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Eroding productivity of walleye populations in northern Wisconsin lakes

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Running Head: Walleye Production Rates

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Abstract

Managing fisheries through rapid environmental change requires diverse approaches for identifying and adapting to novel ecological conditions. For the Wisconsin Ceded Territory, we calculated 473 adult walleye *Sander vitreus* production (P), biomass (B), and P/B estimates, 1990-2012. Frequency distributions for production statistics were right-skewed, indicating the fishery is generally dominated by low production populations. Average P, B, and P/B were significantly elevated in natural recruitment (NR) lakes compared to combination (NR + stocking) and stocked-only lakes. Furthermore, combination populations had significantly higher production compared to stocked-only lakes. In NR lakes, walleye productivity changed little over time, however the proportion of NR populations has declined over time. In combination and stocked-only populations, there were significant temporal declines in P, B and P/B, and the proportion of these lakes has increased through time. This study reveals the crucial link between fish recruitment potential and fish production, helping to explain why the regional walleye fishery is struggling. Causes for walleye recruitment and production declines remain unclear, but long-term shifts in fish habitats are likely involved (e.g., from climate change and indirect food web effects). Decreasing walleye production is a significant and emerging fishery management challenge in the region and portends a need to collaboratively adapt fisheries management systems for future sustainability.

35 **Introduction**

36 The sustainability of inland fisheries is being challenged by global ecological change at all scales
37 (Lynch et al. 2016; Sass et al. 2017). Freshwater fisheries are changing in response to climate
38 change (Chu et al. 2005; Sharma et al. 2011), invasive species (Vander Zanden and Olden 2008),
39 pollution (Herb et al. 2014; Schindler et al. 2016), ecosystem fragmentation (Rypel and Layman
40 2008) and overharvest (Post et al. 2002; Allan et al. 2005). Diverse perspectives and approaches
41 are increasingly needed to understand complex drivers of fisheries change and to develop
42 management strategies for sustainability (Paukert et al. 2016; Poesch et al. 2016; Winfield et al.
43 2016).

44 In the mid-high latitudes of North America, native walleye (*Sander vitreus*) fisheries are
45 rapidly being impacted by widespread ecological change (Hansen et al. 2016; Tsehaye et al.
46 2016; Van Zuiden and Sharma 2016). Walleye fisheries are of exceptional cultural, recreational,
47 and economic importance in Wisconsin and neighboring regions (Beard et al. 2003; Carlin et al.
48 2012; Rypel et al. 2016), but in recent years, walleye recruitment has started to decline (Hansen
49 et al. 2016). In contrast, abundances of other species (e.g., largemouth *Micropterus salmoides*
50 and smallmouth bass *M. dolomieu*) have increased, prompting concern among managers and
51 stakeholders (Hansen et al. 2015c; Rypel et al. 2016). Questions remain as to the potential causes
52 and consequences of walleye recruitment declines in the fishery. For example, it is unclear how
53 declining recruitment might be linked to later fish production (i.e., the elaboration rate of new
54 fish biomass).

55 Studying the spatiotemporal dynamics of fish production has the potential to address
56 important questions surrounding native walleye populations (Rypel et al. 2015). Production

estimates integrate critical vital rates such as abundance, recruitment, growth, and mortality (Waters 1977; Downing 1984; Kwak and Waters 1997). Resultantly, production variables are sensitive indicators of ecological change (Waters 1992; Valentine-Rose et al. 2007; Benke 2010; Myers et al. 2017; Rypel and David 2017). Production is also a measure specifically well-suited to the study of exploited fish populations (Ricker 1946; Waters 1992; Dolbeth et al. 2012; Rypel et al. 2015). Production is based in first principles, and is a direct estimate of energy fixation by organisms, energy flow through food webs, and fisheries services for human societies (Lindeman 1942; Roell and Orth 1993; Benke and Wallace 1997). In many fisheries, managers already track changes in population numbers, size, and growth (i.e., the component parts of production), but production itself is rarely calculated (Rypel et al. 2015; Rypel and David 2017).

The current walleye management system in northern Wisconsin uses a limit reference point method to manage harvest using population abundance (Cichosz 2015). In the absence of population abundance data, recruitment source becomes a critical element to estimating abundances (Cichosz 2015). Thus there is an implicit assumption that recruitment potential is linked to later fisheries production, but this idea has never been investigated using empirical production data. An improved understanding of how recruitment is coupled to actual walleye production might have implications for fisheries management in Wisconsin and nearby regions. The primary goals of our study were to: 1) Understand the distribution of walleye P, B and P/B across recruitment categories; 2) Investigate long-term trends in walleye P, B and P/B within each recruitment category; and 3) Explore the broader utility of production as a tool for inland fisheries management, using Wisconsin walleye as a case example.

Methods

79 *Wisconsin walleye management and data*

80 Walleye are native to large rivers and cool-water glacial lakes in Wisconsin (Becker 1983). In
81 1985, legal affirmation of off-reservation Native American hunting, fishing, and gathering treaty
82 rights reinstated a spring spearing fishery for walleye in the Wisconsin Ceded Territory,
83 approximately the northern 1/3 of the state (Staggs et al. 1990; Nesper 2002). Thus, walleye
84 populations were now subjected to an additional form of fishing mortality. In response, the
85 Wisconsin Department of Natural Resources (WDNR) and the Great Lakes Indian Fish and
86 Wildlife Commission (GLIFWC) launched a region-wide walleye stock-assessment program and
87 management system (Staggs et al. 1990). At the center of this system is the enactment of harvest
88 quotas on individual lakes based on adult walleye population estimates (Hansen 1989; Hansen et
89 al. 1991). A region-wide limit reference point was determined from Escanaba Lake, Wisconsin
90 as 35% of the adult walleye population, and harvest quotas for individual lakes are based on
91 recent population estimates so as to not exceed the limit reference point more than 1-in-40 times
92 minus margins of error (Hansen et al. 1991). Because population estimates are not available for
93 all lakes in each year, adult walleye population abundance estimates are also obtained using
94 regression models of total adult walleye abundance versus lake surface area (Hansen 1989;
95 Hansen et al. 1991; Nate et al. 2000; Hansen et al. 2015b). Separate regression models are used
96 for: 1) lakes sustained primarily by natural reproduction; 2) lakes sustained primarily through
97 stocking; and 3) lakes with low density populations maintained through intermittent natural
98 reproduction (Cichosz 2015).

99 Spring surveys of walleye populations have been conducted annually on Ceded Territory
100 lakes since 1985 and before, but surveys became more closely standardized in 1990. Lakes are
101 selected for surveys using a rotation that prioritizes lakes with a stratified random design based

on lake size, historical harvest, and recruitment status (Cichosz 2015). However, there has been variation in lake selection and the rotation over time. Initially a 5-year rotation was set to cover 1990-1994 and included lakes thought to be important to the fishery at that time. It became clear however that additional sampling was needed on other lakes that were also receiving harvest; thus a second rotation of treaty lakes was developed for 1997-2004 that included a larger pool of lakes. In 2001, plans emerged for a third sampling rotation with a goal of better establishing and examining temporal trends in walleye populations. This rotation, with the exception of some minor adjustments, has been in place until present day. The rotation included a separate lake rotation specifically to provide meaningful data on temporal trends within walleye populations. Sampling on these lakes (termed “trend lakes”) is selected from a list of 57 lakes with good population data (circa 2001), using a stratified randomized design, and occurs roughly every 3 years. Most trend lakes were historically lakes with walleye populations supported exclusively by natural reproduction (NR lakes), but there are increasingly many combination lakes too (NR + stocking). However, it also included a spatial coverage rotation selected from a region-wide list of 856 walleye lakes in the Ceded Territory, also using a stratified randomized design. Thus, some walleye lakes have been sampled numerous times since 1990, while others have been sampled less frequently. Statistical differences in trend and non-trend lakes in this study were partially handled through the use of a mixed effects model approach (see Statistical Analyses section below).

