Canadian Journal of Fisheries and Aquatic Sciences

OPEN ACCESS | Research Article

Diminishing productivity and hyperstable harvest in northern Wisconsin walleye fisheries

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Abstract

Managing fisheries in a changing socio-ecological environment may require holistic approaches for identifying and adapting to novel ecosystem dynamics. Using 32 years of Ceded Territory of Wisconsin (CTWI) walleye (*Sander vitreus*) data, we estimated production (*P*), biomass (*B*), biomass turnover (*P*/*B*), yield (*Y*), and yield over production (*Y*/*P*) and tested for hyperstability in walleye yield. Most CTWI walleye populations showed low *P* and *B*, and $Y/P < 1$. Yet, production overharvest ($Y/P > 1$) was prevalent among Wisconsin walleye recruitment-based management approaches (natural recruitment (NR), sustained only by stocking, combination). Production, *B*, and *P*/*B* have declined in NR populations, while *Y* and *Y*/*P* have remained constant. Walleye *Y* was hyperstable along a production gradient among all management approaches and fishery types (i.e., angling only, angling/tribal harvest combined). Diminishing productivity and hyperstable yield may be jointly contributing to observed walleye declines. We classified lakes into management groups of low, moderate, or high vulnerability to harvest based on *Y*/*P* and *P*/*B* dynamics and identify that harvest may benefit from declines to maintain or increase the adaptive capacity of CTWI walleye.

Key words: yield, production, stability, ecosystem-based fisheries management, adaptive capacity, *Sander vitreus*

