

Eroding productivity of walleye populations in northern Wisconsin lakes

Andrew L. Rypel, Daisuke Goto, Greg G. Sass, and M. Jake Vander Zanden

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 for 1990–2012. Frequency distributions for production statistics were right-skewed, indicating the fishery is generally dominated by low production populations. Mean P , B , and P/B were significantly elevated in natural recruitment (NR) lakes compared with combination (NR + stocking) and stocked-only lakes. Furthermore, combination populations had significantly higher production compared with 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 an important and emerging fishery management challenge in the region and portends a need to adapt fisheries management systems collaboratively for future sustainability.

Résumé : La gestion des ressources halieutiques dans un contexte de changements environnementaux rapides requiert des approches variées pour cerner les nouvelles conditions écologiques et s'y adapter. Pour le Wisconsin Ceded Territory, nous avons calculé 473 estimations de la production (P), de la biomasse (B) et du rapport P/B de dorés jaunes (*Sander vitreus*) adultes pour la période de 1990 à 2012. Les distributions de fréquences des statistiques sur la production étaient asymétriques vers la droite, indiquant que des populations de faible production sont généralement dominantes dans cette pêche. Les valeurs moyennes de P , B et P/B étaient significativement élevées dans les lacs à recrutement naturel (RN) par rapport aux lacs à recrutement combiné (RN + empoissonnement) et aux lacs à empoissonnement seulement. En outre, les populations de lacs à recrutement combiné avaient une production significativement plus élevée que celles des lacs à empoissonnement seulement. Dans les lacs RN, la productivité des dorés jaunes a peu varié dans le temps, alors que la proportion de populations de lacs RN a diminué. Dans les populations de lacs à recrutement combiné et de lacs à empoissonnement seulement, il y a eu des baisses significatives dans le temps des valeurs de P , B et P/B , et la proportion de ces lacs a augmenté au fil du temps. L'étude fait ressortir le lien crucial entre le potentiel de recrutement de poissons et la production de poissons, contribuant à expliquer pourquoi la pêche régionale au doré jaune est en difficulté. Les causes des baisses du recrutement et de la production de dorés jaunes demeurent incertaines, mais des changements à long terme des habitats des poissons y participent vraisemblablement (p. ex. découlant des changements climatiques et d'effets indirects sur les réseaux trophiques). La baisse de la production de dorés jaunes constitue un important nouveau défi pour la gestion de cette ressource dans la région et souligne la nécessité d'une approche collaborative pour adapter les systèmes de gestion afin d'assurer la pérennité de cette pêche. [Traduit par la Rédaction]

Introduction

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

In the mid- to high latitudes of North America, native walleye (*Sander vitreus*) fisheries are rapidly being impacted by widespread ecological change (Hansen et al. 2017; Tsehaye et al. 2016; Van Zuiden and Sharma 2016). Walleye fisheries are of exceptional cultural, recreational, and economic importance in Wisconsin and neighboring regions (Beard et al. 2003; Carlin et al. 2012; Rypel et al. 2016), but in recent years, walleye recruitment has started to decline (Hansen et al. 2017). In contrast, abundances of other species (e.g., largemouth bass (*Micropterus salmoides*) and smallmouth bass (*Micropterus dolomieu*)) have increased, prompting concern among managers and stakeholders (Hansen et al. 2015c; Rypel et al. 2016). Questions remain as to the potential

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causes and consequences of walleye recruitment declines in the fishery. For example, it is unclear how declining recruitment might be linked to later fish production (i.e., the elaboration rate of new fish biomass).

Studying the spatiotemporal dynamics of fish production has the potential to address 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). As a result, production variables are sensitive indicators of ecological change (Waters 1992; Valentine-Rose et al. 2007; Benke 2010; Myers et al. 2018; 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 alongside population abundance estimates (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 (i) understand the distribution of walleye production (P), biomass (B), and P/B across recruitment categories; (ii) investigate long-term trends in walleye P , B , and P/B within each recruitment category; and (iii) explore the broader utility of production as a tool for inland fisheries management, using Wisconsin walleye as a case example.

