolerance of
183 eutrophic conditions (Briland, 2018).

184

185 **METHODS**

186 **Study system**

187 *West basin of Lake Erie*

188 Lake Erie is the smallest of the Laurentian Great Lakes (by volume), but is the most
189 biologically productive, supporting numerous commercial and recreational fisheries (Ludsin et
190 al., 2014; Bunnell et al., 2013). The lake has three distinct basins (west, central, and east), each
191 having unique chemical and physical properties. The focal area of this study, the west basin
192 (Figure 1), is the warmest, shallowest, and most biologically productive of the three (Leach &
193 Nepszy, 1976; Bolsenga & Herdendorf, 1993; Ludsin et al., 2001). Owing to these properties, the
194 west basin has historically provided spawning and nursery habitat for a diversity of fishes
195 including walleye, yellow perch, and white perch (Mion et al., 1998; Ludsin et al., 2001; Jones et
196 al., 2003; Ludsin et al., 2011; DuFour et al., 2015; Farmer et al., 2015, ODW 2017). A major
197 driver of the biologically productive west basin is nutrient inputs from the WLEB watershed and
198 specifically, the Maumee River, which drains the largest watershed in the entire Great Lakes
199 basin (Bolsenga & Herdendorf, 1993). The Maumee River watershed is composed of primarily
200 agricultural land (>70%, USDA NRCS., 2011) and delivers substantial nutrient and sediment
201 inputs to the west basin (Baker & Richards, 2002; Scavia et al., 2014; Keitzer et al., 2016).
202 Excessive phosphorus loading from agricultural runoff in the Maumee River watershed has been
203 identified as the primary driver of Lake Erie's recent re-eutrophication (Scavia et al., 2014;
204 Watson et al., 2016), resulting in efforts to reduce loading via the implementation of ACPs (Ohio
205 EPA 2013). Given that the Maumee River contributes a substantial portion of the total
206 phosphorus load from the WLEB into the west basin of Lake Erie (Scavia et al., 2014; Maccoux,
207 Dove, Backus, & Dolan, 2016), the need exists to understand how ACP implementation in this

208 watershed will impact the resident fish community, especially amidst a changing climate
209 (Keitzer et al., 2016).

210 *Study species*

211 The three focal species in this study are: 1) walleye, which supports Lake Erie's largest
212 recreational fishery and second largest commercial fishery (Kayle, Oldenburg, Murray, Francis,
213 & Markham, 2015; Markham & Knight, 2017; ODW 2017, 2018); 2) yellow perch, which
214 supports Lake Erie's largest commercial fishery and second largest recreational fishery (Belore
215 et al., 2014; ODW 2018); and 3) white perch, an invasive species that is of minor commercial
216 importance but has become the most abundant prey-fish in Lake Erie (FTG 2013; ODW 2017)
217 and is a known predator of walleye and yellow perch during their early life stages (Schaeffer &
218 Margraf, 1987; Ludsin et al., 2011; Carreon-Martinez et al., 2014). In addition to their economic
219 and ecological roles in Lake Erie, walleye, yellow perch, and white perch are common and
220 widespread across North America, and support recreational fisheries across their ranges. These
221 three species also span a gradient of thermal guilds. Although walleye and yellow perch are both
222 considered cool-water species, walleye has a lower optimal temperature range for both spawning
223 and embryo hatching compared to yellow perch (Hokanson, 1977). In Lake Erie, walleye
224 typically spawn during March through mid-May at temperatures of 3-12°C (Roseman et al.,
225 1996; May, 2015) and yellow perch typically spawn during mid-April through May at
226 temperatures of 8-14°C (Collingsworth & Marschall, 2011; Belore et al., 2014; Farmer et al.,
227 2015). Both walleye and yellow perch age-0 (juvenile) abundance indices during August (~ 3-4
228 months post-hatch) are excellent predictors of age-2 abundance when recruitment to the fishery
229 occurs (Belore et al., 2014; Farmer et al., 2015; Kayle et al., 2015), highlighting the importance
230 of early life processes in determining fishery production. Because white perch prefer warmer
231 temperatures compared to walleye and yellow perch, the west basin of Lake Erie is a favorable
232 recruitment environment for this species. White perch spawn in its tributaries (e.g., Maumee
233 River) and shallow (<1.5 m) waters during spring at temperatures of 11-15°C (Hartman, 1972;
234 Boileau, 1985).

235 **Modeling overview**

236 Our modeling approach involved two primary steps (Figure 2). First, we built species-
237 specific predictive recruitment models using historical age-0 (juvenile) abundance data and
238 indices of winter severity, spring warming rate, and Maumee River total phosphorus (TP) loads.

239 Second, we projected future (2020-2065) recruitment under different combinations of anticipated
240 climate change and four levels of ACP implementation in the WLEB watershed, using our
241 predictive models and forecasted values of winter severity, spring warming rate, and Maumee
242 River TP loads that were generated from linked climate, watershed-hydrology, and agricultural-
243 practice-simulation models.

244 **Predictive fish recruitment models**

245 *Fish recruitment indices*

246 We used annual indices of age-0 abundance generated from bottom trawl surveys
247 (typically 10 min duration) conducted by the Ohio Department of Natural Resources-Ohio
248 Division of Wildlife (ODNR-DOW) and the Ontario Ministry of Natural Resources and Forestry
249 (OMNRF) during 1987-2015 (walleye and yellow perch) and 1992-2015 (white perch). The
250 white perch time-series was truncated to avoid the confounding effects of early establishment
251 dynamics (i.e., large boom-bust cycles) during which environmental drivers were likely not the
252 main drivers of population dynamics (Williamson, 1996; Simberloff & Gibbons, 2004). Surveys
253 were conducted during the last two weeks of August, sometimes extending into early September.
254 The agencies used a stratified-random design to sample 56-70 stations annually across the west
255 basin of Lake Erie. To correct for catchability differences, vessel-specific and species-specific
256 fishing power corrections were applied to standardize trawl catches (Tyson, Johnson, Knight, &
257 Bur, 2006). Catches were averaged within each year to generate a basin-wide mean. Herein, we
258 report annual catch per unit effort (CPUE) as the number of individuals per minute of trawling.

259 *Abiotic predictors*

260 We assessed winter severity, spring warming rate, and total springtime (March through
261 May) Maumee River TP loads as potential environmental predictors of walleye, yellow perch,
262 and white perch recruitment. We chose these metrics based on previous research indicating their
263 influence on recruitment for at least one of the three species (Busch et al., 1975; Clady, 1976;
264 Hokanson, 1977; Johnson & Evans, 1990; Mion et al., 1998; Reichert et al., 2010; Jones et al.,
265 2006; Ludsin et al., 2011; Carreon-Martinez et al., 2014; Farmer et al., 2015). We calculated
266 historical winter severity and spring warming rate from observed maximum daily air
267 temperatures during 1987-2015 from stations (N = 29) located throughout the WLEB watershed
268 (National Oceanic and Atmospheric Administration's Daily Global Historical Climatology
269 Network, Menne, Durre Vose, Gleason, & Houston, 2012). Our use of air temperature is

270 justified, as it has often been used as a proxy for water-related thermal metrics (Sharma, Jackson,
271 Minns, & Shuter, 2007; Van Zuiden et al., 2016) and has been used to successfully predict the
272 effects of climate change on fisheries (Van Zuiden et al., 2016). Furthermore, previous research
273 has shown that local air temperature is correlated to Lake Erie water temperature in western Lake
274 Erie (Farmer, 2013). We defined winter severity as the total number of days that the mean daily
275 maximum temperature across the WLEB watershed was $\leq 6^{\circ}\text{C}$ during January through April of
276 each year. Our inclusion of winter severity as a recruitment predictor was based on previous
277 research identifying optimal spawning conditions for percids, which showed that at colder water
278 temperatures, maturation is more likely to result in a spawning event as compared to warmer
279 water temperatures (Hokanson, 1977). Our winter index is also strongly correlated with ice cover
280 indices used in previous studies (e.g., Farmer et al., 2015) that have been shown to explain
281 variation in Lake Erie recruitment success, and it is easily projected using existing climate
282 change models. To calculate spring warming rate ($^{\circ}\text{C}\cdot\text{d}^{-1}$), we fit a linear regression model to the
283 basin-wide mean daily maximum temperature during April through May (the approximate larval
284 production period for all three species) for each year and defined the annual spring warming rate
285 ($^{\circ}\text{C}\cdot\text{d}^{-1}$) as the slope of the least-squares regression line (Busch et al., 1975). Finally, we
286 calculated total annual spring-time TP loading (metric tons) as the sum of the recorded daily
287 (March through May) Maumee River TP loads obtained from the National Center for Water
288 Quality Research housed by Heidelberg University (<https://ncwqr.org/monitoring/>).

289 *Predictive models of fish recruitment*

290 Because environmental driver-biological response relationships are often nonlinear
291 (Hunsicker et al., 2016), we used generalized additive models (GAMs, Hastie & Tibshirani,
292 1987) to examine the relationship between fish recruitment and winter severity, spring warming
293 rate, and Maumee River TP loads. Generalized additive models are an ideal tool because of their
294 flexibility in fitting non-linear relationships that need not be defined *a priori*, and they have
295 previously been used to model fish recruitment (Daskalov, 1999; Cardinale & Arrhenius 2000).
296 We built species-specific GAMs using thin-plate regression splines (Adams, Leaf, Wu, &
297 Hernandez, 2018) and a Gamma distribution with a log-link function. The Gamma distribution is
298 a flexible, continuous distribution, appropriate for skewed data, which has commonly been used
299 in fisheries applications (Maunder & Punt, 2004). Smoothness parameters were estimated with
300 Generalized Cross Validation (GCV). Because fewer years of data were available for white

301 perch, as compared to walleye and yellow perch, we restricted the basis dimension, k (controls
302 the degree of smoothness in the model), to 6 in all white perch models to avoid overfitting
303 (Decker et al., 2013; Quiñones et al., 2015). To avoid the confounding effects of
304 multicollinearity, prior to model construction, we used pairwise correlations to confirm that no
305 substantial ($r > 0.6$, Zuur, 2009) multicollinearity between predictor variables was present.