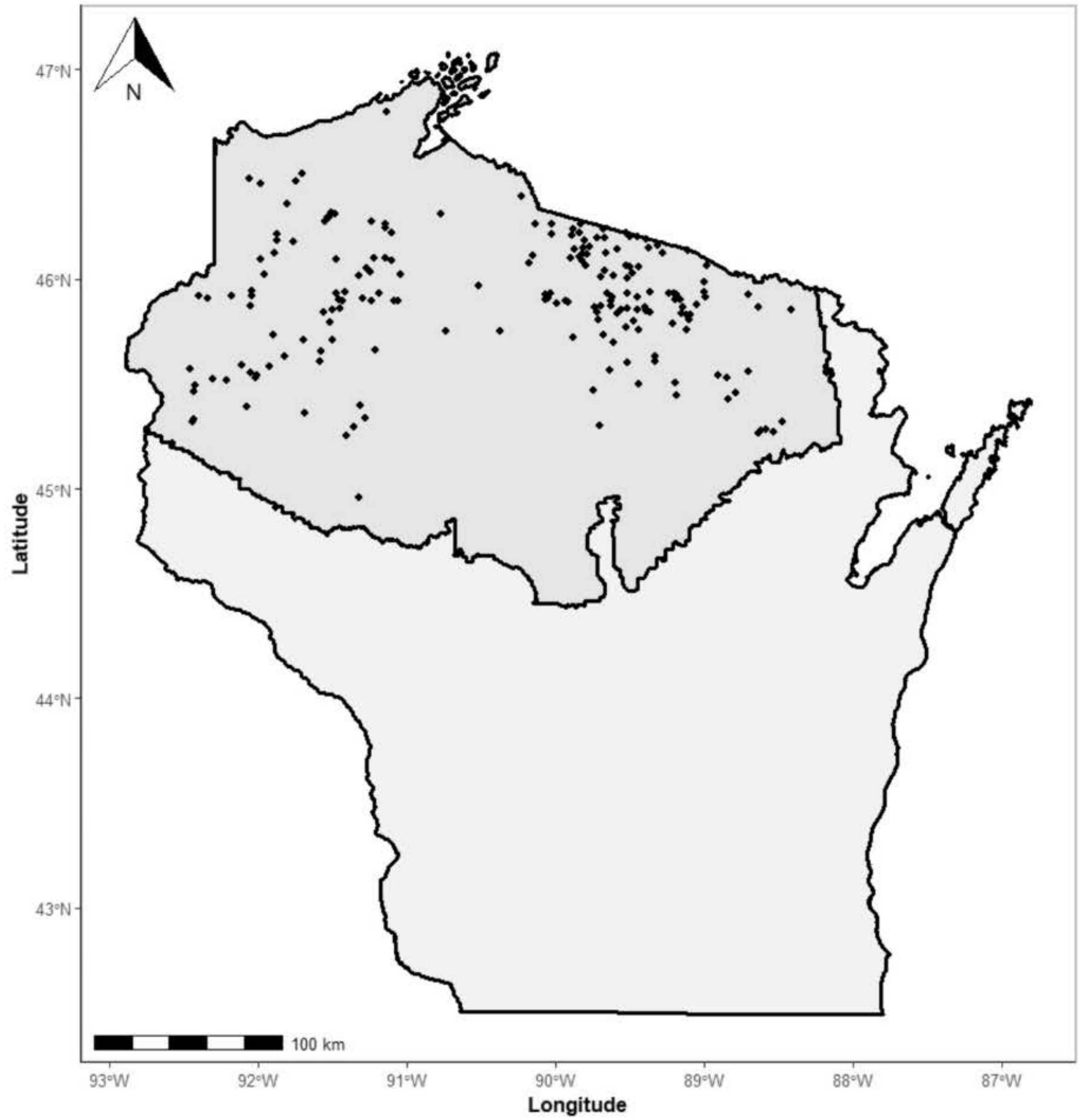
Introduction

The ability of fish populations to provision ecosystem services is being threatened by global environmental change (Carpenter et al. 2011; Lynch et al. 2016). Freshwater fisheries are rapidly changing in response to aquatic invasive species (Walsh et al. 2016; Bernery et al. 2022), climate and habitat changes (Myers et al. 2017; Tingley et al. 2019), and overexploitation (Embke et al. 2019; Cooke et al. 2023). These interactions and potential novel ecosystem dynamics may create a mismatch between existing management frameworks and the current ecosystem regime (Mrnak et al. 2023). Reduction in fish productivity may require management frameworks to shift toward more conservative or protective regulations as consistent harvest on a declining population may lead to recruitment overharvest (Allen et al. 2013; Rypel et al. 2018).Given the complex and often interconnected nature of these drivers, there is a critical need for more holistic ecosystem-based approaches to achieve sustainable fisheries management (Hilborn 2005, 2011; Paukert et al. 2016; Carpenter et al. 2017; Radinger et al. 2023).

Walleye (*Sander vitreus*) populations are in decline and are being negatively influenced by environmental change across their native midwestern USA range (Boehm et al. 2022; Feiner et al. 2022*b*; Krabbenhoft et al. 2023). In the Ceded Territories of Wisconsin (CTWI; Fig. 1), adult walleye production has declined by ~35% over the past 20 years (Hansen et al. 2015*a*, 2018; Rypel et al. 2018; Embke et al. 2019).Rypel et al. (2018) first identified walleye production and biomass-turnover decline across a gradient of walleye stocking regimes. Embke et al. (2019) followed this research and found ~40% of walleye populations experienced production-overharvest (i.e., yield > production) in the CTWI. Natural recruitment (NR) declines and failures and persistent exploitation in these harvest-oriented fisheries have been identified as the critical bottleneck leading to observed declines in adult walleye production (Gaeta et al. 2013; Rypel et al. 2018; Embke et al. 2019; Gostiaux et al. 2022; Krabbenhoft et al. 2023).

Management actions targeted at mitigating the adult walleye decline and restoring NR have largely focused on supplemental stocking to increase adult abundance (Jennings et al. 2005; Raabe et al. 2020; Feiner et al. 2022*b*; Lawson et al. 2022). The efficacy of this stocking program remains largely debated as it has been shown that sex ratios of stocked walleye are skewed female and thus might not be capable of rehabilitating NR (Sass et al. 2022*a*). Further, Elwer et al. (2023) found that no current stocking conditions (i.e., density of

Fig. 1. Map of Wisconsin with the Ceded Territories of Wisconsin highlighted in grey. All lakes used in this study are represented by a point on the map. Note that the same lake may be sampled in multiple years. Base map source: Great Lakes Indian Fish and Wildlife Commission.



stocked fish + stocked fish survival rates) resulted in the naturally reproducing population density standard being met.

Instituting conservative harvest regulations for walleye to reduce adult exploitation (i.e., reduced bag limit, increased minimum length limits, protected no-harvest slot length limits) and liberalized regulations to incentivize harvest of other species (e.g., no minimum length limit, increased bag limit for largemouth bass *Micropterus salmoides*) are management actions frequently used to combat walleye decline (Krueger and Hrabik 2005; Hansen et al. 2015*c*; Sullivan et al. 2020; Krogman et al. 2022). Despite management interventions, current system stressors are independently or jointly driving Wisconsin walleye populations away from being self-sustaining (i.e., declines in recruitment, recruitment failures; Rypel et al. 2018; Krabbenhoft et al. 2023). Loss of population sustainability may be attributable to the large role that humans play in the social–ecological systems in which walleye exist (Post et al. 2002; Ostrom 2009; Golden et al. 2022). For example, production overharvest (Embke et al. 2019; Sass et al. 2022*b*) and angler/tribal (hereafter "fisher") behavior have been linked to observed walleye declines (Gaeta et al. 2013; Mrnak et al. 2018; Sass and Shaw 2020).