Methods

Wisconsin walleye management and data

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

Spring surveys of walleye populations have been conducted annually on Ceded Territory lakes since 1985 and before, but surveys became more closely standardized in 1990. Lakes are 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, again 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 nontrend 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 nearshore 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 marked by tagging or fin-clipping and released. Recaptures are then made using boat electrofishing, and population estimates are generated using Chapman's modification of the Petersen estimator (Chapman 1951). In some cases, initial marks were made with electrofishing (i.e., shock–shock population estimates). Total length (TL, mm) of all captured walleye are recorded, and mass data for some populations were occasionally available. Calcified hard structures were collected from a subsample of fish from each population for age estimation. Dorsal fin spines were used to estimate age from walleye ≥ 508 mm TL, and scales were used for fish < 508 mm TL. In general, ages were estimated without knowledge of fish identity by two experienced WDNR biologists, and a consensus read was used to settle between-reader discrepancies. Walleye growth data has been collected for decades across multiple field offices; thus, we are aware of slight deviations in methodologies, but ultimately view these as minor (Pedersen et al. 2018).

Production calculations

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

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

where P is the total walleye production ($\text{kg}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$), G is instantaneous growth rate for the year (i.e., $\ln\left(\frac{\text{mean mass at time } t}{\text{mean mass at time } t+1}\right)$), \bar{B} is mean standing stock biomass during the year ($\text{kg}\cdot\text{ha}^{-1}$), and i is age class. The instantaneous growth method appears to originally be attributable to

Table 1. Example calculation of walleye (*Sander vitreus*) production from a Ceded Territory of Wisconsin lake.

Age	<i>n</i>	Total mass (kg)	Mean mass (kg)	<i>B</i> (kg·ha ⁻¹)	\bar{B} (kg·ha ⁻¹)	<i>G</i>	<i>P</i> (kg·ha ⁻¹ ·year ⁻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

Note: *B* = total annual biomass, \bar{B} = mean biomass between age classes, *G* = instantaneous growth rate, and *P* = production rate.

*Production estimates initiated at age-3 when sexually mature walleye become vulnerable to sampling gears.

Ricker (1946), but was independently formulated by Allen (1949) using a graphical approach (i.e., “the 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 semivoltine (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 subannual 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, 2011; Myers et al. 2014, 2018; Rypel et al. 2015).

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 mass-at-age using a stock-specific mass-TL regression. Although TL data were always available, mass data were not. When mass or length-at-age data were insufficient to develop a mass-TL regression for a unique lake-year combination, we developed and used a lake-specific mass-TL regression by integrating all walleye mass-TL data across all years in a lake. If no mass data were available for a lake, we used a regional mass-TL regression for the eastern and western portions of the Ceded Territory of Wisconsin based on all available walleye mass-TL data. Mass data were ultimately available for a total of 324 of the study lakes. Our analysis included mass information on a total of 52 328 individual walleye (out of a total of 95 248) and covered the full study period (1990–2012).

Population estimates for each lake-year combination were converted to age-specific population estimates by estimating a proportion of fish in each age class from size and age-structure data (Rypel et al. 2015). Although used in management decisions, population estimates from lake area regressions (e.g., Nate et al. 2000;