Walleye surveys are conducted by state and tribal fisheries biologists when adults move into near-shore habitats for spawning, shortly after ice-out. Adult walleye (i.e., sexable fish or walleye typically ≥ 381 mm total length) are initially captured in standard fyke nets set overnight at likely spawning locations, usually in an effort to maximize catch. Captured walleye are

125 marked by tagging or fin-clipping and released. Recaptures are then made using boat
126 electrofishing and population estimates are generated using Chapman's modification of the
127 Petersen estimator (Chapman 1951). In some cases, initial marks were made with electrofishing
128 (i.e., shock-shock population estimates). Total length (TL, mm) of all captured walleye are
129 recorded and weight data for some populations were occasionally available. Calcified hard
130 structures were collected from a sub-sample of fish from each population for age estimation.
131 Dorsal fin spines were used to estimate age from walleye ≥ 508 mm TL and scales were used for
132 fish < 508 mm TL. In general, ages were estimated without knowledge of fish identity by two
133 experienced WDNR biologists and a consensus read was used to settle between-reader
134 discrepancies. Walleye growth data has been collected for decades across multiple field offices;
135 thus, we are aware of slight deviations in methodologies, but ultimately view these as minor
136 (Pedersen et al. 2017).

137 *Production calculations*

138 Production calculations for each lake and year combination were made using the instantaneous
139 growth method:

$$140 \quad (1) \quad P = \sum G_i \bar{B}_i$$

141 where P is the total walleye production ($\text{kg ha}^{-1} \text{ y}^{-1}$), G is instantaneous growth rate for the year
142 i.e., $\ln\left(\frac{\text{Mean weight at time } t}{\text{Mean weight at time } t+1}\right)$, $\bar{B}$ is mean standing stock biomass during the year (kg ha^{-1}), and i
143 is age class. The instantaneous growth method appears to originally be attributable to Ricker
144 (1946), but was independently formulated by Allen (1949) using a graphical approach, i.e., "the
145 Allen curve". The instantaneous growth method has since been applied to a wide variety of taxa

and is the predominant form of production estimation reported for freshwater fishes (Whitworth and Strange 1983; Kwak and Waters 1997; Waters 1999).

As with all production estimation approaches, there are assumptions in the method (Waters 1977; Dolbeth et al. 2012). Most importantly, the instantaneous growth method is a “snapshot” estimate unlike other production approaches where mortality and biomass are tracked through time using multiple samples (Waters 1977; Benke 1979; Freeman and Freeman 1985; Benke 2010). Yet, the instantaneous growth method remains the standard method for fishes, likely because most fishes are semi-voltine (take > 1 year to complete a life-cycle), and ages can be estimated using calcified hard structures that produce reliable annuli (Mann 1971; Kempinger and Carline 1977; Valentine-Rose et al. 2007). Ultimately, the work required to develop sub-annual production estimates in lake fish populations is cost-prohibitive (e.g., monthly estimates of walleye population size in lakes). Thus, we are assuming that P and B, as a snapshot, remain stable prior to recruitment of the following young-of-year cohort, an assumption also made in other studies (Valentine-Rose et al. 2007; Valentine-Rose et al. 2011; Myers et al. 2014; Rypel et al. 2015; Myers et al. 2017).

For each population, we reconstructed age-structure of all captured fish using field-collected TL data (size-structure) in combination with consensus length-at-age estimates. Using measured TL and the survey specific age-length key, we assigned ages to all sampled fish of unknown age. Mean TL-at-age values for each population were converted to mean weight-at-age using a stock-specific weight-TL regression. Although TL data were always available, weight data were not. When weight or length-at-age data were insufficient to develop a weight-TL regression for a unique lake-year combination, we developed and used a lake-specific weight-TL regression by integrating all walleye weight-TL data across all years in a lake. If no weight data

169 were available for a lake, we used a regional weight-TL regression for the eastern and western
170 portions of the Ceded Territory of Wisconsin based on all available walleye weight-TL data.
171 Weight data were ultimately available for a total of 324 of the study lakes. Our analysis included
172 weight information on a total of 52328 individual walleye (out of a total of 95248), and covered
173 the full study period (1990-2012).

174 Population estimates for each lake-year combination were converted to age-specific
175 population estimates by estimating a proportion of fish in each age class from size and age-
176 structure data (Rypel et al. 2015). Although used in management decisions, population estimate
177 from lake area regressions, population estimates from lake area regressions (e.g., Nate et al.
178 2000; Hansen et al. 2015b) were not used in any production, biomass or P/B estimations for this
179 study; only empirical mark-recapture population estimates were used. Age-specific biomass (B)
180 was estimated as the product of age-specific population estimates and mean weight of
181 individuals by age class (Table 1). Thus, total B for any lake-year combination was represented
182 by the sum of all age-specific B estimates. Mean biomass (i.e., $\bar{B}$) was calculated as average B
183 between adjacent age classes. Production rates (P) for walleye in each age class were calculated
184 using eq. 1 and the sum of all age-specific production values was adult walleye production (see
185 example calculation in Table 1). P/B (turnover rate) was estimated as the ratio of P to B and is
186 expressed in units of inverse time (i.e., y^{-1}). For all production estimates, we excluded age classes
187 0-2 because immature walleye of these sizes are not consistently vulnerable to capture by
188 standard fyke nets (Hansen et al. 1991) or harvest by anglers (Newby et al. 2000). Therefore, our
189 production values represent adult walleye production, a convention that is common in the fish
190 production literature (Kempinger and Carline 1977; Mosindy et al. 1987). Furthermore, because
191 the Ceded Territory of Wisconsin walleye fishery is harvest-oriented towards sexually mature

fish, adult production, biomass and P/B values represent a more direct measure of productivity and biomass available for harvest in the actual fishery.

Statistical analyses

To test for differences in productivity among lakes of varying recruitment status, we grouped lakes into three broad walleye recruitment categories; “natural recruitment”, “combination”, and “stocked-only lakes”. We defined “natural recruitment” (NR) lakes as those that maintained an NR recruitment code by WDNR managers over the available period of record. Thus, natural recruitment lakes have had little to no known walleye stocking over time and include most of the higher profile walleye fisheries for anglers in Wisconsin. We defined “combination” lakes as those with recruitment codes reflecting both stocking and natural recruitment within the same waterbody. We defined “stocked-only” lakes as those sustained solely through stocking. Walleye populations with “remnant” recruitment codes ($n = 29$) were dropped from analyses because of low sample size and because previous research has shown these populations to be distinct from other recruitment categories (Nate et al. 2000; 2001). Because we calculated rates of “adult production” (i.e., walleye 3+), biomass production of adults in one year in fact reflects recruitment processes from past years. This is especially relevant for cases where recruitment codes in a lake may have changed over those past three years. As one example, adult walleye production walleye for Yellow Lake (Burnett County WI) in the year 2008, in fact, reflects recruitment processes from 2005. Therefore, if the code was NR in 2005 but changed to combination by 2008, the code used in our 2008 adult production analysis should probably be NR (not combination), as the adult production reflects NR dynamics from 2005 and not the stocking + NR dynamic that occurred in 2008. In such cases (which were limited; ~15% of all lake years), classifications that were ≤ 3 years old were reverted to their prior classification in

215 this manner. Finally, because the sample of lakes analyzed for production annually represents
216 only a small sub-set of lakes, we also summarized lake recruitment data across the entire
217 Wisconsin Ceded Territory ($n \approx 732$). Separation of these trends provides contrast between trends
218 observed in the production lakes with those observed across the larger management region. We
219 recognize that changing recruitment codes may be confusing to some readers. However, we note
220 that these codes are important in the management system for walleye in the Ceded Territory of
221 Wisconsin. Managers use these codes as a “tracking system” for walleye recruitment potential,
222 and for setting harvest regulations by way of the lake area-population estimate regressions
223 (Cichosz 2015; Hansen et al. 2015b). Therefore, we use these codes as important categories that
224 link production information developed in our analyses directly to the recruitment potential of
225 lakes identified in the management system for setting fishery regulations and policies over the
226 landscape.

227 We constructed frequency histograms for each production statistic grouped by
228 recruitment category. We used Shapiro-Wilk tests to evaluate whether distributions for each
229 statistic were normally distributed. Tests for statistical differences among recruitment categories
230 in P, B, and P/B were assessed using three mixed effect models with Tukey’s *post-hoc* tests. In
231 each model, the production variable of interest (P, B or P/B) was the dependent variable,
232 recruitment category was the independent variable, and lake was a random effect. All P, B and
233 P/B values were $\log_{10}$ -transformed prior to analysis to meet assumptions of normality.

234 We developed mixed effect regression models to test whether P, B, and P/B changed
235 significantly over time in each recruitment category. Thus, for each recruitment category (NR,
236 combination, and stocked-only), we developed three mixed effect models for P, B and P/B. In
237 these models, the $\log_{10}$ -transformed production statistic of interest was the dependent variable,

year was an independent variable, and lake was a random effect. The use of a mixed effect model with lake as a random effect was critical to statistically handling the problem of changing lake selection as part of the changing rotation (details outlined above). For example, the mixed effect models portray regional trends in walleye productivity that were more evenly influenced by lake-specific trends than by temporal trends in lake selection. Using the final resultant models, we estimated % change over time by calculating the average annual value of each production statistic and a % change between 1990 and 2012. All statistical computations were conducted using SAS statistical software (Version 9.4, SAS Institute Inc., Cary, North Carolina, USA) and considered significant at $\alpha < 0.05$.