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

308 $CPUE \sim s(TP) + s(\text{spring warming rate}) + s(\text{winter severity})$,

309 was constructed and fit for each species where s represents the smoothing function. Model fit and
310 temporal autocorrelation were assessed using standard diagnostics (Anderson & Burnham,
311 2002). To determine the most supported predictive model for each species, we constructed model
312 formulations with all possible combinations of predictor variables (Burnham & Anderson, 2003)
313 and considered the most supported model for each species as the one with the lowest sample
314 size-corrected Akaike information criteria (AICc) value. If models were equally supported
315 ($\Delta AICc < 2$), we chose the model with the greatest predictive ability. All GAM analyses were
316 conducted using the 'mgcv' package in R 3.3.0 (Wood & Wood, 2015; R Core Team, 2019).

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

327 **Future projections**

328 *Climate change scenarios: thermal metrics*

329 We projected future (2020-2065) winter severity and spring warming rate using daily
330 maximum air temperature values from global circulation models (GCMs) used in the IPCC's
331 Fifth Assessment Report (IPCC, 2014). We included two greenhouse gas emission

332 (Representative Concentration Pathway, RCP) scenarios: a moderate-reductions scenario
333 (RCP4.5, 18 GCMs) and a “business-as-usual” scenario (i.e., status quo, RCP8.5, 17 GCMs). For
334 each GCM, multiple ensembles (slightly different versions of a GCM model) were run to
335 generate a range of future climate conditions. (RCP4.5, N = 38; RCP8.5, N = 37, Table S1). The
336 use of multiple GCMs and ensembles is a common way to incorporate uncertainty in future
337 climate conditions and to better reflect the range of possible future outcomes (Sharma, Vander
338 Zander, Magnuson, & Lyons, 2011; Van Zuiden et al., 2016). The GCM data spatially
339 overlapped the 29 stations that were used to calculate historical winter severity and spring
340 warming rate.

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

357 *Agricultural conservation practice (ACP) scenarios*

358 To generate future TP loads that resulted from different levels of implementation of
359 nutrient and sediment reduction strategies in the watershed, we applied a set of previously
360 developed watershed-hydrology and agricultural-simulation models (Arnold, Srinivasan,
361 Muttiah, & Williams, 1998; Gassman et al., 2009; USDA NRCS, 2011; Wang, Kannan, Santhi,
362 Potter, Williams, & Arnold, 2011; Daggupati et al., 2015; Yen et al., 2016). Briefly, we used

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

380 The SWAT is a commonly used watershed-hydrology model and has been used in
381 multiple WLEB studies to explore the impact of climate change and ACP implementation on
382 river flow and agricultural runoff (e.g., Bosch et al., 2013; Keitzer et al., 2016). In our study,
383 SWAT inputs were nutrient loads from cultivated fields simulated by APEX (under each level of
384 ACP implementation) and meteorological data from each climate change model. We used an
385 approach similar to the one used for our thermal metrics to bias-correct the TP forecasts from the
386 SWAT, with some notable differences. In this case, we built scenario-specific and month-
387 specific (March-May) linear models because the observed biases were month-specific. After
388 forecasting spring-time TP loads, we calculated the proportional change between the forecasted
389 value and the hindcasted (1987-2015) median value for that specific-scenario. Regardless of the
390 level of ACP implementation, we used the baseline ACP median in each emission scenario,
391 which simulated historical nutrient and erosion control practices. Finally, we multiplied the
392 proportional change by the historical median to obtain the forecasts that were used to predict
393 recruitment. We chose to use proportional change for TP to account for precipitation-driven

394 changes in TP loading in the climate models, as simply adding or subtracting load differences
395 would not make sense. The results of this modeling effort were projections of Maumee River TP
396 loads for each combination of climate change and ACP implementation scenario, analogous to
397 the historical Maumee River TP loads in regards to timing (spring) and spatial scale.

398 *Forecasting fish recruitment*

399 We used our predictive recruitment models to forecast walleye, yellow perch, and white
400 perch recruitment under both RCP scenarios and the four ACP implementation scenarios. Under
401 each combination of climate and ACP implementation scenario (total N = 8), species-specific
402 recruitment values were projected from winter severity, spring warming rate, and/or Maumee
403 River TP loads annually and subsequently summarized by decade.

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

417

418 **RESULTS**

419 **Predictive models of fish recruitment**

420 *Fish recruitment indices*

421 Lake Erie walleye, yellow perch, and white perch recruitment, as indexed by age-0
422 abundance (i.e., year-class strength), varied by up to an order of magnitude during the historical
423 time period (Figure 3 A-C). Annual age-0 walleye trawl CPUE ranged from 0.09 to 5.2
424 individuals·min⁻¹, with a median CPUE of 0.5. The strongest walleye recruitment events

425 occurred in 1993, 1996, 2003, and 2015 (Figure 3A). Age-0 yellow perch CPUEs ranged from
426 0.7 to 66.4 individuals·min⁻¹, with a median value of 7.4 individuals·min⁻¹ (Figure 3B). The three
427 strongest recruitment events occurred during years similar to walleye (1996, 2003, and 2015;
428 Figure 3B). Age-0 white perch CPUE also varied by an order of magnitude with annual CPUEs
429 ranging from 9.5 to 117.0 individuals·min⁻¹, with a median value of 46.3 individuals·min⁻¹. White
430 perch recruitment was highest during the 2000s with the strongest recruitment events occurring
431 in 2004 and 2012 (Figure 3C).

432

433 *Abiotic predictors*

434 Winter severity, spring warming rate, and Maumee River TP loads also varied throughout
435 the historical period (Figure 3D-F). Winter severity (number of days with a maximum
436 temperature $\leq 6^{\circ}\text{C}$) ranged 43 to 76 d, with a median winter severity of 62 d (Figure 3E).
437 Extremely mild winters occurred in 2002 and 2012, whereas severe winters occurred in 1993,
438 2003, and during 2013-2015. Spring warming rate varied throughout the period, ranging from
439 0.06 to 0.31 $^{\circ}\text{C}\cdot\text{d}^{-1}$ (Figure 3D). Generally, warming rates were lower in the middle of the time-
440 series (1996-2006) compared to the early and late periods (Figure 3D). The median springtime
441 Maumee River TP load was 807.0 MT and ranged from 172.1 to 2208.8 MT (Figure 3F).
442 Notably, the 2011 TP load was very high, approximately double the next highest load. Because
443 no substantial collinearity between these environmental variables existed ($r < 0.4$), all were
444 included as potential predictors of recruitment in our species-specific models.

445 *Predictive models of fish recruitment*

446 Based on standard, qualitative diagnostics (Anderson & Burnham, 2002) all three final
447 models of fish recruitment displayed good fit with no obvious patterns in the residuals (Figure
448 S1) and no significant temporal autocorrelation based on autocorrelation function (ACF) plots
449 (Figure S2, Zuur et al., 2009). Based on our defined AICc and predictive ability criteria, the most
450 supported predictive model of walleye recruitment included only winter severity (Table S2). Our
451 resampling analysis revealed that, as winter severity increased, so did walleye recruitment, with
452 exponentially higher walleye recruitment occurring after severe winters (Figure S3). The final
453 walleye model explained 31.3% overall deviance in walleye recruitment (Table 1). The most
454 supported predictive model of yellow perch recruitment included winter severity and Maumee
455 River TP as predictors (Table S2). The partial response of yellow perch recruitment to winter

456 severity was similar to the walleye partial response; as winter severity increased, so did yellow
457 perch recruitment (Figure S4). The partial response of yellow perch recruitment to TP was dome-
458 shaped (unimodal) with the greatest positive effect occurring at intermediate TP loads (Figure
459 S4). The final yellow perch predictive model explained 51.1% of the overall deviance in yellow
460 perch recruitment (Table 1). The most supported predictive model of white perch recruitment
461 included spring warming rate and Maumee River TP as predictor variables (Table S2). In
462 general, white perch recruitment increased with increasing spring warming rate (Figure S5).
463 Although the partial response of white perch recruitment to Maumee River TP was nonlinear, as
464 TP increased white perch recruitment generally decreased (Figure S5), a finding that ran counter
465 to our expectations. The final white perch recruitment model explained 55.4% of the variation in
466 observed recruitment (Table 1).

467 **Future projections**

468 *Forecasts of winter severity and spring warming rate*

469 As expected, winter severity decreased through time in both the RCP4.5 and RCP8.5
470 emission scenarios, although the declines varied in their magnitude, especially during later
471 decades (Figure 4A). Median winter severity decreased by 5 d during the 2020s and 7 d during
472 the 2030s relative to the median historical winter severity (62 d) in the RCP4.5 emission
473 scenario. Similarly, it decreased 4 d during the 2020s and 8 d during the 2030s relative to the
474 median historical winter severity (62 d) in the RCP8.5 emission scenario. After the 2030s,
475 however, the two emission scenarios diverged, with winter severity decreasing more in the
476 RCP8.5 scenario compared to the RCP4.5 emission scenario (Figure 4A). By the 2060s,
477 projected median winter severity decreased by 13 d in the RCP4.5 emission scenario and 18 d in
478 the RCP8.5 emission scenario, representing a 21% and 29% reduction, respectively, relative to
479 the historical period. In contrast to winter severity, no obvious temporal trends in projected
480 spring warming rate were apparent, with differences between emission scenarios also being
481 negligible (Figure 4B). Median spring warming rates under the RCP4.5 emission scenario were
482 slightly higher than the historical median, although the projected rates were variable (Figure 4B).