Hansen et al. 2015b) were not used in any *P*, *B*, or *P/B* estimations for this study; only empirical mark-recapture population estimates were used. Age-specific *B* was estimated as the product of age-specific population estimates and mean mass of individuals by age class (Table 1). Thus, total *B* for any lake-year combination was represented by the sum of all age-specific *B* estimates. Mean biomass (i.e., \bar{B}) was calculated as average *B* between adjacent age classes. Production rates (*P*) for walleye in each age class were calculated using eq. 1, and the sum of all age-specific production values was adult walleye production (see example calculation in Table 1). *P/B* (turnover rate) was estimated as the ratio of *P* to *B* and is expressed in units of inverse time (i.e., year⁻¹). For all production estimates, we excluded age classes 0–2 because immature walleye of these sizes are not consistently vulnerable to capture by standard fyke nets (Hansen et al. 1991) or harvest by anglers (Newby et al. 2000). Therefore, our production values represent adult walleye production, a convention that is common in the fish production literature (Kempinger and Carline 1977; Mosindy et al. 1987). Furthermore, because the Ceded Territory of Wisconsin walleye fishery is harvest-oriented towards sexually mature fish, adult *P*, *B*, 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, NR 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 age 3+), biomass production of adults in 1 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 3 years. As one example, adult walleye production walleye for Yellow Lake (Burnett County, Wisconsin) in the year 2008, in fact, reflects recruitment processes from 2005. Therefore, if the code was NR in 2005 but

Table 2. Summary of lake characteristics used in analysis of production changes over time.

Year	No. of 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 (15.0)	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)

Note: For area, depth, shoreline length, and Secchi depth, values represent ranges of values with mean values in parentheses.

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

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

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

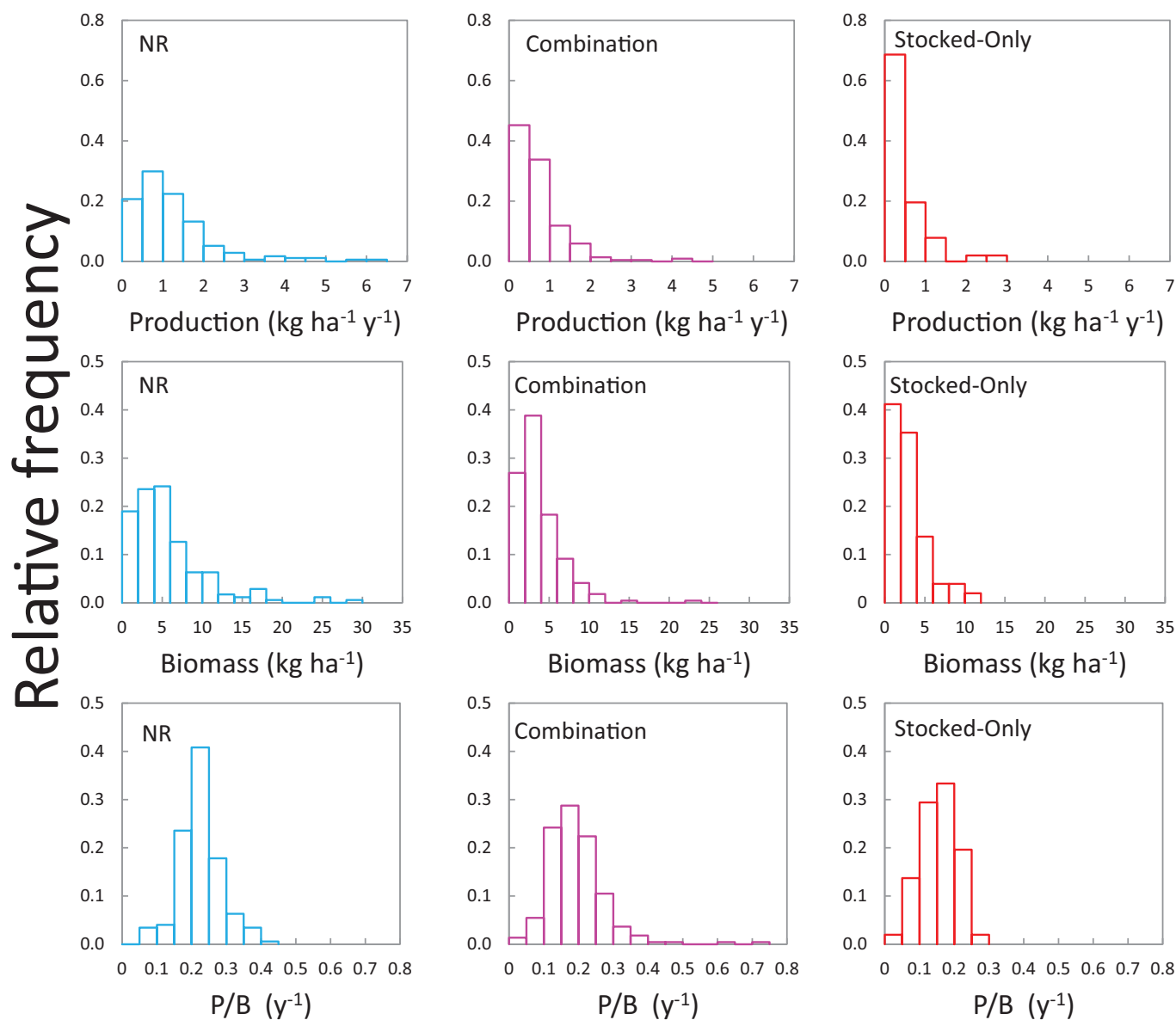
We developed mixed effect regression models to test whether P , B , and P/B changed significantly over time in each recruitment category. Thus, for each recruitment category (NR, combination, and stocked-only), we developed three mixed effect models for P , B and P/B . In these models, the \log_{10} -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 percent change over time by calculating the mean annual value of each production statistic and a percent 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 (refer to online Supplementary data¹; 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 values < 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-