A critical assumption of recreational fisheries as social–ecological systems is the potential to self-regulate and maintain a desired regime for the long-term without allowing for instability and population collapse (i.e., sustainability; Post et al. 2002; Ostrom 2009). For Wisconsin walleye fisheries, sustainable populations have been defined as those with an adult density ≥ 7.4 adults/ha (United States Department of the Interior 1991). Walleye recreational and subsistence fisheries were believed to self-regulate in a sustainable feedback loop where fisher effort responded proportionally to population declines or increases (Post et al. 2002; Golden et al. 2022). However, nonlinear relationships between fishery dynamics and fisher behavior are prevalent and often create challenges for sustainable fisheries management if catch or harvest remains relatively constant while the exploitation rate increases as the population declines (Carpenter et al. 1994; Erisman et al. 2011; Johnston et al. 2018; Mrnak et al. 2018; Feiner et al. 2020; Mosley et al. 2022). Nonlinear relationships may occur when fishers maintain catch or yield rates across wide ranges in fish abundance or production, resulting in a curvilinear or asymptotic relationship. These relationships demonstrate hyperstability (i.e., catch rate is maintained during declining abundance, but rapidly declines once a critical, low abundance threshold is reached) or hyperdepletion (i.e., catch rates increase exponentially with abundance; Ward et al. 2013; Golden et al. 2022). Hyperstable relationships may mask population collapse (Harley et al. 2001; Post et al. 2002; Maggs et al. 2016). Many Wisconsin fisheries have demonstrated hyperstability of catch and harvest (Dassow et al. 2020; Feiner et al. 2020; Mosley et al. 2022), including the joint CTWI walleye fishery (e.g., angling catch rates and tribal spearfishing harvest rates; Hansen et al. 2000; Mrnak et al. 2018).

Fish production estimates integrate population vital rates such as abundance, recruitment, growth, and mortality (Waters 1977; Downing 1984; Kwak and Waters 1997) and are specifically suited to study exploited fish populations (Ricker 1946; Waters 1992; Rypel et al. 2015, 2018; Embke et al. 2019). Thus, variables incorporated into fish production estimates are powerful indicators of socio-ecological change (Waters 1992; Valentine-Rose et al. 2007; Benke 2010; Rypel and David 2017; Myers et al. 2018; Rypel et al. 2018) and therefore represent an ecosystem-based approach to fisheries management and assessment (Mrnak et al. 2023; Radinger et al. 2023). Two former studies applied an ecosystem-based production approach to address CTWI walleye abundance and recruitment declines and attempted to identify drivers of such declines (Rypel et al. 2018; Embke et al. 2019). Rypel et al. (2018) calculated production, biomass, and biomass turnover for CTWI walleye lakes during 1990–2012 and found production metrics to be declining over time in lakes supplemented or sustained by walleye stocking and empirically revealed a link between walleye recruitment potential and walleye production. Rypel et al. (2018) did not incorporate fisheries-dependent data (Mrnak et al. 2018; Embke et al. 2019; Sass and Shaw 2020). Embke et al. (2019) incorporated fisheries-dependent data by examining biomass harvest (yield) and production overharvest (yield/production) and reported that ∼40% of CTWI walleye populations were production overharvested. Embke et al. (2019) provided a critical piece of information for CTWI walleye management as they empirically showed fisheries overharvest in the declining CTWI walleye fishery through a production approach. However, the relationship between yield and production and the differences among Wisconsin's recruitment-based management approaches (i.e., sustained by NR only; sustained by a combination of NR and stocking (C); sustained only by stocking (ST); see Cichosz (2022b) for more details) have never been examined (Embke et al. 2019). Neither Rypel et al. (2018) nor Embke et al. (2019) applied their ecosystem-based approach to classify a lake's vulnerability to harvest to be broadly applied for management.

Our objectives were to: (1) extend research on CTWI walleye production dynamics (Rypel et al. 2018) by updating previously developed models with 10 years of new data to reevaluate production (*P*; annual rate of new biomass accumulation), biomass (*B*; empirically estimated standing stock biomass), and biomass turnover (*P*/*B*) rates and relationships among walleye populations supported by different recruitment-based management approaches (i.e., NR, C, or ST; see Cichosz (2022b) for more details); (2) evaluate the temporal dynamics of walleye yield (*Y*; empirical annual biomass harvest estimates) and yield in relation to production (*Y*/*P*; Embke et al. 2019); (3) assess the relationship between *Y* and *P*, and test for hyperstability in walleye *Y* for each recruitment-based management approach and fishery type (i.e., recreational angling only, angling/tribal harvest combined); and (4) classify lakes into management groups of low, moderate, or high vulnerability to harvest based upon yield and production metrics. Linking these recruitment designations to various walleye dynamics (e.g., production, yield) may be useful to managers applying policy and regulation across the landscape. These findings can be used by managers to identify vulnerable fisheries and better inform sustainable management practices, particularly if fishery production is in decline and fisher exploitation is consistent (or increasing).