483 *Forecasts of total phosphorus loading*

484 Three general patterns emerged from our projected Maumee River TP loads (Figure 5).
485 First, as expected, increased levels of ACP implementation (i.e., more farm acres treated with
486 nutrient and erosion control practices) resulted in lower TP loads. For example, implementing

487 ACPs in all farm acres (ENM) resulted in a 45.4% reduction in TP loading during the 2020s
488 under the RCP4.5 emission scenario and a reduction of 39.2% under the RCP8.5 emission
489 scenario, relative to the historical period. Second, TP loads increased through time, within each
490 level of ACP implementation, indicating that anticipated climate change can be expected to
491 reduce the effect of ACP implementation during later decades. Finally, during most decades and
492 ACP implementation scenarios, the RCP8.5 emission scenario had greater median expected TP
493 loads compared to the corresponding RCP4.5 emission scenario, likely because of greater
494 projected increases in springtime precipitation, and subsequent TP loading, under the RCP8.5
495 emission scenario (N. Aloysius, unpublished data). However, the differences in median
496 forecasted TP loads between emissions scenarios were modest, especially when compared to the
497 differences that we observed among ACP implementation scenarios. The implementation of
498 ACPs influenced TP loading more than the projected changes in climate in the two highest levels
499 of ACP implementation (ENMA and ENM). For example, substantial reductions (e.g., 27.6%
500 during the 2060s, RCP4.5, ENM scenario) in TP loading could still be achieved in the far-term,
501 despite the overall increasing trends in climate-driven TP loading through time (Figure 5).
502 However, in the ACP implementation scenarios where current levels of implementation were
503 carried into the future or only acres in critical need were treated, TP loads were forecasted to
504 increase above the historical median levels (Figure 5).

505 *Forecasts of fish recruitment*

506 Walleye. The final walleye recruitment model only included winter severity as a
507 predictor. Thus, walleye recruitment was not projected under different levels of ACP
508 implementation, only under different greenhouse gas emission (RCP) scenarios. In general,
509 median annual projections of recruitment decreased through time in both the moderate reductions
510 (RCP4.5) and business-as-usual (RCP8.5) scenarios (Figure 6). Interestingly, the projected
511 median annual recruitment values during earlier decades (2020s to 2040s for RCP4.5, 2020s and
512 2030s for RCP8.5) were 3% to 50% higher than the historical median, owing to more variable
513 forecasts that resulted in projected severe winters during earlier decades. However, during
514 subsequent decades (2040s-2060s), both emission scenarios had projected median annual
515 recruitment values lower than the historical median (Figure 6). During the 2060s under the
516 RCP8.5 emission scenario, which represents the “worst-case scenario” in our projections, median
517 annual recruitment decreased by 38% relative to the historical median. By contrast, the

518 frequency of a projected strong (\geq historical 75th percentile) annual walleye recruitment event
519 (year-class) during a decade was lower than 25% (the expected frequency) during all decades,
520 under both emission scenarios (Figure 7), except under the RCP8.5 emission scenario during the
521 2020s. Under the RCP4.5 emission scenario, the median frequency of a projected annual strong
522 recruitment event decreased from 18% during the 2020s to 5% during the 2060s. The decline
523 was more severe under the RCP8.5 emission scenario during which the median value was only
524 5% and 4% in the 2050s and 2060s, respectively. The median frequency of strong recruitment
525 events was slightly higher early in the projected period under the RCP8.5 emission scenario
526 compared to the RCP4.5 one, owing to a slightly higher occurrence of projected severe winters
527 during early decades. Overall, under both future greenhouse gas emission scenarios, the
528 projected frequency of strong walleye recruitment events decreased substantially compared to
529 the past.

530 Yellow perch. Our analysis of yellow perch recruitment yielded four major findings.
531 First, median annual recruitment was projected to be lower than the historical median across all
532 decades under all climate change \times ACP implementation scenarios, except for one (RCP8.5,
533 ENMC, 2020s; Figure 8). These reductions ranged from 3.3% (RCP8.5, Baseline, 2020s) to 61%
534 (RCP8.5, ENM, 2060s) relative to the historical median. Second, projected median annual
535 yellow perch recruitment declined *through time* in all future climate and ACP implementation
536 scenarios (Figure 8). Generally, the reductions were greater under the RCP8.5 emission scenario
537 during any decade at any level of ACP implementation relative to the RCP4.5 emission scenario;
538 however, some exceptions to this pattern existed (e.g., ENMC, 2020s). The greatest reductions in
539 median annual yellow perch recruitment (56.5-60%) occurred during the 2060s under the
540 RCP8.5 emissions scenario. Third, increasing the level of ACP implementation (i.e., reducing TP
541 loads) exacerbated the climate-driven decline in median annual yellow perch recruitment. For
542 example, during the 2020s, we documented a 4.6% decline in median annual yellow perch
543 recruitment under the RCP4.5-Baseline scenario. By contrast, we observed a 27.3% reduction in
544 median annual yellow perch recruitment in the 2020s under the RCP4.5-ENM (all acres treated)
545 scenario. This trend was similar across all decades and combinations of climate and ACP
546 implementation scenarios (Figure 8). Fourth, similar trends emerged for the projected frequency
547 of strong (\geq historical 75th percentile) yellow perch recruitment events (Figure 9). Projected
548 strong yellow perch recruitment events decreased through time, decreased with increasing levels

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

554 White perch. Unlike walleye and yellow perch, recruitment of invasive white perch was
555 projected to be near or above the historical median across all climate and ACP implementation
556 scenarios (Figure 10). The projected increases in the median annual recruitment values were
557 typically greatest during the near-term (2020s and 2030s) at the two highest levels of ACP
558 implementation (ENMA and ENM; Figure 10). Although temporal trends in median white perch
559 recruitment were less apparent relative to yellow perch and walleye, white perch recruitment was
560 projected to be slightly higher during the 2020s relative the 2060s under any given climate and
561 ACP implementation scenario (Figure 10). Even so, during all decades, under all future
562 scenarios, annual median recruitment was projected to be greater than the historical median at
563 the two highest levels of ACP implementation. Unlike yellow perch, median white perch
564 recruitment was projected to increase with increasing levels of ACP implementation under both
565 emission scenarios, a finding that ran counter to our expectations. However, the projected trends
566 in the frequency of strong (\geq historical 75th percentile) annual recruitment events differed from
567 the trends in median recruitment. At the two lowest levels of ACP implementation, the
568 proportion of strong recruitment events was lower than the expected frequency across all
569 decades. However, during all decades under both emission scenarios, at the highest level of ACP
570 implementation, the frequency of strong white perch recruitment events was projected to be
571 above the expected frequency (25% based on the historical occurrence of strong recruitment
572 events), ranging from 27% to 54% (Figure 11).

573

574 **DISCUSSION**

575 Predicting the effects of anthropogenic stressors such as climate change and agricultural-
576 derived non-point source (NPS) pollution has been identified as a critical research need that
577 could benefit fisheries management in the face of future ecosystem change (Arvai et al., 2006;
578 Pritt et al., 2014; DeVanna Fussell et al., 2014). The Great Lakes, and specifically Lake Erie, is
579 an ideal study system for such work because it has experienced these anthropogenic stressors,

580 supports valuable fisheries, and is data-rich (Ludsin et al., 2014; Pritt et al., 2014; Scavia et al.,
581 2014; Farmer et al., 2015). In this study, we forecasted how the recruitment of three ecologically
582 and/or economically important western Lake Erie fish populations, which span a gradient of
583 thermal preferences, might vary under future scenarios of climate change and agricultural
584 conservation practice (ACP) implementation in the western Lake Erie basin (WLEB) watershed.
585 Our modeling showed that, in general, walleye and yellow perch recruitment can be expected to
586 decrease and that white perch recruitment can be expected to remain stable or increase during the
587 next several decades, relative to the recent past. Interestingly, our modeling also revealed
588 offsetting effects between climate change and ACP implementation, highlighting the potential
589 for tradeoffs between improving water quality, maintaining fisheries production, and controlling
590 invasive species in the face of potential climate change. Although attaining a complete
591 understanding of future recruitment dynamics is impossible (Schindler & Hilborn, 2015), and
592 more research is encouraged to verify some of our suggested mechanistic linkages and
593 recruitment projections, our study presents a useful modeling framework to forecast fish
594 population dynamics, specifically recruitment, and provides a range of potential outcomes for
595 resource management agencies and policy makers that can help them develop adaptive and
596 resilient management strategies in the face of continued ecosystem change (Heller & Zavaleta
597 2009; Lynch et al., 2016; Paukert et al., 2016,).

598 Our results support previous studies, which have predicted that climate warming will
599 differentially affect species with varying thermal preferences. Similar to other studies (Chu,
600 Mandrak, & Minns, 2005; Farmer 2013; Van Zuiden et al., 2016; Hansen et al., 2017), we
601 projected declines in recruitment for walleye and yellow perch, which are considered cool-water
602 species, and increased or stable recruitment in white perch, an invasive warm-water species.
603 Although previous research has suggested that habitat conditions for *adult*, cool-water fishes,
604 such as walleye, would increase with continued warming, especially in northern latitudes (e.g.,
605 Chu et al., 2005; Wiley et al., 2010), our research demonstrates the importance of considering
606 other life stages (e.g., juvenile) and specific biological processes (e.g., reproduction and ovary
607 development) that require cold temperatures, and therefore, are more likely to be affected by
608 warming. Understanding the influence of warming is especially critical for populations such as
609 Lake Erie walleye and yellow perch, the recruitment dynamics of which have been shown to be
610 influenced by temperature, which in turn drives variability in the fishery (Shuter & Koonce

611 1977; Farmer et al., 2015; WTG 2017). In fact, species that are sensitive to winter conditions
612 (such as walleye and yellow perch) may be the first to be affected by climate change (Shuter,
613 Minns & Lester, 2002).

614 *Walleye recruitment*

615 Based on our findings, western Lake Erie walleye recruitment, especially episodically
616 strong recruitment events that keep the recreational and commercial fisheries viable (Vandergoot
617 et al., 2010), were predicted to decline, owing to a projected reduction in winter severity.
618 Recruitment declines were greatest further into the 21st century and in the “business-as-usual”
619 greenhouse gas emission scenario (RCP8.5), relative to the moderate-reduction (RCP4.5)
620 scenario. Although we documented an overall decreasing trend in projected walleye recruitment
621 in the future, median walleye recruitment was generally projected to be at or above the historical
622 median during the 2020s through 2040s. Even so, the projected frequency of strong walleye
623 recruitment events was below the “expected” proportion (25%) during these and subsequent
624 decades, under both greenhouse gas emission scenarios.