¹Supplementary data are available with the article through the journal Web site at <http://nrcresearchpress.com/doi/suppl/10.1139/cjfas-2017-0311>.

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



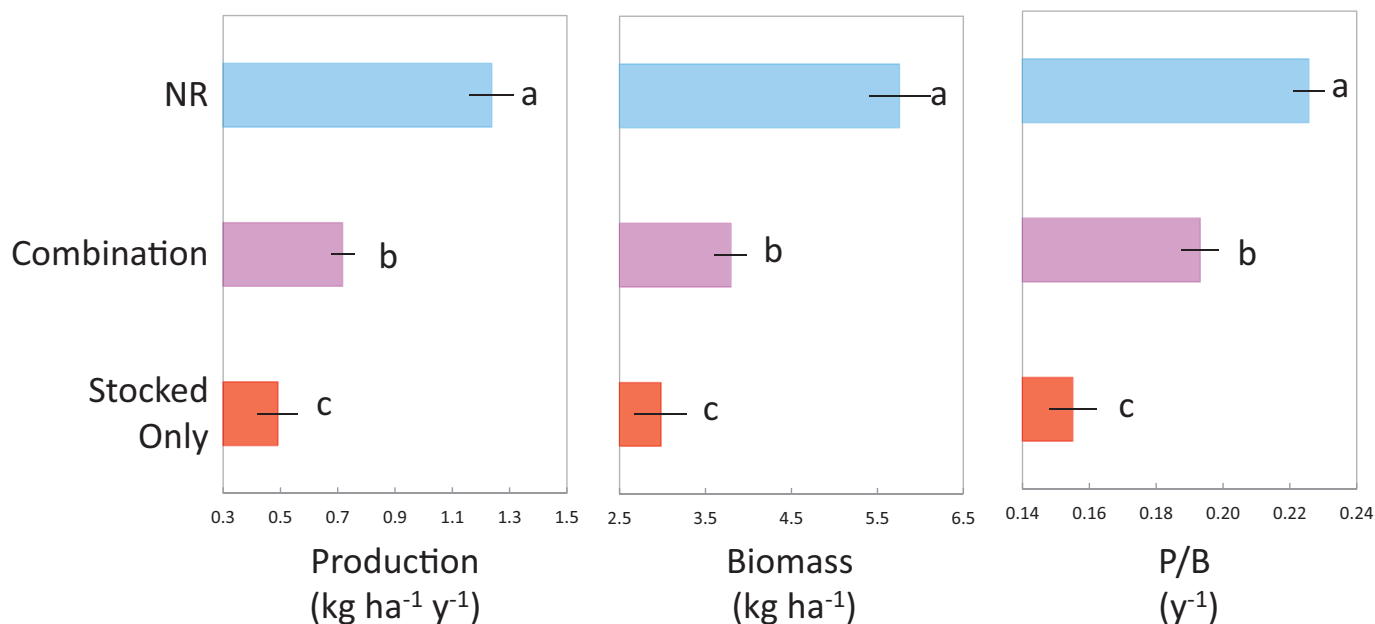
only lakes (Shapiro–Wilk test $P = 0.84$; Fig. 1). Thus, P/B ratios were more normally distributed across walleye populations than were either P or B were alone. Across all recruitment categories and years, P/B had a modal peak at ~ 0.20 ; thus, walleye B turns over every 5 years in most lakes.