Results

We estimated P, B, and P/B for 473 unique lake-year combinations, representing 260 walleye populations during 1990-2012 (Table 2). P and B values were uniformly non-normal in their statistical distribution, and this pattern applied across all recruitment categories (Shapiro-Wilk tests, all P 's < 0.0001 , Fig. 1). P and B distributions were right-skewed, with peaks at low values, and long tails. Thus, there were many low production systems and only a few highly productive ones. P/B estimates were right-skewed for NR (Shapiro-Wilk test $P = 0.002$, Fig. 1) and combination lakes (Shapiro-Wilk test $P < 0.0001$, Fig. 1), but were normally distributed in the stocked-only lakes (Shapiro-Wilk test $P = 0.84$, Fig. 1). Thus P/B ratios were more normally distributed across walleye populations than were either P or B were alone. Across all recruitment categories and years, P/B had a modal peak at ~ 0.20 ; thus walleye B turns over every 5 years in most lakes.

Estimates of walleye P, B, and P/B were significantly higher in NR lakes relative to combination and stocked-only categories (Fig. 2, mixed effect models, all Tukey's P 's < 0.0001). Similarly, average walleye P, B, and P/B in combination lakes were significantly higher than stocked-only lakes (Fig. 2, Mixed effect models, all Tukey's P 's < 0.0001). Mean production in NR, combination, and stocked-only lakes was $1.24 (\pm 0.08 SE)$, $0.71 (\pm 0.04 SE)$, and $0.49 (\pm 0.07 SE)$ $\text{kg ha}^{-1} \text{y}^{-1}$, respectively. Mean B was $5.76 \text{ kg ha}^{-1} (\pm 0.36 SE)$ in NR lakes, $3.80 \text{ kg ha}^{-1} (\pm 0.19 SE)$ in combination lakes, and $2.98 \text{ kg ha}^{-1} (\pm 0.31 SE)$ kg ha^{-1} in stocked-only lakes. Thus, average P/B in NR, combination, and stocked only lakes was $0.23 (\pm 0.005 SE)$, $0.19 (\pm 0.006 SE)$, and $0.16 (\pm 0.007 SE) \text{y}^{-1}$, respectively. NR lakes exhibited no apparent change in P or B over time, and P/B increased significantly over the 22 y study period (Table 2, Fig. 3a-c). In combination lakes, P, B, and P/B declined by 47%, 32%, and 25%, respectively (Table 3, Fig. 3). In stocked-only lakes, P declined 46%, B declined 51%, and P/B declined 29% (Table 3, Fig. 3).

The proportion of lakes classified as NR has declined over time. The percentage of lakes included in our production calculations (production lakes) that were classified as NR declined strongly over time (Fig. 4). A downward trend in NR classification across all Wisconsin Ceded Territory lakes was also still apparent, but was not nearly as severe (Fig. 4). The proportion of lakes classified as combination generally increased over time. In the production lakes, this trend was again extremely strong (Fig. 4). However again, a similar trend was observable across all Ceded territory lakes, but the strength was not as strong. The proportion of stocked-only production lakes increased through time, however there was high amount of year-to-year variance, and the temporal trend across the entire Wisconsin Ceded Territory was essentially flat (Fig. 4). Combined these results show a general decline in the number of NR lakes, and a general increase in the number of combination lakes.

282 Discussion

283 NR walleye populations were more productive than combination or stocked-only walleye
284 populations. In most cases, the strongest correlate of P will often be B or abundance, i.e.,
285 population size or density (Neves and Pardue 1983; Hayes et al. 2007; Rypel et al. 2015).
286 Recruitment drives population growth, and thus also secondary production (Benke 1979; Ranta
287 et al. 1997; Van Der Meer et al. 2001). It was reassuring to observe that patterns of walleye P in
288 Wisconsin so closely mirrored recruitment classifications because recruitment codes are directly
289 used in the management of walleye. For example, although the limit reference point remains
290 35%, harvest quotas can shift because different recruitment codes have different population size-
291 lake area regression models (Cichosz 2015; Hansen et al. 2015b). Furthermore, many of the most
292 intensively managed lakes (e.g., spearing + angling) tend to be NR lakes where production is
293 correspondingly high. Therefore, walleye productivity patterns across the Wisconsin Ceded
294 Territory should be re-assuring to managers because they show that the current management
295 system is capturing key empirical dynamics of production.

296 The productivity of walleye populations was right-skewed across all types of populations.
297 Therefore, low P and B populations dominate the landscape, whereas high P and B systems are
298 rare. This information is pertinent because high P in certain populations is occasionally raised as
299 an example of what other populations might be capable of delivering. Dating back to Lindeman
300 (1942), freshwater lakes have been conceptualized as possessing finite quantities of solar energy,
301 nutrients, and carbon to support the production of higher order heterotrophs (Pace et al. 2004).
302 Thus, it has long been known that the productive capacity of lakes and fish populations is limited
303 and influenced by habitat change (Moyle 1949; Rawson 1952; Downing et al. 1990; Jones et al.
304 1996; Randall and Minns 2000). For example, habitat restorations might improve production

(Sass et al. 2012; Sass et al. 2017), whereas environmental degradations might decrease fish production (Sass et al. 2006; Valentine-Rose et al. 2007; Valentine-Rose et al. 2011; Gaeta et al. 2014). Secondary production provides a lens through which the production of walleye and other fish populations might be quantified and considered explicitly by managers (Randall and Minns 2000; Rypel and David 2017). For example, whereas production of most walleye populations in northern Wisconsin is low, the few productive walleye populations might be those most important for future walleye conservation.

On average, walleye P, B and P/B in combination and stocked-only lakes declined over time. However, declining growth rates do not account for the regional decline in walleye productivity. In a recent study, Pedersen et al. (2017) showed that growth rates of young walleye have actually increased in recent years compared to earlier years. Growth rates of older walleye have declined compared to earlier years. Pedersen et al. (2017) attributed the increase in growth rates of younger walleye to a potential release from density-dependent constraints on growth caused by recent declines in natural recruitment. Importantly though, increased growth for young walleye highlights that declining production for Ceded Territory of Wisconsin walleye is more strongly connected to declining recruitment and recruitment potential than to growth.

The proportion of lakes classified as NR in our analysis declined. Further, the proportion of all lakes classified as NR across the Ceded Territory also declined, though not as severe as observed in the production lakes. Discrepancies in the severity of recruitment declines in production lakes versus the whole Ceded Territory might be due to the response time of the recruitment classifications, or other idiosyncrasies. For example, changes in the recruitment status of a lake may lag biological changes by many years. Furthermore, the production lakes in general represent a small sample of more highly managed lakes whereas the many lakes across

the Wisconsin Ceded Territory often receive less management attention, and thus without new information, may remain in the same recruitment category for some time. Taken together, our results again highlight that walleye production is strongly linked to recruitment, and declines in recruitment can mean later declines in fishery production. And even though stocking in many lakes has increased over time, walleye turnover (i.e., P/B) in these systems remains in decline, likely because of declining recruitment. We do not suggest that stocking is the cause for walleye production declines. In fact, evaluation of stocking records for walleye in Wisconsin shows increasing numbers of lakes being stocked through time; thus more likely, is that lakes with declining recruitment and habitat quality are now increasingly being stocked. Indeed, the finding that P, B and P/B in stocked-only lakes have uniformly declined over time, even though stocking has increased, provides strong evidence that the habitats that have traditionally supported higher walleye production and recruitment are changing. There are a variety of potential factors that might underlie walleye P and recruitment declines:

1. *Direct effects of climate change.* Water temperatures have been increasing in Wisconsin lakes over the last century (Magnuson et al. 2000; Sharma et al. 2011; Read et al. 2014) and warmer limnetic waters have been linked to walleye recruitment declines (Fayram et al. 2014; Hansen et al. 2015a; Hansen et al. 2016). Yet despite warmer water temperatures, many lakes still retain quality thermal habitat for walleye growth and survival (J. Lyons, unpublished data). Effects of temperature change on walleye recruitment are likely both cumulative (Venturelli et al. 2010; Sharma et al. 2016), and synergistic/additive with other climate- and human-mediated effects below (Pedersen et al. 2017).
2. *Indirect food web effects of increased water temperatures.* A temperature effect on walleye could still manifest as reduced walleye productivity despite suitable thermal conditions if the

effect were indirect and mediated through food web interactions (Stenseth et al. 2002; Boehm 2016). For example, one of the strongest predictors of walleye recruitment declines tends to be largemouth bass abundance (Hansen et al. 2016). Largemouth bass could negatively affect walleye P through predation on juvenile walleye, but Kelling et al. (2016) found little evidence for this. Alternatively, negative competitive interactions (Forney 1977), or predation on other aspects of the food web may negatively affect walleye growth and survival (Van Zuiden and Sharma 2016).