625 Our modeling results are consistent with other modeling studies that have forecasted
626 walleye recruitment under a changing climate. For example, Hansen et al. (2017) showed that the
627 projected number of Wisconsin (USA) lakes likely to support walleye recruitment decreased in
628 the future, owing to increases in the number of annual degree days under future warming
629 scenarios. Likewise, Van Zuiden et al. (2016) concluded that projected warming should lead to
630 an increase in unsuitable habitat at the southern range of walleye, resulting in a general
631 northward shift in their distribution. While we fully expect western Lake Erie to continue to
632 support walleye fisheries, our modeling suggests that the strong recruitment events (year-classes)
633 that drive order of magnitude differences in the fishable population (Vandergoot et al., 2010)
634 may decline with continued climate warming.

635 Our predictive model explained 31.3% of the variation in walleye recruitment, which is
636 similar to or better than studies that have correlated walleye recruitment to abiotic and/or biotic
637 factors (e.g., Madenjian, Tyson, Knight, Kershner, & Hansen, 1996; Shuter & Koonce 1977;
638 Zhao, Kocovsky, & Madenjian, 2013; Shaw, Sass, & VanDeHey, 2018). Historically, explaining
639 walleye recruitment variability using various measures of spawning-stock biomass has yielded
640 poor results (Madenjian et al., 1996; Shaw et al., 2018), and considering environmental drivers
641 of recruitment has consistently yielded better results (Busch et al., 1975; Shuter & Koonce 1977;

642 Madenjian et al., 1996; Roseman et al., 1999; Zhao et al., 2009). Much work on Lake Erie
643 walleye recruitment has suggested the rate of spring warming is significantly and positively
644 related to walleye recruitment (Busch et al., 1975; Madenjian et al., 1996; Roseman et al., 1999;
645 Zhao et al., 2013). Although we considered spring warming rate, it was not included in our final
646 predictive model of walleye recruitment. The lack of inclusion of spring warming rate as a
647 recruitment driver is not, however, inconsistent with all previous Lake Erie walleye recruitment
648 work. For example, Zhao et al. (2009) used a three-dimensional hydrodynamic model to
649 demonstrate that walleye recruitment was more strongly associated with wind speed and
650 direction than it was with spring warming rate. Data like wind speed, however, are not available
651 from climate models and were therefore not considered in this study.

652 In addition to abiotic factors, biotic factors are also likely to affect walleye recruitment,
653 which we did not consider. For example, prey abundance, specifically, age-0 gizzard shad
654 (*Dorosoma cepedianum*) abundance has been correlated to Lake Erie walleye recruitment
655 (Madenjian et al., 1996), but not with consistent, replicable results (Zhao et al., 2013). It is also
656 possible that climate change could have indirect effects on walleye recruitment that is mediated
657 by biotic factors such as zooplankton prey availability to larvae (Ludsin et al., 2014). Ultimately,
658 our understanding of walleye recruitment in Lake Erie remains largely speculative and is based
659 primarily on correlative work. While the use of winter severity to predict walleye recruitment is
660 partially supported by mechanistic evidence, as walleye prefer cooler incubation and fertilization
661 temperatures (Koenst & Smith, 1976), exactly why the relationship between winter severity and
662 walleye recruitment exists remains incomplete (Fedor, 2008). We therefore recommend more
663 research into this linkage, as well as how climate change might affect walleye through other
664 direct and indirect pathways.

665 *Yellow perch recruitment*

666 Similar to walleye, our modeling projected that Lake Erie yellow perch recruitment will
667 decline under future climate warming scenarios. Furthermore, it suggests that this decline would
668 be exacerbated by efforts to reduce nutrient inputs (i.e., total phosphorus, TP) into Lake Erie via
669 the implementation of ACPs in the WLEB watershed. The prominent driver of the projected
670 yellow perch recruitment decline was reduced winter severity, with the level of ACP
671 implementation having a secondary negative effect. Although yellow perch recruitment
672 displayed a unimodal, dome-shaped response to Maumee River TP inputs, future anticipated

673 ACP implementation led to TP loads that were lower than the optimum for strong recruitment
674 events to occur. Previous studies of yellow perch recruitment have suggested that rapid warming
675 during the spring can positively (Eshenroder 1977) and negatively (Zhang, Reid, & Nudds, 2016)
676 influence yellow perch recruitment, whereas it was not identified as a useful predictor in our
677 final model.

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

693 Our yellow perch model explained 51.1% of the variation in recruitment and included
694 both winter severity and Maumee River TP as environmental predictors. Similar to walleye,
695 various measures of spawning-stock size have not consistently explained yellow perch
696 recruitment variation (Henderson 1985; Henderson & Nepszy, 1988; Zhang et al., 2016) and
697 yellow perch recruitment synchrony throughout the Great Lakes region indicate that regional-
698 scale environmental factors, such as the ones included in this study, are more likely than stock-
699 size to drive recruitment (Honsey et al., 2016). The two environmental drivers of yellow perch
700 recruitment that we identified are consistent with findings from previous correlative and
701 mechanistic studies (Hokanson, 1977; Hall & Rudstam, 1999; Reichert et al., 2010; Ludsin et al.,
702 2011; Carreon-Martinez et al., 2014; Farmer et al., 2015). For example, a greater percentage of
703 yellow perch successfully spawn at colder water temperatures and after long chill durations

704 (Hokanson, 1977) compared to warmer temperatures, indicating a benefit of long, cold winters
705 for yellow perch. This finding is supported by experimental research, which has demonstrated
706 that short warm winters cause reduced egg hatching success and reduced egg and larvae size and
707 quality (Farmer et al., 2015). Declines in yellow perch abundance have also previously been
708 correlated with reduced TP availability (Hall & Rudstam, 1999).

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

726 *White perch recruitment*

727 White perch recruitment (both median levels and the frequency of strong recruitment
728 events) was forecasted to be close to or greater than the historical median across all scenarios
729 during all decades, and increased levels of ACP implementation (i.e., reduced TP loading)
730 resulted in generally higher white perch recruitment. Substantially less information exists on the
731 drivers of white perch recruitment relative to walleye or yellow perch, especially in ecosystems
732 where this species is invasive (e.g., Lake Erie). However, our finding that climate warming may
733 lead to higher white perch recruitment is generally consistent with the literature that does exist.
734 For example, Johnson & Evans (1990) speculated that climate warming would cause higher

735 recruitment and ultimately expansion of white perch in the Great Lakes by reducing overwinter
736 mortality. Although, winter severity was not included in the final predictive model of white
737 perch recruitment, climate warming could possibly result in a longer growing season and
738 improve overwinter survival (Johnson & Evans, 1990). The generally negative (although non-
739 linear) relationship between Maumee River TP and white perch recruitment was the opposite of
740 our expectation, as white perch generally prefer eutrophic waters over oligotrophic ones
741 (Boileau, 1985). Adult white perch abundance has also previously been shown to be positively
742 associated with high turbidity and eutrophic conditions in other ecosystems (Hawes & Parrish,
743 2003), indicating a need for more research to understand our observed association.

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

759 Regardless of the ultimate mechanism, increases in white perch recruitment, could have
760 serious ecological effects that warrant further study. For example, white perch are known
761 predators of walleye eggs (Schaeffer & Margraf, 1987), and increased white perch abundance
762 could potentially negatively affect walleye recruitment. Also, yearling and adult white perch are
763 known predators of yellow perch larvae (Ludsin et al., 2011; Carreon-Martinez et al., 2014), and
764 increased predation from an even more abundant white perch population in the future could
765 further exacerbate the projected negative effects of climate warming and ACP implementation on

766 western Lake Erie's yellow perch population. Although we did not account for biotic interactions
767 in our study, collectively, our results highlight the need to understand how warm-water invasive
768 species, such as white perch, which are likely to thrive in a warmer future climate, might impact
769 native cool-water fishes in temperate ecosystems such as Lake Erie.

770 *Study limitations*

771 As with all forecasting studies, our approach has several limitations. Although the
772 proportions of variance in recruitment that our predictive models explained were similar to or
773 better than those reported in the literature (see species-specific examples above), they certainly
774 did not explain all, or in some cases the majority of recruitment variation. Still, such models can
775 be useful in assessing the impacts of climate change (Guisan & Thuiller, 2005), although we
776 strongly encourage managers to consider the breadth of information available when making
777 future management and conservation decisions. Furthermore, care should be taken when
778 extrapolating recruitment responses to environmental conditions outside the range of observed
779 historical conditions, as species-environment relationships may not be stationary (Schindler &
780 Hilborn, 2015; Zhang, Reid, & Nudds, 2018). We also caution against interpreting the exact
781 magnitude of our future recruitment values in a “predict and prescribe” approach (Schindler &
782 Hilborn 2015), given mechanistic uncertainties associated our predictive models. Even so, we
783 feel comfortable interpreting the general trends and drivers apparent in our results and their use
784 as guidance for future management.

785 Forecasting future population dynamics will always be incomplete, uncertain, and a
786 simplification of reality, regardless of the ecosystem. However, studies like ours provide a range
787 of possible outcomes that can be used as tools for resource managers (Schindler & Hilborn
788 2015). While we do not know the true magnitude or extent of future warming, by modeling
789 multiple greenhouse gas emission scenarios, using a suite of climate ensembles, we could
790 propagate some of that future uncertainty into our recruitment forecasts (Hansen et al., 2017).
791 This “ensemble approach” to forecasting future dynamics is ubiquitous and is an accepted way of
792 acknowledging the uncertainty in future predictions (Hollowed et al., 2009; Lindegren et al.,
793 2010; Bartolino et al., 2014), although we recognize this approach does not account for all of the
794 uncertainty associated with forecasting future recruitment.