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 values < 0.0001). Similarly, mean walleye P , B , and P/B in combination lakes were significantly higher than that in stocked-only lakes (Fig. 2; mixed effect models, all Tukey's P values < 0.0001). Mean (\pm SE) production in NR, combination, and stocked-only lakes was 1.24 (± 0.08), 0.71 (± 0.04), and 0.49 (± 0.07) $\text{kg}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$, respectively. Mean (\pm SE) B was 5.76 $\text{kg}\cdot\text{ha}^{-1}$ (± 0.36 $\text{kg}\cdot\text{ha}^{-1}$) in NR lakes, 3.80 $\text{kg}\cdot\text{ha}^{-1}$ (± 0.19 $\text{kg}\cdot\text{ha}^{-1}$) in combination lakes, and 2.98 $\text{kg}\cdot\text{ha}^{-1}$ (± 0.31 $\text{kg}\cdot\text{ha}^{-1}$) in stocked-only lakes. Thus, mean (\pm SE) P/B in NR, combination, and stocked only lakes was 0.23 (± 0.005), 0.19 (± 0.006), and 0.16 (± 0.007) year^{-1} , respectively. NR lakes exhibited no apparent change in P or B over time, and P/B increased significantly over the 22-year study period (Table 2; Fig. 3). 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.

Fig. 2. Mean walleye (*Sander vitreus*) production (P), biomass (B), and P/B across recruitment categories in Ceded Territory of Wisconsin lakes, 1990–2012. Bars and whiskers represent the mean \pm 1 SE, and letters in each panel denote means that differed statistically (mixed effect model Tukey's $P < 0.05$). NR, natural recruitment lakes.



Discussion

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

The productivity of walleye populations was right-skewed across all types of populations. Therefore, low P and B populations dominate the landscape, whereas high P and B systems are rare. This information is pertinent because high P in certain populations is occasionally raised as an example of what other populations might be capable of delivering. Dating back to Lindeman (1942), freshwater lakes have been conceptualized as possessing finite quantities of solar energy, nutrients, and carbon to support the production of higher-order heterotrophs (Pace et al. 2004). Thus, it has long been known that the productive capacity of lakes and fish populations is limited and influenced by habitat change (Moyle 1949; Rawson 1952; Downing et al. 1990; Jones et al. 1996; Randall and Minns 2000). For example, habitat restorations might improve fish production (Sass et al. 2012, 2017), whereas environmental degradations might decrease fish production (Sass et al. 2006; Valentine-Rose et al. 2007, 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. (2018) showed that growth rates of young walleye have actually increased in recent years compared with earlier years. Growth rates of older walleye have declined compared with earlier years. Pedersen et al. (2018) 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 walleye in Ceded Territory of Wisconsin 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 currently 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

Fig. 3. Trends in walleye (*Sander vitreus*) production (P), biomass (B), and P/B for Ceded Territory of Wisconsin lakes, 1990–2012. Left column = natural reproduction (NR) populations; middle column = combination populations; right column = stocked-only populations. For the three productivity values, each data point represents a yearly mean across all sampled lakes ± 1 SE. Regression lines reflect significant mixed effect models fit to the data using lake as a random effect. “Change” values represent percent change in modeled production statistics from 1990 compared with 2012; “n.s.” = nonsignificant. Significance and coefficients for all regressions can be viewed in Table 3.