3. *Harvest*. Wisconsin walleye populations provide an important recreational and tribal fishery (USA Department of the Interior 1991; Nesper 2002). The relationship between harvest and P was not a focal topic for our research, but extensions of the secondary production approach to harvest-oriented fisheries like walleye would be fertile grounds for future research (Waters 1992; Rypel et al. 2015). Harvest has long been known to have potential effects on recruitment and P in exploited species (Larkin 1977; Fogarty et al. 1991). For example, large predatory fish crop down forage species that are potential competitors of their own juveniles, i.e., cultivation (Walters and Kitchell 2001). In reverse, when large fish are removed through fishing, prey species are released from predation and increase in abundance, leading to reduced juvenile survival through interspecific competition and predation effects, i.e., depensation (Walters and Kitchell 2001). Furthermore, size and reproductive fitness of parental fish and effects on harvest on these individuals could be key; e.g., maternal effects (Scott et al. 1999; Heyer et al. 2001; Venturelli et al. 2009).

4. *Changes in stocking practices*. Stocking and fish culture practices are constantly evolving, and walleye are no exception (Harder et al. 2014; Suedel et al. 2014; Davidson et al. 2016). In Wisconsin, a recent switch has taken place towards large-scale stocking of extended

growth fingerlings during the fall (dubbed “the Wisconsin Walleye Initiative”). This effort was partly triggered by a perception among biologists that spring fingerling walleye were not surviving at the same rate as they were during the 1980s and 1990s. During these earlier periods, sizes of spring fingerlings were larger, and declined as hatcheries shifted to lined ponds. In addition, stocking recommendations were reduced from 50 to 35 small fingerlings per acre (Fayram 2005; Fayram et al. 2005). Changing stocking practices do not explain why recruitment may begin failing in a previously NR lake, but could potentially magnify the severity of production declines, and represents a potential topic for future research.

5. *Non-native dreissenid mussels*. Dreissenid mussels (zebra mussels *Dreissena polymorpha* and quagga mussels *Dreissena bugensis*) have spread rapidly across commercial, and now, inland waterbodies throughout the midwestern USA. Dreissenid invasions are associated with clarification of the water column and benthification of food webs (Zhu et al. 2006; Higgins and Vander Zanden 2010). Such changes are notably problematic for walleye as the species is typically associated with cool and dark thermal-optical habitats/lakes (Chu et al. 2004; Lester et al. 2004). Importantly, the vast majority of walleye lakes examined in this study have not been invaded by dreissenid mussels (and some may never be) due to insufficient calcium concentrations. Therefore, declining walleye productivity across northern Wisconsin is occurring independent of known dreissenid effects, even though dreissenids represent additional challenges to some walleye fisheries in the future.

6. *Other anthropogenic effects*. Lake ecosystems across the globe are increasingly being influenced by an array of other human effects including residential development of riparian zones, pollution, other species invasions, effects of drought, habitat fragmentation (Christensen et al. 1996; Vitousek et al. 1997; Schindler et al. 2000; Vander Zanden and

Olden 2008; Rypel 2010; DeBoer et al. 2013). All of the above disturbances have been documented in Wisconsin lakes and therefore could be involved in shifting habitat conditions and productivity for walleye.

Overall, high production walleye populations were rare. This is important because the limited number of high production lakes tends to be the well-studied lakes for information on walleye biology and management. Indeed, Escanaba Lake is the most well-studied walleye population in Wisconsin, in large part because of a continuous compulsory creel survey since 1946. Based on our data however, this lake is apparently also the most productive walleye population in Wisconsin (average $P = 6.5 \text{ kg ha}^{-1} \text{ y}^{-1}$ and $B = 26.3 \text{ kg ha}^{-1}$) (Rypel et al. 2015). It is worth noting that in some years, P and B were substantially higher in Escanaba Lake with values approaching $12 \text{ kg ha}^{-1} \text{ y}^{-1}$ and 50 kg ha^{-1} , respectively (i.e., ~double the 2nd most productive estimate for the Ceded Territory of Wisconsin and values that dwarf even the NR category average presented in Fig. 2). However, these values are not extreme when compared to those reported from more northern regions in Canada where production rates are similar (Mosindy et al. 1987; Rypel et al. 2015; Rypel and David 2017). These findings raise important questions, namely: Are fisheries patterns from highly productive populations applicable to less productive ones in the same region?

Estimates of P , B , and P/B are likely useful tools for assessing the general productive capacity of diverse populations. We hypothesize that fish production estimates have become rarer over time because of the misconception that the data needed to calculate P are time-consuming and costly to gather. This might be true if a single investigator were starting a new sampling program from scratch with little support. However, as was observed in our study, all the information needed to estimate P , B , and P/B were already available in existing databases

because management of walleye here was focused on the component parts of production, without ever calculating production directly. Although these datasets likely represent some of the premiere datasets available for this species in the world, there are probably many others that could be analyzed in a similar way. Furthermore, the 2012 Fisheries Act in Canada shifted conservation and management priorities towards direct measures of “fisheries production”. Thus our study represents an example of how fish production can be quantified to investigate broad-scale ecological and management issues.

Declining natural recruitment, production, and P/B in walleye populations represents a significant and emerging management challenge for the region. In combination lakes, production was almost halved from $0.91 \text{ kg ha}^{-1} \text{ y}^{-1}$ in 1990 to $0.48 \text{ kg ha}^{-1} \text{ y}^{-1}$, and P/B eroded from ~ 0.22 (or 1/4.5 y) to 0.17 (1/6 y); thus, it currently takes 1.5 y longer to replace the same amount of walleye biomass now versus 1990. In 1990, NR walleye populations were more abundant on the landscape but have decreased – an opposite pattern compared to combination populations, which have increased. Therefore, regional trends in walleye productivity are linked to broad-scale declines in walleye recruitment (Hansen et al. 2016), the underlying cause of which remains elusive. Government agencies and management systems will need to adapt to meet the challenges posed by these trends. To an extent they already have, e.g., by increasing hatchery capacity and stocking of fall fingerling walleye. Yet adaptation to novel conditions may ultimately require highly collaborative and landscape-scale strategies that capitalize on a diversity of rehabilitation options (Rypel and Magnuson 2018). Potential management actions might include habitat restoration aimed at raising the productive potential for walleye in lakes, food web management, and reductions in harvest as yield approaches production (Rypel et al. 2015; McMeans et al. 2016; Carpenter et al. 2017).

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455 **Literature Cited**

- 456 Allan, J.D., Abell, R., Hogan, Z., Revenga, C., Taylor, B.W., Welcomme, R.L., and Winemiller,
457 K. 2005. Overfishing of inland waters. *BioScience* **55**(12): 1041-1051.
- 458 Allen, K.R. 1949. Some aspects of the production and cropping of fresh waters. *Transactions*
459 of the Royal Society of New Zealand **77**: 222-228.
- 460 Beard, T.D., Cox, S.P., and Carpenter, S.R. 2003. Impacts of daily bag limit reductions on
461 angler effort in Wisconsin walleye lakes. *North American Journal of Fisheries*
462 Management **23**(4): 1283-1293.
- 463 Becker, G.C. 1983. *Fishes of Wisconsin*. University of Wisconsin Press, Madison, WI USA.