795 Another limitation to our study is that our methods were correlative and did not verify the
796 underlying mechanisms by which winter severity, spring warming rate, and TP loads can alter

797 recruitment dynamics. Thus, while we provided mechanistic support for their inclusion in our
798 predictive models, which strengthens the confidence in our results (Hilborn 2016), the possibility
799 exists that the metrics included in this study encompass several underlying mechanisms (Hansen
800 et al., 2017) or are actually proxies for other correlated environmental drivers. For example,
801 because Maumee River TP loads into Lake Erie are highly correlated with Maumee River
802 inflows and total suspended sediment loads, TP itself may not be the exact mechanistic driver of
803 yellow perch or white perch recruitment. Owing to the difficulty in implementing and designing
804 rigorous, experimental approaches to determine causal relationships over large spatial and
805 temporal extents (Hilborn 2016), correlative studies such as ours remain the most reasonable
806 approach to forecasting recruitment on large spatial and temporal scales (Guisan & Thuiller,
807 2005; Hansen et al., 2017).

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

817 *Conclusions*

818 Our modeling allowed us to explore how anticipated climate change and ACP
819 implementation designed to reduce non-point source nutrient loading might interact to affect the
820 recruitment dynamics of ecologically and economically important fish populations in Lake Erie.
821 By including two emission scenarios, four levels of ACP implementation, and numerous GCMs
822 and ensembles, we forecasted a range of future outcomes to better equip resource managers to
823 make decisions that can promote sustainable and resilient fisheries in the future (Lynch et al.,
824 2016; Paukert et al., 2016). Our findings highlight the importance of climate as a driver of fish
825 recruitment dynamics and indicate that, in the future, native cool-water species such as walleye
826 and yellow perch may be detrimentally affected by climate change, whereas nonnative warm-
827 water species such as white perch might benefit. Our modeling also suggests that reducing

828 nutrient inputs to improve water quality (though ACP implementation) may lead to inadvertent
829 tradeoffs that could negatively affect the production of valued fisheries (Ney, 1996; Ludsin,
830 2000, Ludsin et al., 2001; Kao, Richards, & Bunnell, 2018). For example, our modeling provided
831 evidence to suggest that reduced nutrient (or possibly sediment) runoff from the WLEB
832 watershed—resultant of ACP implementation—could exacerbate anticipated climate-driven
833 reductions in western Lake Erie yellow perch recruitment. Simultaneously, these same
834 conditions were projected to promote invasive white perch, which is a known predator on
835 walleye and yellow perch early life stages (Schaeffer & Margraf 1987; Carreon-Martinez et al.,
836 2014).

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

850

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862

863 **DATA AVAILABILITY STATEMENT**

864 Data used to build the recruitment models are available as a separate file. The climate data are
865 available at https://gdo-dcp.ucllnl.org/downscaled_cmip_projections/dcpInterface.html.

866

867 **CONFLICT OF INTEREST STATEMENT**

868 The authors report no conflicts of interest.

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FIGURE LEGENDS

Figure 1. Map of the western Lake Erie basin watershed (MI, IN, OH, USA) and the west basin of Lake Erie (USA-Canada). Trawling stations are denoted by solid black circles, weather stations by black triangles, and the Maumee River gauge station used to validate the SWAT model by a gold star.

Figure 2. Conceptual modeling 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) watershed. Predictive models of fish recruitment were built using generalized 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 climate ensemble forecasts and linked Soil and Water Assessment Tool (SWAT) and Agricultural Policy/Environmental eXtender (APEX) models.

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⁻¹) in western Lake Erie and D) spring warming rate (°C·d⁻¹, during April through May), E) winter severity (number of days with a maximum temperature ≥ 6°C during January through May), and F) Maumee River total phosphorus load (TP, metric tons, March through 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.

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 not summarized (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 through May) or median spring warming rate ($^{\circ}\text{C}\cdot\text{d}^{-1}$, during April through May). The horizontal line represents the historical (1987 – 2015) median.

Figure 5. Violin plot of projected (2020-2065) Maumee 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 unsummarized (all years, all ensembles) data with the black lines representing the median springtime TP load (total March-May TP load, MT).

Figure 6. Boxplot of projected (2020-2065) median annual walleye recruitment (year-class strength, CPUE, individuals $\cdot\text{min}^{-1}$) 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, CPUE, individuals $\cdot\text{min}^{-1}$) in western Lake Erie under the RCP4.5 (grey) and RCP8.5 (white) emission scenarios by decade and agricultural conservation practice (ACP) implementation scenario. See Figure 5 legend for a description of each ACP scenario.

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

(ACP) 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 ACP scenario.

Figure 10. Boxplot of projected (2020-2065) median annual western Lake Erie white perch recruitment (year-class strength, CPUE, individuals·min⁻¹) under the RCP4.5 (grey) and RCP8.5 (white) emission scenarios by decade and agricultural conservation practice (ACP) implementation scenario. See the Figure 5 legend for a description of each ACP scenario.

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 (ACP) 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 ACP scenario.

SUPPLEMENTAL FIGURE LEGENDS

Figure S1. Diagnostic model fit plots for the most supported generalized additive models to predict walleye, yellow perch, and white perch recruitment in western Lake Erie. Each species-specific set of four plots includes a quantile-quantile plot, a plot of the residuals against fitted values, a histogram of the residuals, and response vs fitted values plot.

Figure S2. Diagnostic temporal autocorrelation (ACF) plots of walleye (we), yellow perch (yp), and white perch (wp) recruitment in western Lake Erie. Black vertical bars (Lag > 0), extending beyond the blue dotted lines indicate significant temporal autocorrelation. No significant temporal autocorrelation was observed for each species-specific model.

Figure S3. Partial response of western Lake Erie walleye recruitment to winter severity based on resampling procedure described in methods. Winter severity was the only predictor included in the final predictive walleye recruitment model, based on AICc analysis. First,

we generated a separate, simulated sequence ($N = 250$) of each predictor variable using its observed range as bounds. Next, we resampled the other two predictor variables (with replacement) from the original data to generate three new resampled data sets, 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).

Figure S4. Partial responses of western Lake Erie yellow perch recruitment to winter severity (left) and Maumee River total phosphorus (TP, right) using resampling procedure described in methods and in the Figure S3 legend. Winter severity and TP were the two predictors included in the final yellow perch recruitment model.

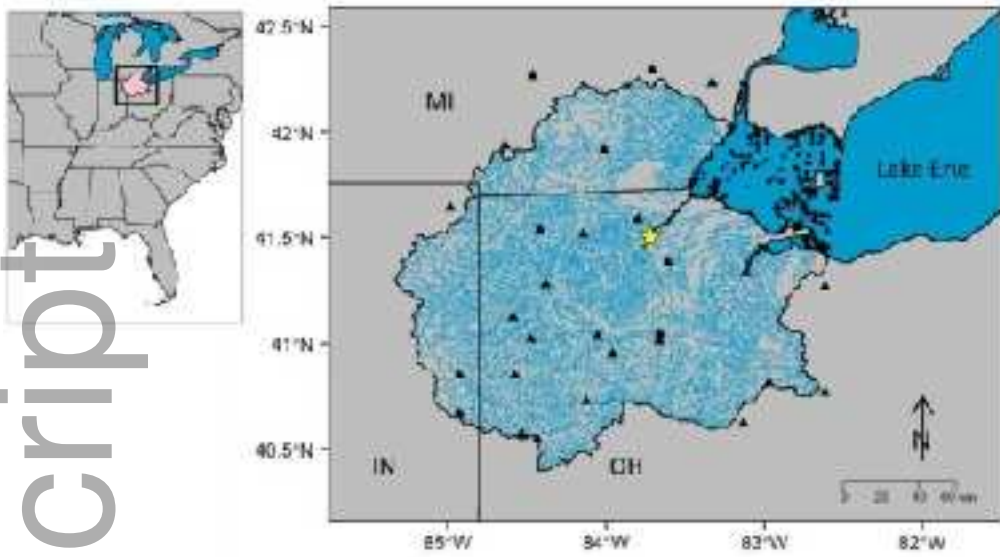
Figure S5. Partial responses of western Lake Erie white perch recruitment to spring warming rate (top) and Maumee River TP (bottom) using resampling procedure described in methods and in the Figure S3 legend. Spring warming rate and TP were the two predictors included in the final predictive white perch recruitment model.

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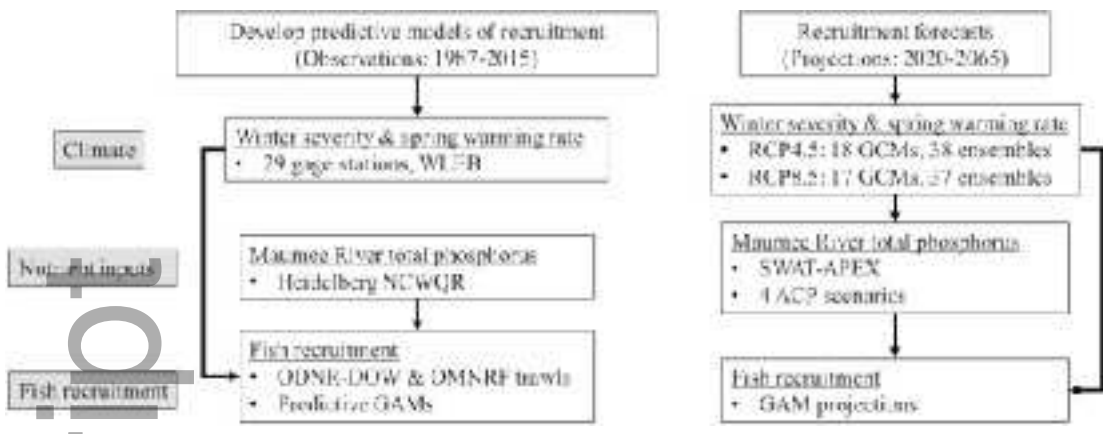
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Table 1. Summary of final generalized additive models used to predict walleye, yellow perch, and white perch recruitment in western Lake Erie. Possible predictors included winter severity (the total number of days that the mean daily maximum temperature across the western Lake Erie watershed was $\leq 6^\circ\text{C}$ during January through May of each year), spring warming rate ($^\circ\text{C}\cdot\text{d}^{-1}$), 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 AIC_c model selection. All included smooth terms have $p < 0.05$