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, 2017). 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. 2018).

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. 2017). 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

Fig. 4. Proportion of walleye (*Sander vitreus*) lakes classified into natural reproduction (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. [Colour online.]

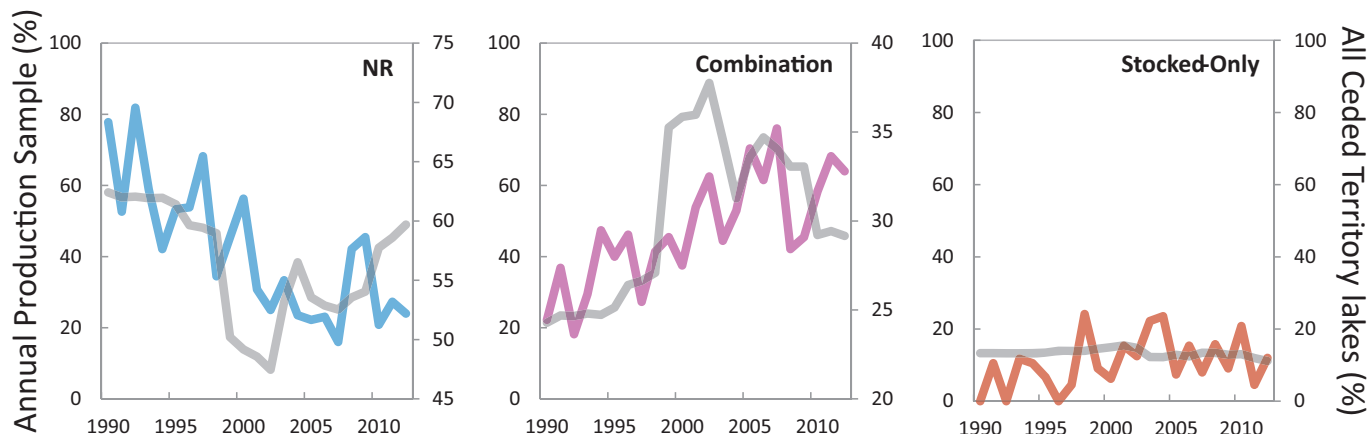


Table 3. Results of mixed effect models evaluating temporal change in walleye (*Sander vitreus*) P , B , and P/B in northern Wisconsin lakes.

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

Note: Variables with significant ($P < 0.05$) trends are highlighted in bold. Note that all data, and thus all regression coefficients, are \log_{10} transformed.

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 (US 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 triggered partly 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 (1 acre = 0.405 ha) (Fayram 2005; Fayram et al. 2005). Changing stocking practices does not explain why recruitment may begin failing in a previously NR lake, but could potentially magnify the severity of production declines.

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, and 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 finding 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 (mean $P = 6.5 \text{ kg}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$ and $B = 26.3 \text{ kg}\cdot\text{ha}^{-1}$; Rypel et al. 2015). It is worth noting that in

some years, P and B were substantially higher in Escanaba Lake with values approaching $12 \text{ kg}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$ and $50 \text{ kg}\cdot\text{ha}^{-1}$, respectively (i.e., approximately double the second most productive estimate for the Ceded Territory of Wisconsin and values that dwarf even the NR category mean presented in Fig. 2). However, these values are not extreme when compared with 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 an important question: 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 data sets likely represent some of the premiere data sets 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 substantial and emerging management challenge for the region. In combination lakes, production was almost halved from $0.91 \text{ kg}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$ in 1990 to $0.48 \text{ kg}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$, and P/B eroded from ~ 0.22 (or $1/4.5 \text{ year}^{-1}$) to 0.17 ($1/6 \text{ year}^{-1}$); thus, it currently takes 1.5 years 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 with combination populations, which have increased. Therefore, regional trends in walleye productivity are linked to broad-scale declines in walleye recruitment (Hansen et al. 2017), 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 2019). 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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