- 464 Benke, A.C. 1979. A modification of the Hynes method for estimating secondary production
465 with particular significance for multivoltine populations. *Limnology and Oceanography*
466 **24**: 168-171.
- 467 Benke, A.C. 2010. Secondary production. *Nature Education Knowledge* **1 (8)**: 1-5.
- 468 Benke, A.C., and Wallace, J.B. 1997. Trophic basis of production among riverine caddisflies:
469 implications for food web analysis. *Ecology* **78**(4): 1132-1145.
- 470 Boehm, H. 2016. Identifying recruitment bottlenecks for walleyes in northern Wisconsin lakes,
471 University of Wisconsin-Stevens Point, MS Thesis.
- 472 Carlin, C., Schroeder, S.A., and Fulton, D.C. 2012. Site choice among Minnesota Walleye
473 anglers: the influence of resource conditions, regulations and catch orientation on lake
474 preference. *North American Journal of Fisheries Management* **32**(2): 299-312.
- 475 Carpenter, S.R., Brock, W.A., Hansen, G.J.A., Hansen, J.F., Hennessy, J.M., Isermann, D.A.,
476 Pedersen, E.J., Perales, K.M., Rypel, A.L., Sass, G.G., Tunney, T.D., and Vander
477 Zanden, M.J. 2017. Defining a safe operating space for recreational fisheries. *Fish and*
478 *Fisheries*: Published Online.
- 479 Chapman, D.G. 1951. Some properties of the hypergeometric distribution with applications to
480 zoological sample censuses. *In* University of California Publications in Statistics.
481 University of California Press. pp. 130-160.
- 482 Christensen, D.L., Herwig, B.R., Schindler, D.E., and Carpenter, S.R. 1996. Impacts of
483 lakeshore residential development on coarse woody debris in north temperate lakes.
484 *Ecological Applications* **6**(4): 1143-1149.

- 485 Chu, C., Mandrak, N.E., and Minns, C.K. 2005. Potential impacts of climate change on the
486 distributions of several common and rare freshwater fishes in Canada. *Diversity and*
487 *Distributions* **11**(4): 299-310.
- 488 Chu, C., Minns, C.K., Moore, J.E., and Millard, E.S. 2004. Impact of oligotrophication,
489 temperature, and water levels on walleye habitat in the Bay of Quinte, Lake Ontario.
490 *Transactions of the American Fisheries Society* **133**(4): 868-879.
- 491 Cichosz, T.A. 2015. Wisconsin Department of Natural Resources 2013-2014 Ceded Territory
492 Fishery Assessment Report. Wisconsin Department of Natural Resources, Treaty
493 Fisheries Assessment Unit, Bureau of Fisheries Management, Administrative Report
494 #78, Madison, WI USA.
- 495 Davidson, J., Summerfelt, R., Barrows, F., Gottsacker, B., Good, C., Fischer, G., and
496 Summerfelt, S. 2016. Walleye *Sander vitreus* performance, water quality, and waste
497 production in replicated recirculation aquaculture systems when feeding a low
498 phosphorus diet without fishmeal versus a traditional fishmeal-based diet. *Aquacultural*
499 *Engineering* **75**: 1-13.
- 500 DeBoer, J.A., Pope, K.L., and Koupal, K.D. 2013. Environmental factors regulating the
501 recruitment of walleye *Sander vitreus* and white bass *Morone chrysops* in irrigation
502 reservoirs. *Ecology of Freshwater Fish* **22**(1): 43-54.
- 503 Dolbeth, M., Cusson, M., Sousa, R., and Pardal, M.A. 2012. Secondary production as a tool for
504 better understanding of aquatic ecosystems. *Canadian Journal of Fisheries and Aquatic*
505 *Sciences* **69**(7): 1230-1253.

- 506 Downing, J.A. 1984. Assessment of secondary production: the first step. *In* A manual on the
507 assessment of secondary production in fresh waters IBP handbook No. 16. *Edited by* J.A.
508 Downing and J.A. Rigler. Blackwell Scientific Publications, Oxford, UK. pp. 1-18.
- 509 Downing, J.A., Plante, C., and Lalonde, S. 1990. Fish production correlated with primary
510 productivity, not the morphoedaphic index. *Canadian Journal of Fisheries and Aquatic*
511 *Sciences* **47**(10): 1929-1936.
- 512 Fayram, A.H. 2005. Walleye stocking in Wisconsin lakes: species interactions, changes in
513 angler effort, optimal stocking rates, and effects on community maturity, PhD
514 Dissertation. University of Wisconsin-Milwaukee.
- 515 Fayram, A.H., Hansen, M.J., and Nate, N.A. 2005. Determining optimal stocking rates using a
516 stock–recruitment model: an example using walleye in northern Wisconsin. *North*
517 *American Journal of Fisheries Management* **25**(4): 1215-1225.
- 518 Fayram, A.H., Tober Griffin, J.D., and Wendel, J.L. 2014. Effects of localized temperature and
519 precipitation on historic Walleye recruitment in Wisconsin, USA with implications for
520 climate change. *Aquatic Ecosystem Health & Management* **17**(2): 115-121.
- 521 Fogarty, M.J., Sissenwine, M.P., and Cohen, E.B. 1991. Recruitment variability and the
522 dynamics of exploited marine populations. *Trends in Ecology & Evolution* **6**(8): 241-
523 246.
- 524 Forney, J.L. 1977. Evidence of inter-and intraspecific competition as factors regulating walleye
525 (*Stizostedion vitreum vitreum*) biomass in Oneida Lake, New York. *Journal of the*
526 *Fisheries Board of Canada* **34**(10): 1812-1820.
- 527 Freeman, B.J., and Freeman, M.C. 1985. Production of fishes in a subtropical blackwater
528 ecosystem: the Okefenokee Swamp. *Limnology and Oceanography* **30**(3): 686-692.

- 529 Gaeta, J.W., Sass, G.G., and Carpenter, S.R. 2014. Drought-driven lake level decline: effects on
530 coarse woody habitat and fishes. *Canadian Journal of Fisheries and Aquatic Sciences*
531 **71**(2): 315-325.
- 532 Hansen, G.J.A., Carpenter, S.R., Gaeta, J.W., Hennessy, J.M., and Vander Zanden, M.J. 2015a.
533 Predicting walleye recruitment as a tool for prioritizing management actions. *Canadian*
534 *Journal of Fisheries and Aquatic Sciences* **72**(5): 661-672.
- 535 Hansen, G.J.A., Hennessy, J.M., Cichosz, T.A., and Hewett, S.W. 2015b. Improved models for
536 predicting walleye abundance and setting safe harvest quotas in northern Wisconsin
537 lakes. *North American Journal of Fisheries Management* **35**(6): 1263-1277.
- 538 Hansen, G.J.A., Read, J.S., Hansen, J.F., and Winslow, L.A. 2016. Projected shifts in fish
539 species dominance in Wisconsin lakes under climate change. *Global Change Biology*:
540 Published Online. DOI: 10.1111/gcb.13462.
- 541 Hansen, J.F., Sass, G.G., Gaeta, J.W., Hansen, G.J.A., Isermann, D.A., Lyons, J., and Vander
542 Zanden, M.J. 2015c. Largemouth bass management in Wisconsin: intra- and inter-
543 specific implications of abundance increases. *In* Black bass diversity: multidisciplinary
544 science for conservation. *Edited by* M.D. Tringali, J.M. Long, T.W. Birdsong and M.S.
545 Allen. American Fisheries Society, Bethesda, Maryland, USA.
- 546 Hansen, M.J. 1989. A walleye population model for setting harvest quotas. Wisconsin
547 Department of Natural Resources, Fish Management Report 143.
- 548 Hansen, M.J., Staggs, M.D., and Hoff, M.H. 1991. Derivation of safety factors for setting
549 harvest quotas on adult walleyes from past estimates of abundance. *Transactions of the*
550 *American Fisheries Society* **120**(5): 620-628.

- 551 Harder, T.M., Gotsch, G.G., and Summerfelt, R.C. 2014. Growth response of juvenile walleyes
552 after cold banking. *North American Journal of Aquaculture* **76**(3): 255-260.
- 553 Hayes, D.B., Bence, J.R., Kwak, T.J., and Thompson, B.E. 2007. Abundance, biomass, and
554 production. *In* *Analysis and Interpretation of Freshwater Fisheries Data. Edited by C.S.*
555 *Guy and M.L. Brown. American Fisheries Society, Bethesda, MD. pp. 327-374.*
- 556 Herb, W.R., Johnson, L.B., Jacobson, P.C., and Stefan, H.G. 2014. Projecting cold-water fish
557 habitat in lakes of the glacial lakes region under changing land use and climate regimes.
558 *Canadian Journal of Fisheries and Aquatic Sciences* **71**(9): 1334-1348.
- 559 Heyer, C.J., Miller, T.J., Binkowski, F.P., Caldarone, E.M., and Rice, J.A. 2001. Maternal
560 effects as a recruitment mechanism in Lake Michigan yellow perch (*Perca flavescens*).
561 *Canadian Journal of Fisheries and Aquatic Sciences* **58**(7): 1477-1487.
- 562 Higgins, S.N., and Vander Zanden, M.J. 2010. What a difference a species makes: a meta-
563 analysis of dreissenid mussel impacts on freshwater ecosystems. *Ecological Monographs*
564 **80**(2): 179-196.
- 565 Jones, M.L., Randall, R.G., Hayes, D., Dunlop, W., Imhof, J., Lacroix, G., and Ward, N.J.R.
566 1996. Assessing the ecological effects of habitat change: moving beyond productive
567 capacity. *Canadian Journal of Fisheries and Aquatic Sciences* **53**: 446-457.
- 568 Kelling, C.J., Isermann, D.A., Sloss, B.L., and Turnquist, K.N. 2016. Diet overlap and predation
569 between largemouth bass and walleye in Wisconsin lakes using DNA barcoding to
570 improve taxonomic resolution. *North American Journal of Fisheries Management* **36**(3):
571 621-629.