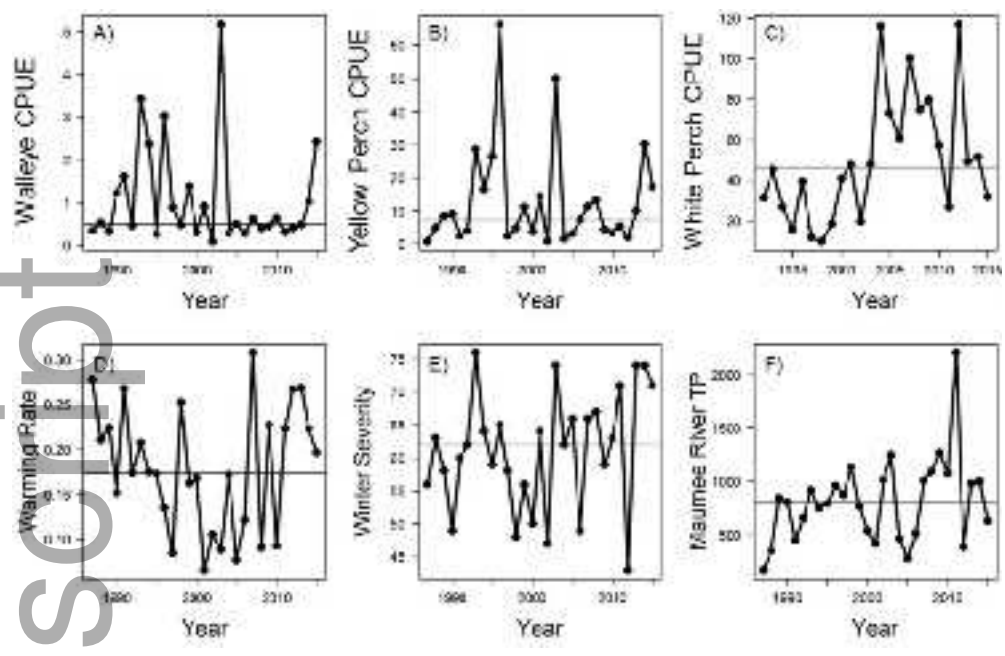
Species	EDF			
	Winter Severity	Spring Warming Rate	Maumee River TP	Overall Deviance Explained (%)
Walleye	1.00	NA	NA	31.3
Yellow Perch	1.00	NA	2.587	51.1
White Perch	NA	1.00	4.523	55.4



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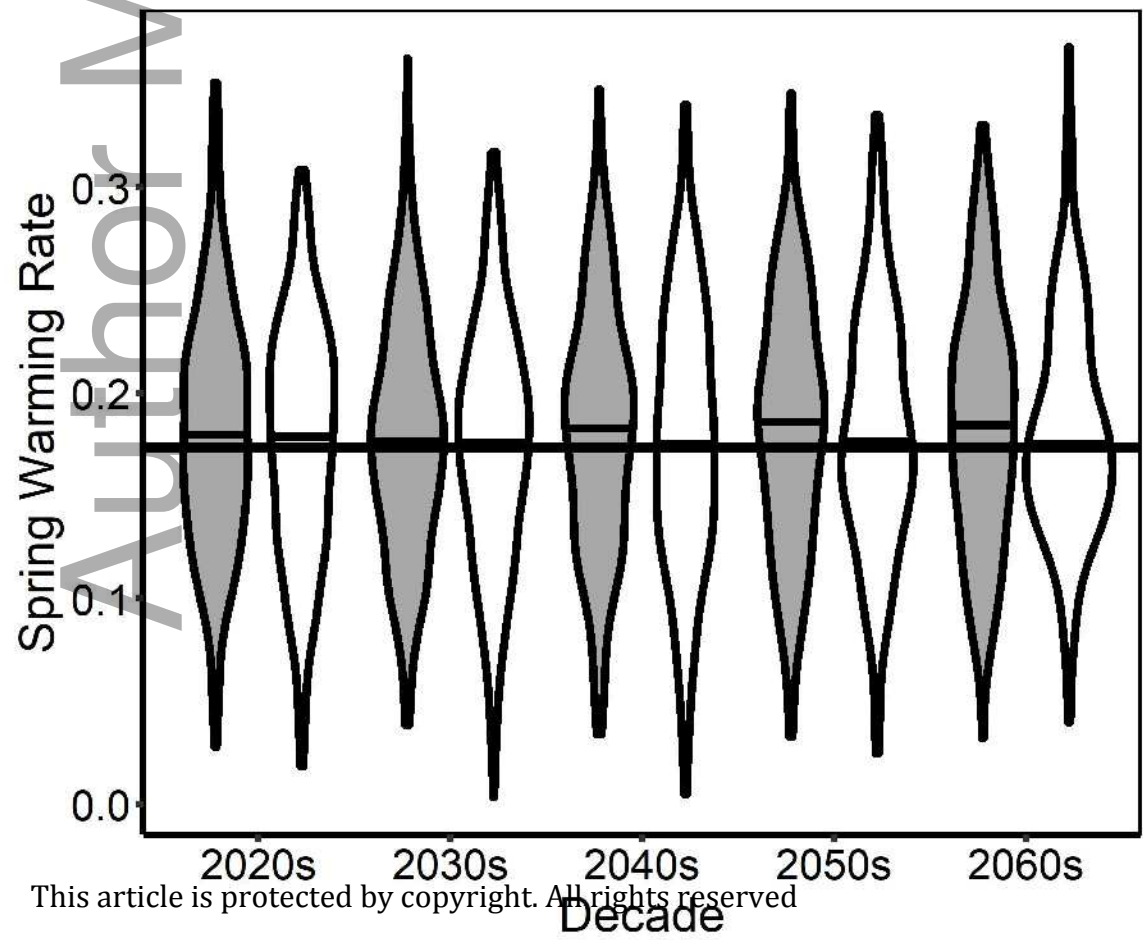
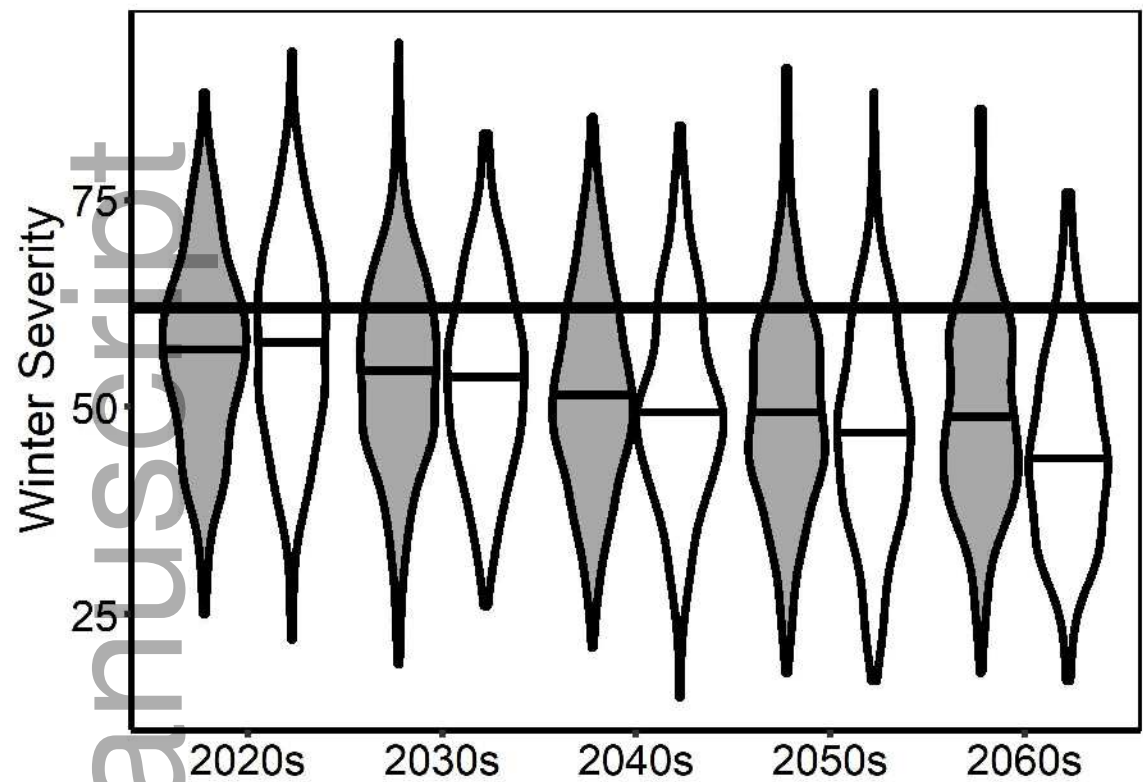


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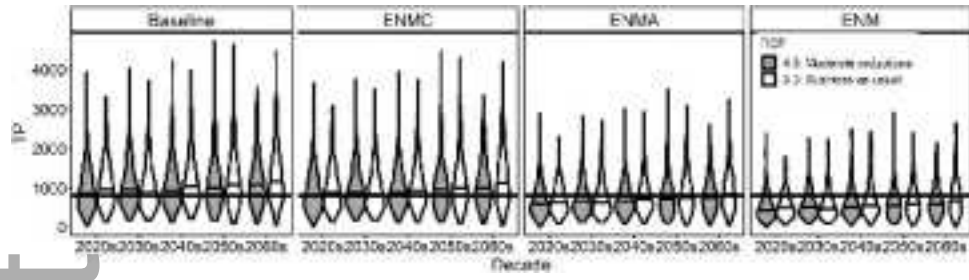