- 572 Kempinger, J.J., and Carline, R.F. 1977. Dynamics of the walleye (*Stizostedion vitreum*
573 *vitreum*) population in Escanaba Lake, Wisconsin, 1955-72. Journal of the Fisheries
574 Board of Canada **34**(10): 1800-1811.
- 575 Kwak, T.J., and Waters, T.F. 1997. Trout production dynamics and water quality in Minnesota
576 streams. Transactions of the American Fisheries Society **126**(1): 35-48.
- 577 Larkin, P.A. 1977. An epitaph for the concept of maximum sustained yield. Transactions of the
578 American Fisheries Society **106**(1): 1-11.
- 579 Lester, N.P., Dextrase, A.J., Kushneriuk, R.S., Rawson, M.R., and Ryan, P.A. 2004. Light and
580 temperature: key factors affecting walleye abundance and production. Transactions of
581 the American Fisheries Society **133**(3): 588-605.
- 582 Lindeman, R.L. 1942. The trophic-dynamic aspect of ecology. Ecology **23**(4): 399-417.
- 583 Lynch, A.J., Myers, B.J.E., Chu, C., Eby, L.A., Falke, J.A., Kovach, R.P., Krabbenhoft, T.J.,
584 Kwak, T.J., Lyons, J., and Paukert, C.P. 2016. Climate change effects on North
585 American inland fish populations and assemblages. Fisheries **41**(7): 346-361.
- 586 Magnuson, J.J., Robertson, D.M., Benson, B.J., Wynne, R.H., Livingstone, D.M., Arai, T.,
587 Assel, R.A., Barry, R.G., Card, V., and Kuusisto, E. 2000. Historical trends in lake and
588 river ice cover in the Northern Hemisphere. Science **289**(5485): 1743-1746.
- 589 Mann, R. 1971. The populations, growth and production of fish in four small streams in
590 southern England. The Journal of Animal Ecology **40**: 155-190.
- 591 McMeans, B.C., McCann, K.S., Tunney, T.D., Fisk, A.T., Muir, A.M., Lester, N., Shuter, B.,
592 and Rooney, N. 2016. The adaptive capacity of lake food webs: from individuals to
593 ecosystems. Ecological Monographs **86**(1): 4-19.

- 594 Mosindy, T.E., Momot, W.T., and Colby, P.J. 1987. Impact of angling on the production and
595 yield of mature walleyes and northern pike in a small boreal lake in Ontario. *North*
596 *American Journal of Fisheries Management* **7**(4): 493-501.
- 597 Moyle, J.B. 1949. Some indices of lake productivity. *Transactions of the American Fisheries*
598 *Society* **76**(1): 322-334.
- 599 Myers, B.J.E., Dolloff, C.A., and Rypel, A.L. 2014. Rainbow trout versus brook trout biomass
600 and production under varied climate regimes in small southern Appalachian streams. *In*
601 *Proceedings of the Wild Trout XI Symposium. Edited by R.F. Carline and C. LoSapio,*
602 *Bozeman, MT USA. pp. 127-134.*
- 603 Myers, B.J.E., Dolloff, C.A., Webster, J.R., Nislow, K.H., Fair, B., and Rypel, A.L. 2017. Fish
604 assemblage production estimates in Appalachian streams across a latitudinal and
605 temperature gradient. *Ecology of Freshwater Fish: Published Online, DOI*
606 *10.1111/eff.12352.*
- 607 Nate, N.A., Bozek, M.A., Hansen, M.J., and Hewett, S.W. 2000. Variation in walleye
608 abundance with lake size and recruitment source. *North American Journal of Fisheries*
609 *Management* **20**(1): 119-126.
- 610 Nate, N.A., Bozek, M.A., Hansen, M.J., and Hewett, S.W. 2001. Variation of adult walleye
611 abundance in relation to recruitment and limnological variables in northern Wisconsin
612 lakes. *North American Journal of Fisheries Management* **21**(3): 441-447.
- 613 Nesper, L. 2002. *The Walleye War: The Struggle for Ojibwe Spearfishing and Treaty Rights.*
614 *University of Nebraska Press, Lincoln, NE.*
- 615 Neves, R.J., and Pardue, G.B. 1983. Abundance and production of fishes in a small Appalachian
616 stream. *Transactions of the American Fisheries Society* **112**(1): 21-26.

- 617 Newby, J.R., Hansen, M.J., Newman, S.P., and Edwards, C.J. 2000. Catchability of walleyes to
618 angling in Escanaba Lake, Wisconsin, 1980–1995. *North American Journal of Fisheries*
619 *Management* **20**(4): 873-881.
- 620 Pace, M.L., Cole, J.J., Carpenter, S.R., Kitchell, J.F., Hodgson, J.R., Van de Bogert, M.C.,
621 Bade, D.L., Kritzberg, E.S., and Bastviken, D. 2004. Whole-lake carbon-13 additions
622 reveal terrestrial support of aquatic food webs. *Nature* **427**(6971): 240-243.
- 623 Paukert, C.P., Glazer, B.A., Hansen, G.J., Irwin, B.J., Jacobson, P.C., Kershner, J.L., Shuter,
624 B.J., Whitney, J.E., and Lynch, A.J. 2016. Adapting inland fisheries management to a
625 changing climate. *Fisheries* **41**(7): 374-384.
- 626 Pedersen, E.J., Goto, D., Gaeta, J.W., Hansen, G.J.A., Sass, G.G., Vander Zanden, M.J., and
627 Rypel, A.L. 2017. Long-term growth trends in northern Wisconsin walleye populations
628 under changing biotic and abiotic conditions. *Canadian Journal of Fisheries and Aquatic*
629 *Sciences*: Published Online, DOI 10.1139/cjfas-2017-0084.
- 630 Poesch, M.S., Chavarie, L., Chu, C., Pandit, S.N., and Tonn, W. 2016. Climate change impacts
631 on freshwater fishes: a Canadian perspective. *Fisheries* **41**(7): 385-391.
- 632 Post, J.R., Sullivan, M., Cox, S., Lester, N.P., Walters, C.J., Parkinson, E.A., Paul, A.J.,
633 Jackson, L., and Shuter, B.J. 2002. Canada's recreational fisheries: the invisible
634 collapse? *Fisheries* **27**(1): 6-17.
- 635 Randall, R., and Minns, C. 2000. Use of fish production per unit biomass ratios for measuring
636 the productive capacity of fish habitats. *Canadian Journal of Fisheries and Aquatic*
637 *Sciences* **57**(8): 1657-1667.
- 638 Ranta, E., Kaitala, V., Lindström, J., and Helle, E. 1997. The Moran effect and synchrony in
639 population dynamics. *Oikos* **78**: 136-142.

- 640 Rawson, D.S. 1952. Mean depth and the fish production of large lakes. *Ecology* **33**(4): 513-521.
- 641 Read, J.S., Winslow, L.A., Hansen, G.J.A., Van Den Hoek, J., Hanson, P.C., Bruce, L.C., and
642 Markfort, C.D. 2014. Simulating 2368 temperate lakes reveals weak coherence in
643 stratification phenology. *Ecological Modelling* **291**: 142-150.
- 644 Ricker, W.E. 1946. Production and utilization of fish populations. *Ecological Monographs*
645 **16**(4): 373-391.
- 646 Roell, M.J., and Orth, D.J. 1993. Trophic basis of production of stream-dwelling smallmouth
647 bass, rock bass, and flathead catfish in relation to invertebrate bait harvest. *Transactions*
648 *of the American Fisheries Society* **122**(1): 46-62.
- 649 Rypel, A.L. 2010. Mercury concentrations in lentic fish populations related to ecosystem and
650 watershed characteristics. *Ambio* **39**(1): 14-19.
- 651 Rypel, A.L., and David, S.R. 2017. Pattern and scale in latitude-production relationships for
652 freshwater fishes. *Ecosphere* **8**(e01660): 1-26.
- 653 Rypel, A.L., Goto, D., Sass, G.G., and Vander Zanden, M.J. 2015. Production rates of walleye
654 and their relationship to exploitation in Escanaba Lake, Wisconsin, 1965–2009.
655 *Canadian Journal of Fisheries and Aquatic Sciences* **72**: 834-844.
- 656 Rypel, A.L., and Layman, C.A. 2008. Degree of aquatic ecosystem fragmentation predicts
657 population characteristics of gray snapper (*Lutjanus griseus*) in Caribbean tidal creeks.
658 *Canadian Journal of Fisheries and Aquatic Sciences* **65**(3): 335-339.
- 659 Rypel, A.L., Lyons, J., Griffin, J.D.T., and Simonson, T.D. 2016. Seventy-year retrospective on
660 size-structure changes in the recreational fisheries of Wisconsin. *Fisheries* **41**: 230-243.

- 661 Rypel, A.L., and Magnuson, J.J. 2018. Rehabilitation and a safe operating space for freshwater
662 fisheries. *In Lake Restoration Handbook: A New Zealand Perspective. Edited by D.*
663 *Hamilton, K. Collier, C. Howard-Williams and J. Quinn. Springer, Switzerland.*
- 664 Sass, G.G., Carpenter, S.R., Gaeta, J.W., Kitchell, J.F., and Ahrenstorff, T.D. 2012. Whole-lake
665 addition of coarse woody habitat: response of fish populations. *Aquatic Sciences* **74**(2):
666 255-266.
- 667 Sass, G.G., Kitchell, J.F., Carpenter, S.R., Hrabik, T.R., Marburg, A.E., and Turner, M.G. 2006.
668 Fish community and food web responses to a whole-lake removal of coarse woody
669 habitat. *Fisheries* **31**(7): 321-330.
- 670 Sass, G.G., Rypel, A.L., and Stafford, J.D. 2017. Inland fisheries habitat management: Lessons
671 learned from wildlife ecology and a proposal for change. *Fisheries* **42**: 197-209.
- 672 Schindler, D.E., Geib, S.I., and Williams, M.R. 2000. Patterns of fish growth along a residential
673 development gradient in north temperate lakes. *Ecosystems* **3**(3): 229-237.
- 674 Schindler, D.W., Carpenter, S.R., Chapra, S.C., Hecky, R.E., and Orihel, D.M. 2016. Reducing
675 phosphorus to curb lake eutrophication is a success. *Environmental Science and*
676 *Technology* **50**: 8923–8929.
- 677 Scott, B., Marteinsdottir, G., and Wright, P. 1999. Potential effects of maternal factors on
678 spawning stock–recruitment relationships under varying fishing pressure. *Canadian*
679 *Journal of Fisheries and Aquatic Sciences* **56**(10): 1882-1890.
- 680 Sharma, S., Magnuson, J.J., Batt, R.D., Winslow, L.A., Korhonen, J., and Aono, Y. 2016. Direct
681 observations of ice seasonality reveal changes in climate over the past 320–570 years.
682 *Scientific Reports* **6**: 25061.

- 683 Sharma, S., Vander Zanden, M.J., Magnuson, J.J., and Lyons, J. 2011. Comparing climate
684 change and species invasions as drivers of coldwater fish population extirpations. PLOS
685 ONE **6**(8): e22906.
- 686 Staggs, M.D., moody, R.C., Hansen, M.J., and Hoff, M.H. 1990. Spearing and sport angling for
687 walleye in Wisconsin's Ceded Territory. Wisconsin Department of Natural Resources,
688 Fish Management Administrative Report no. 31.
- 689 Stenseth, N.C., Mysterud, A., Ottersen, G., Hurrell, J.W., Chan, K.-S., and Lima, M. 2002.
690 Ecological effects of climate fluctuations. Science **297**(5585): 1292-1296.
- 691 Suedel, B.C., Clarke, J.U., Lutz, C.H., Clarke, D.G., Godard-Coding, C., and Maul, J. 2014.
692 Suspended sediment effects on walleye (*Sander vitreus*). Journal of Great Lakes
693 Research **40**(1): 141-148.
- 694 Tsehaye, I., Roth, B.M., and Sass, G.G. 2016. Exploring optimal walleye exploitation rates for
695 northern Wisconsin Ceded Territory lakes using a hierarchical Bayesian age-structured
696 model. Canadian Journal of Fisheries and Aquatic Sciences **73**: 1413-1433.
- 697 USA Department of the Interior. 1991. Casting light upon the waters: a joint fishery assessment
698 of the Wisconsin Ceded Territory. Bureau of Indian Affairs, Minneapolis, Minnesota.
699 102 pp.
- 700 Valentine-Rose, L., Layman, C., Arrington, D., and Rypel, A. 2007. Habitat fragmentation
701 decreases fish secondary production in Bahamian tidal creeks. Bulletin of Marine
702 Science **80**(3): 863-877.
- 703 Valentine-Rose, L., Rypel, A.L., and Layman, C.A. 2011. Community secondary production as
704 a measure of ecosystem function: a case study with aquatic ecosystem fragmentation.
705 Bulletin of Marine Science **87**(4): 913-937.

- 706 Van Der Meer, J., Beukema, J.J., and Dekker, R. 2001. Long-term variability in secondary
707 production of an intertidal bivalve population is primarily a matter of recruitment
708 variability. *Journal of Animal Ecology* **70**(1): 159-169.
- 709 Van Zuiden, T.M., and Sharma, S. 2016. Examining the effects of climate change and species
710 invasions on Ontario walleye populations: can walleye beat the heat? *Diversity and*
711 *Distributions* **22**(10): 1069-1079.
- 712 Vander Zanden, M.J., and Olden, J.D. 2008. A management framework for preventing the
713 secondary spread of aquatic invasive species. *Canadian Journal of Fisheries and Aquatic*
714 *Sciences* **65**(7): 1512-1522.
- 715 Venturelli, P.A., Lester, N.P., Marshall, T.R., and Shuter, B.J. 2010. Consistent patterns of
716 maturity and density-dependent growth among populations of walleye (*Sander vitreus*):
717 application of the growing degree-day metric. *Canadian Journal of Fisheries and Aquatic*
718 *Sciences* **67**(7): 1057-1067.
- 719 Venturelli, P.A., Shuter, B.J., and Murphy, C.A. 2009. Evidence for harvest-induced maternal
720 influences on the reproductive rates of fish populations. *Proceedings of the Royal*
721 *Society of London B: Biological Sciences* **276**(1658): 919-924.
- 722 Vitousek, P.M., Mooney, H.A., Lubchenco, J., and Melillo, J.M. 1997. Human domination of
723 Earth's ecosystems. *Science* **277**(5325): 494-499.
- 724 Walters, C., and Kitchell, J.F. 2001. Cultivation/depensation effects on juvenile survival and
725 recruitment: implications for the theory of fishing. *Canadian Journal of Fisheries and*
726 *Aquatic Sciences* **58**(1): 39-50.
- 727 Waters, T.F. 1977. Secondary production in inland waters. *Advances in Ecological Research* **10**:
728 91-164.

- 729 Waters, T.F. 1992. Annual production, production/biomass ratio, and the ecotrophic coefficient
730 for management of trout in streams. *North American Journal of Fisheries Management*
731 **12**(1): 34-39.
- 732 Waters, T.F. 1999. Long-Term Trout Production Dynamics in Valley Creek, Minnesota.
733 *Transactions of the American Fisheries Society* **128**(6): 1151-1162.
- 734 Whitworth, W.E., and Strange, R.J. 1983. Growth and production of sympatric brook and
735 rainbow trout in an Appalachian stream. *Transactions of the American Fisheries Society*
736 **112**(4): 469-475.
- 737 Winfield, I.J., Baigún, C., Balykin, P.A., Becker, B., Chen, Y., Filipe, A.F., Gerasimov, Y.V.,
738 Godinho, A.L., Hughes, R.M., and Koehn, J.D. 2016. International perspectives on the
739 effects of climate change on inland fisheries. *Fisheries* **41**(7): 399-405.
- 740 Zhu, B., Fitzgerald, D.G., Mayer, C.M., Rudstam, L.G., and Mills, E.L. 2006. Alteration of
741 ecosystem function by zebra mussels in Oneida Lake: impacts on submerged
742 macrophytes. *Ecosystems* **9**(6): 1017-1028.
- 743
- 744

745 Table 1. Example calculation of walleye (*Sander vitreus*) production from a Ceded Territory of
746 Wisconsin lake. B = total annual biomass, $\bar{B}$ = mean biomass between age classes, G =
747 instantaneous growth rate, and P = production rate.