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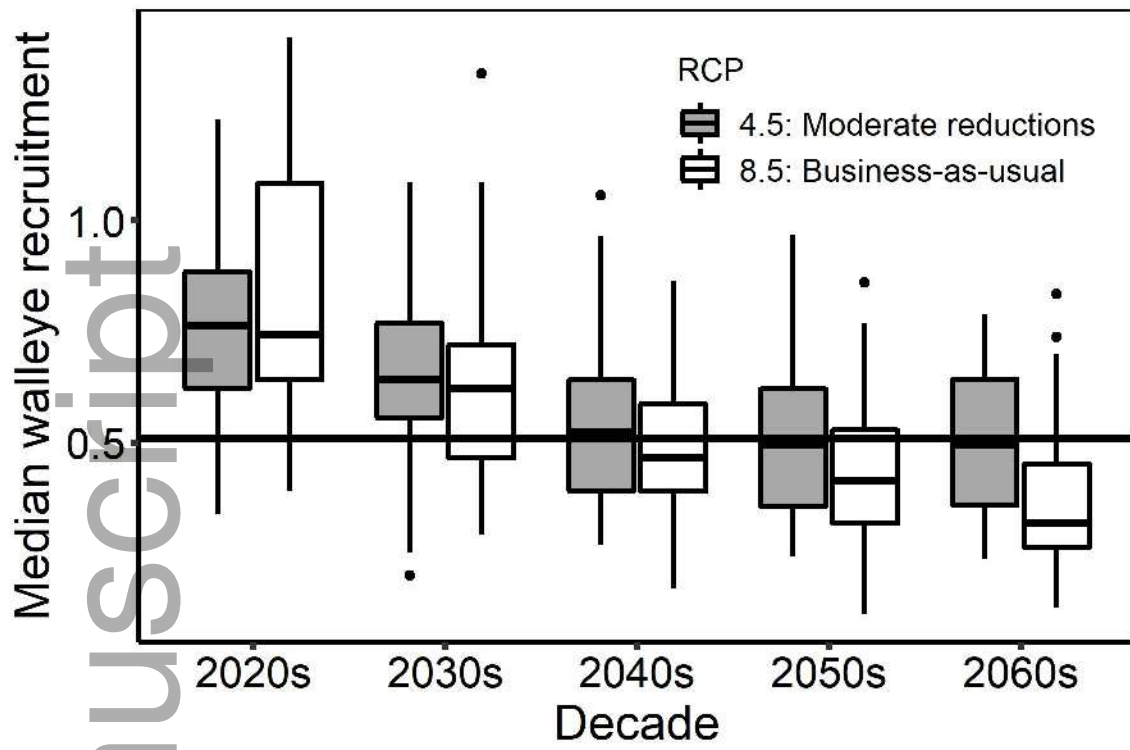
RCP 4.5: Moderate reductions 8.5: Business-as-usual



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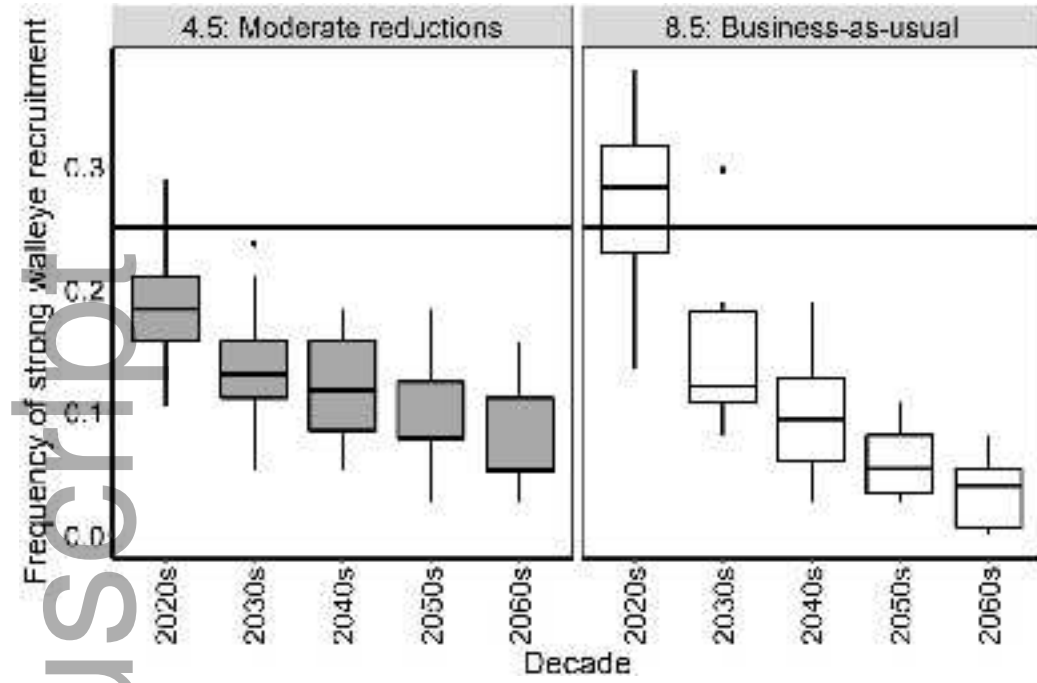


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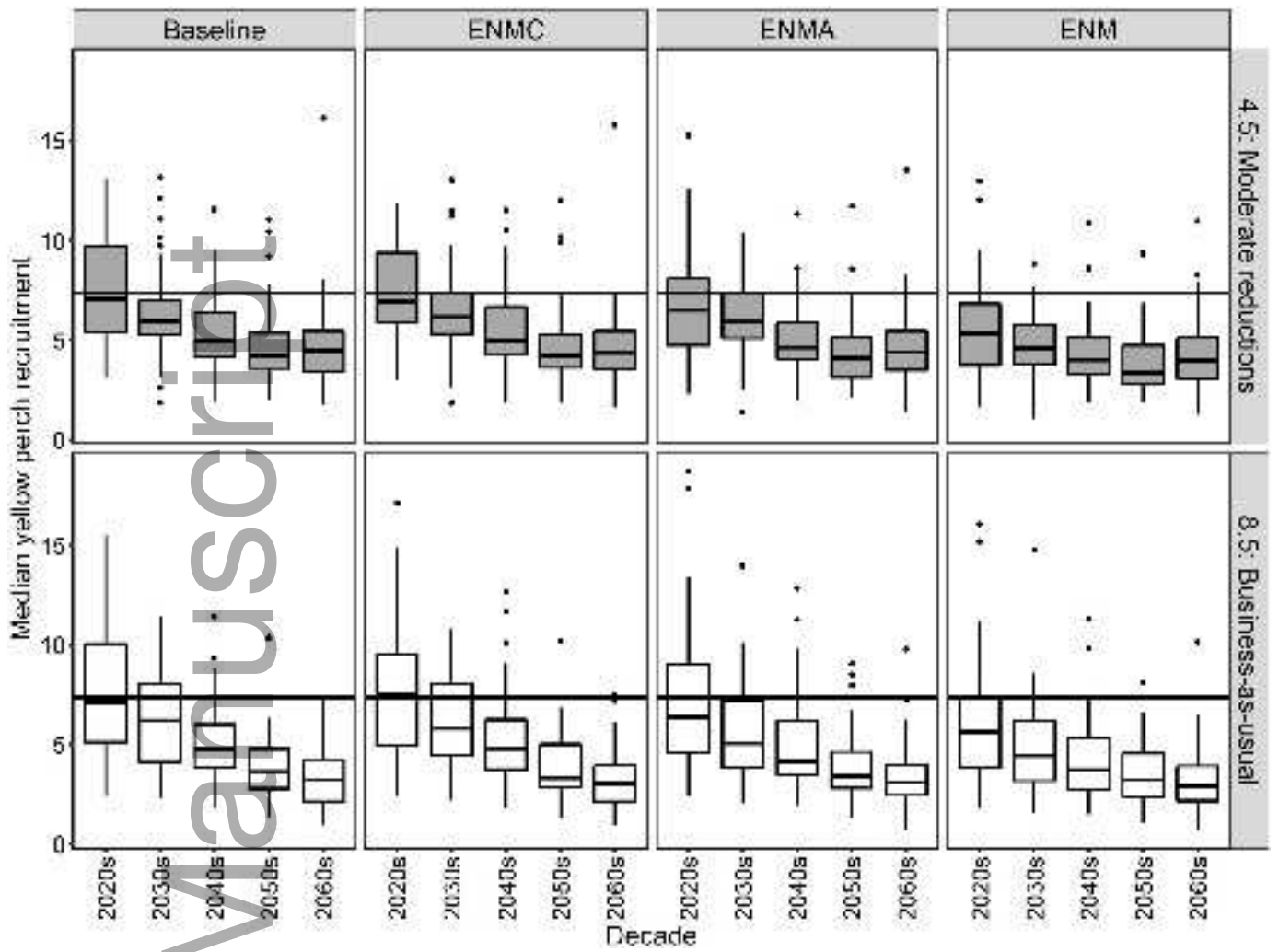


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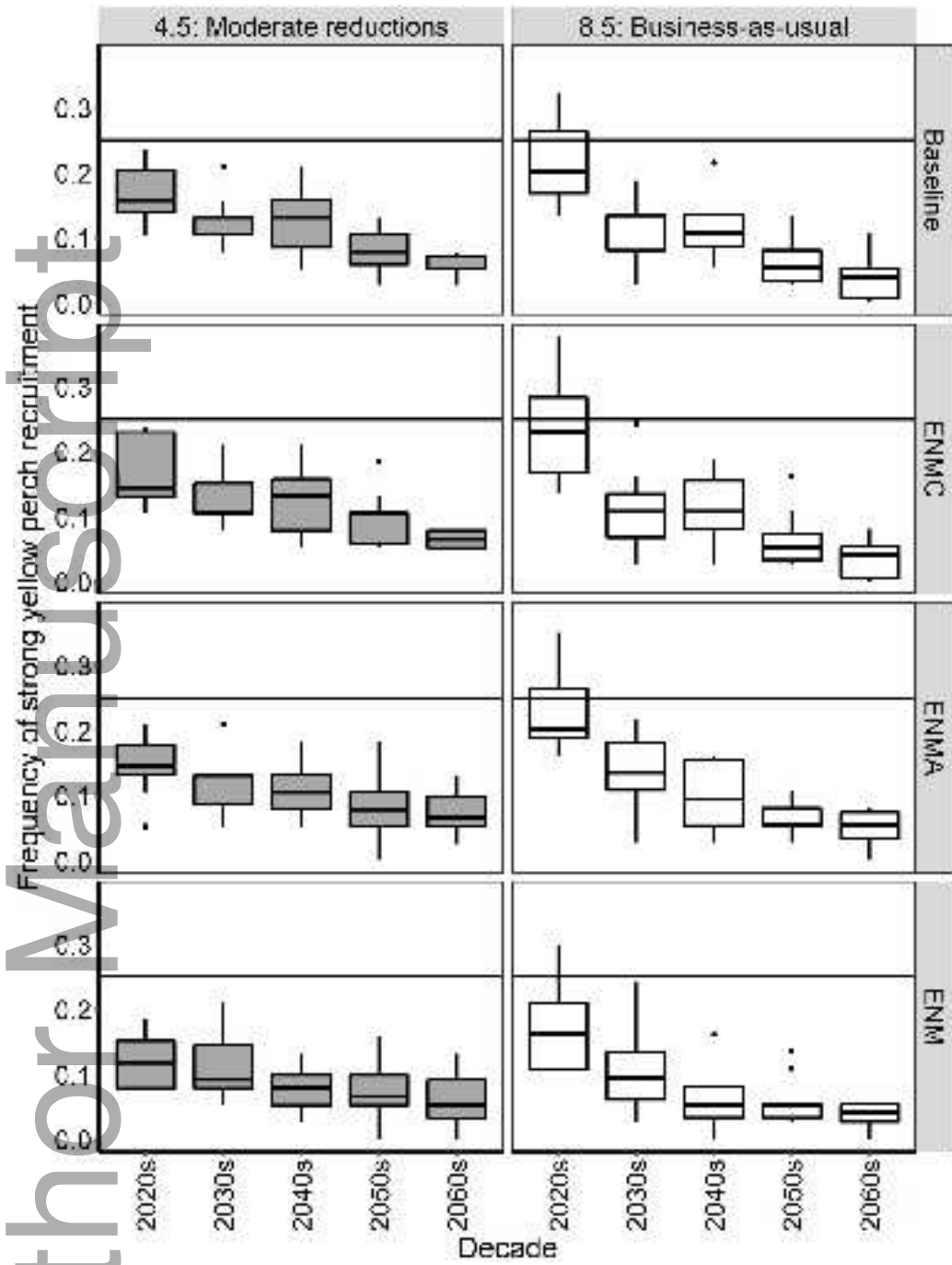
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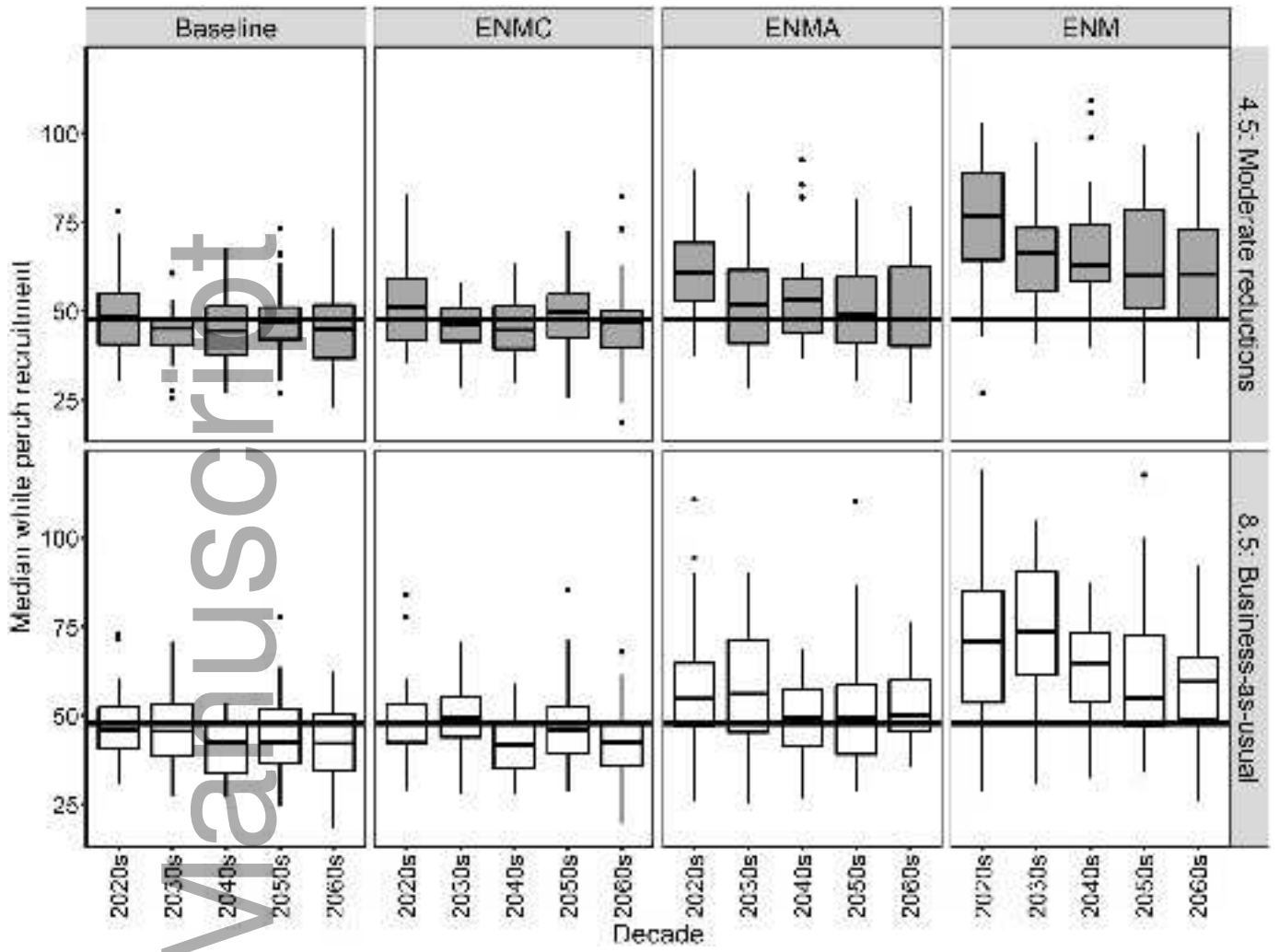
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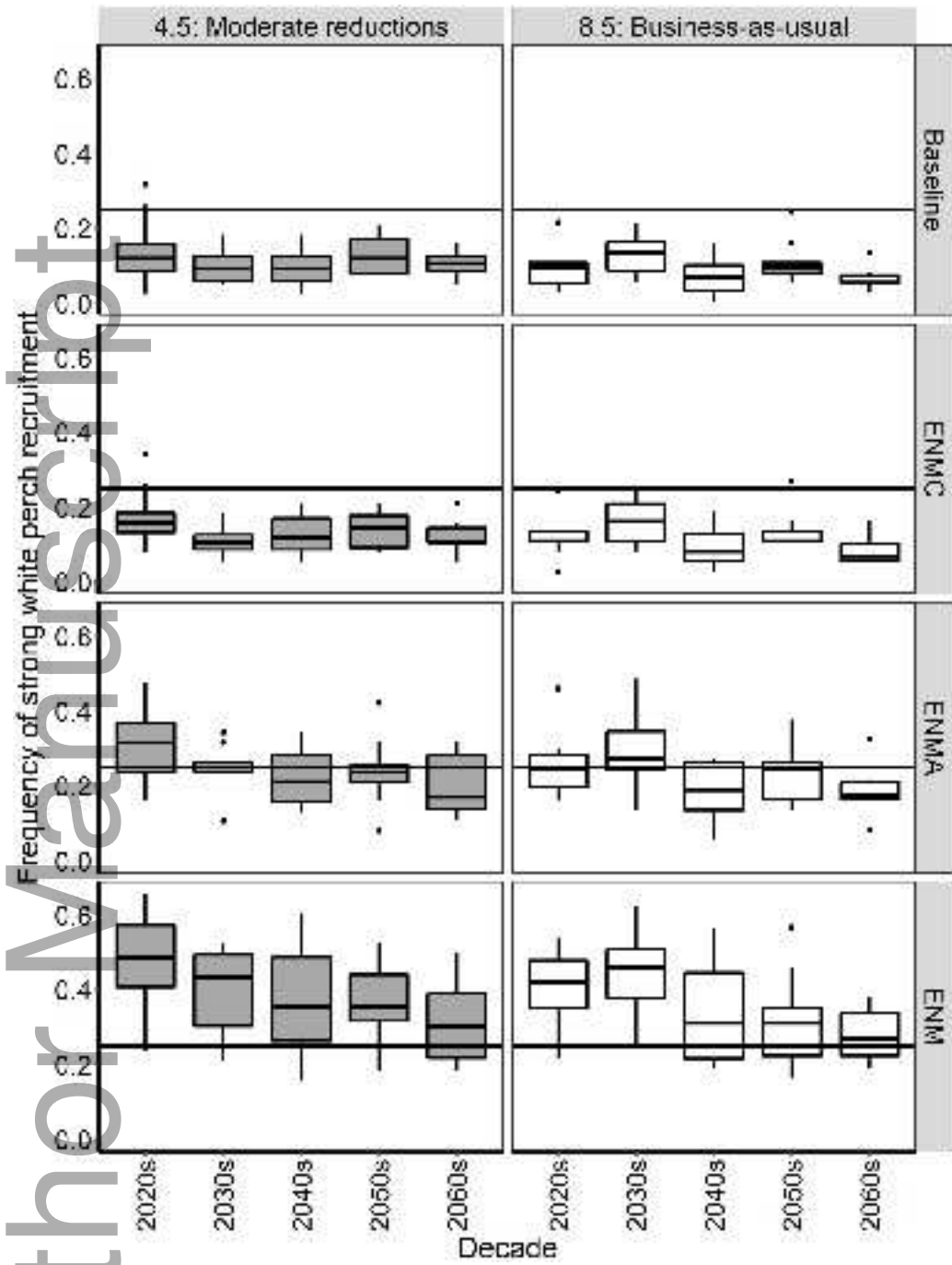


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