Age	Number	Total weight (kg)	Mean Weight (kg)	B (kg ha ⁻¹)	$\bar{B}$ (kg ha ⁻¹)	G	P (kg ha ⁻¹ y ⁻¹)
3 [*]	520	121	0.23	0.69			
4	334	123	0.37	0.70	1.41	0.46	0.32
5	594	376	0.63	2.13	2.30	0.54	0.76
6	520	437	0.84	2.47	2.48	0.28	0.65
7	371	440	1.18	2.49	2.34	0.34	0.85
8	260	389	1.50	2.20	1.88	0.23	0.55
9	149	277	1.86	1.57	1.90	0.22	0.41
10	186	396	2.13	2.24	2.05	0.14	0.26
11	111	327	2.94	1.85	3.07	0.32	0.65
12	223	759	3.41	4.29	4.29	0.15	0.46
Totals				20.6			4.9

748 ^{*} Production estimates initiated at age-3 when sexually mature walleye become vulnerable to
749 sampling gears.

750 Table 2. Summary of lake characteristics used in analysis of production changes over time. For
 751 area, depth, shoreline length, and Secchi depth, values represent ranges of values with mean
 752 values in parentheses.

Year	No. Lakes	Area (ha)	Max Depth (m)	Shoreline Length (km)	Secchi Depth (m)*
1990	21	25.1 - 5905.6 (653)	4.9 - 29.0 (11.7)	3.6 - 401.8 (34.7)	1.2 - 4.5 (2.2)
1991	19	45.7 - 2079.9 (362.1)	2.4 - 31.1 (11.3)	3.5 - 41.2 (12.2)	1.6 - 4.4 (2.6)
1992	12	121.2 - 5237.6 (821.1)	4.0 - 18.3 (11.9)	9.6 - 336.8 (48.6)	1.5 - 3.6 (2.4)
1993	17	60.5 - 1269.7 (405.8)	4.0 - 32.3 (15.7)	6.1 - 120.1 (24.2)	2.0 - 4.2 (3.0)
1994	19	102.6 - 1706.6 (616.8)	4.9 - 35.7 (15.4)	5.6 - 159.5 (28.0)	1.6 - 4.2 (2.8)
1995	15	87.2 - 630.9 (267.1)	4.6 - 30.8 (13.5)	5.8 - 56.0 (14.3)	1.5 - 3.8 (2.7)
1996	13	63.6 - 2488.2 (439.7)	4.6 - 29.0 (16.2)	3.8 - 82.9 (18.6)	1.5 - 4.7 (2.7)
1997	22	72.2 - 5237.6 (539.5)	1.5 - 20.7 (11.6)	4.2 - 336.8 (28.8)	1.1 - 3.7 (2.3)
1998	29	37.7 - 1333.0 (315.7)	2.4 - 22.6 (11.4)	3.2 - 62.0 (14.7)	1.2 - 4.1 (2.5)
1999	12	45.7 - 5905.6 (701.2)	7.6 - 28.0 (14.5)	4.6 - 401.8 (43.2)	1.9 - 4.5 (3.0)
2000	16	78.8 - 1285.4 (311.0)	4.6 - 30.8 (15.9)	5.2 - 27.4 (13.2)	1.9 - 4.5 (2.9)
2001	15	53.5 - 2079.9 (497.3)	5.2 - 35.7 (16.8)	4.1 - 70.9 (17.2)	2.3 - 4.1 (3.2)
2002	18	58.7 - 1172.4 (280.1)	6.7 - 32.0 (14.1)	4.0 - 120.1 (18.9)	1.7 - 4.1 (2.8)
2003	19	33.0 - 2568.8 (450.0)	2.7 - 25.3 (9.8)	3.2 - 109.4 (17.9)	0.8 - 3.9 (2.3)
2004	20	42.5 - 1563.8 (331.0)	6.4 - 35.7 (14.0)	2.6 - 67.2 (14.3)	1.2 - 3.8 (2.6)
2005	30	34.0 - 769.5 (263.7)	3.7 - 31.1 (13.4)	3.7 - 53.4 (1.50)	1.5 - 4.5 (2.6)
2006	26	47.5 - 2488.2 (429.0)	2.7 - 32.3 (14.4)	3.8 - 82.9 (14.7)	1.6 - 4.7 (2.9)
2007	28	30.3 - 1563.8 (327.9)	2.7 - 35.7 (13.6)	2.4 - 41.2 (11.2)	1.0 - 4.2 (2.5)
2008	21	75.7 - 1706.6 (410.6)	3.0 - 30.8 (13.6)	4.8 - 159.5 (23.9)	1.5 - 4.3 (2.5)
2009	26	39.9 - 5237.6 (592.9)	4.0 - 31.1 (13.1)	3.0 - 336.8 (29.2)	1.5 - 4.4 (2.7)
2010	26	54.9 - 2079.9 (383.9)	3.7 - 35.7 (13.3)	4.0 - 41.2 (13.5)	0.9 - 4.1 (2.6)
2011	23	42.1 - 5905.6 (636.7)	4.0 - 28.0 (12.8)	2.6 - 401.8 (32.3)	1.3 - 4.1 (2.4)
2012	26	33.1 - 1625.7 (403.6)	3.7 - 30.8 (12.1)	3.4 - 70.9 (16.8)	0.8 - 3.9 (2.3)
All Years	473	25.1 - 5905.6 (466.7)	1.5 - 35.7 (13.7)	2.4 - 401.8 (22.5)	0.8 - 4.7 (2.6)

753 * Secchi values based from long-term averages of Secchi depth estimates for ~10,000 Wisconsin
 754 lakes acquired using remotely sensed imagery and calibrations.

755

Table 3. Results of mixed effect models evaluating temporal change in walleye (*Sander vitreus*) P, B and P/B in northern Wisconsin lakes. Variables with significant trends are highlighted in bold. Note that all data, and thus all regression coefficients, are log₁₀-transformed.

Recruitment Category	Intercept	Slope	Model <i>P</i>
<i>NR</i>			
P	4.070	-0.002	0.169
B	3.429	-0.001	0.651
P/B	-0.067	0.00008	<0.0001
<i>Combination</i>			
P	10.244	-0.005	<0.0001
B	12.301	-0.006	<0.0001
P/B	1.911	-0.001	0.005
<i>Stocked-only</i>			
P	12.415	-0.006	0.005
B	20.935	-0.010	0.035
P/B	1.901	-0.001	0.020

Figure Legend

Fig. 1.—Frequency histograms of walleye (*Sander vitreus*) production, biomass, and P/B by recruitment category across the Ceded Territory of Wisconsin, 1990-2012.

Fig. 2.—Mean walleye (*Sander vitreus*) production, biomass, and P/B across recruitment categories in Ceded Territory of Wisconsin lakes, 1990-2012. Errors bars represent the mean $\pm$ 1 SE and letters in each panel denote means that differed statistically (mixed effect model Tukey's $P < 0.05$). “Comb.” = Combination recruitment category.

Fig. 3.—Trends in walleye (*Sander vitreus*) production, biomass, and P/B for Ceded Territory of Wisconsin lakes, 1990-2012. Blue circles = natural reproduction populations. Pink chartreuse circles = combination populations. Red circles = stocked-only populations. For the three productivity values, each data point represents a yearly mean across all sampled lakes $\pm$ 1 SE. Regression lines reflect significant mixed effect models fit to the data using lake as a random effect. “Change” values represent % change in modeled production statistics from 1990 compared to 2012. n.s. = non-significant. Significance and coefficients for all regressions can be viewed in Table 3.

Fig. 4.—Proportion of walleye (*Sander vitreus*) lakes classified into NR, combination and stocked recruitment categories. Walleye lakes across the entirety of the Wisconsin Ceded Territory are plotted on the secondary y-axis as a dashed gray line. Production lakes (i.e., lakes where data were available for production calculations) are plotted on the primary y-axis in color.

Fig. 1

Fig. 2

Fig. 3

Fig. 4