Methods

Walleye datasets and fisheries

We used walleye population datasets and angler/tribal member creel surveys conducted by the Wisconsin Department of Natural Resources (WDNR) and Great Lakes Indian Fish and Wildlife Commission (GLIFWC) during 1990–2022 to address our objectives. Information collected as part of these standardized surveys included mark-recapture population estimates for a wide variety of walleye lakes in the CTWI, walleye demographic information (total length (TL), weight, sex, age estimates), and records of catch and harvest for a subset of lakes (see Beard et al. 1997; Mrnak et al. 2018). These standardized surveys were intended to represent the range of available lake types and are designed to survey all exploited populations at least once per generation time (Beard et al. 1997; Mrnak et al. 2018). Most lakes were sampled in a stratified random manner while others were randomly sampled across key strata (e.g., region, recruitment source; Cichosz 2022b).

Adult mark-recapture walleye population estimates were completed during 1990–2022 on 25–30 lakes per year (stratified random process) in the CTWI (Mrnak et al. 2018; Cichosz 2022b). These population estimates are used to establish a 35% adult walleye exploitation limit reference point for the following year's harvest season (Hansen et al. 1991). For

WDNR surveys, large-frame fyke nets were placed in littoral spawning habitat of selected lakes following ice-out and all captured walleye were marked with a year-specific fin clip. Fyke netting continued until about 10% of the adult walleye population was captured and marked based on previous population estimates. Fish were recaptured using an alternating current boom-electroshocking recapture run during peak walleye spawning. The GLIFWC used a two-night pulsed direct-current electroshocking survey to generate walleye population estimates. Walleye were captured and marked on the first night and then recaptured on the second night. Walleye population abundance was estimated via Chapman's modification of the Petersen mark-recapture estimator (Ricker 1975). Only walleye population estimates with a coefficient of variation ≤ 0.4 were used for analyses to reduce and mitigate the regression dilution effect (Beard et al. 1997; Harley et al. 2001). In total, 399 lake-years were used for analysis: 179 lake-years for lakes sustained by NR only, 187 lake-years for lakes sustained by a combination of NR and stocking, and 33 lake-years for lakes sustained only by stocking.

All WDNR and GLIFWC surveys measured all walleye for TL and weight, which we used to develop lake-year-specific length–weight regressions (Embke et al. 2019). Sex was recorded for mature individuals expressing gametes. An age structure (scale or dorsal fin spine) was collected for a subset of walleye based on lake-specific sex and available 13 mm TL bins. Walleye age structures were then examined in the laboratory to produce an age estimate and lake-specific age–length key (Embke et al. 2019).

Lake-specific walleye yield was based on reported tribal harvest from GLIFWC and angler creel surveys conducted by the WDNR. Spring tribal spearfishing harvest most often occurs during peak walleye spawning. During spring tribal harvest, nightly permits were issued by tribal agents, where an individual tribal member may obtain more than one permit until the tribal harvest quota is fulfilled for a given lake. Regulations on tribal spearfishing allow for the harvest of any length walleye with only two fish per permit $\geq$ 508 mm. Lakes that were spearfished were declared daily by the representative tribal agency, and a tribal creel clerk was present at the declared lake the night the lake was spearfished. The tribal creel clerk issued individual permits to tribal members and recorded the numbers of hours spent fishing under each permit. Harvested walleye were examined by the tribal creel clerk with TL, weight, and sex being recorded.

Angler creel surveys in the CTWI were conducted by the WDNR based on a stratified roving access design (Hansen et al. 2000). Surveys can only be conducted on a subset of lakes each year. Lakes that have an adult walleye population abundance estimate were prioritized to have a creel survey in the same year (Beard et al. 1997; Hansen et al. 2000; Cichosz 2022*b*). Angler creel surveys began the first Saturday in May, concurrent with the start of the recreational angler walleye harvest season and end the first Sunday in March of the following year, when the recreational angler walleye harvest season closes. Creel clerks made instantaneous counts of the number of fishers on a lake and conducted interviews on a subset of fishers. During the interview, the creel clerk recorded hours fished, total catch by species, harvest, species targeted, and demographic information from harvested fish (i.e., TL, weight; Hansen et al. 2000). From this information, walleye angler effort, catch rates, and harvest were calculated. The standard CTWI recreational angling walleye regulation is a three fish per day bag limit, with a 381 mm minimum length limit, a protected 508–610 mm no harvest slot length limit, with only one fish $\geq$ 601 mm allowed. Various other harvest regulations are used on specific water bodies based on walleye abundance, individual growth rates, population size-structure, or recruitment status, some of which are summarized in Mrnak et al. (2018).

Following methods and criteria from Rypel et al. (2018), we grouped lakes into three recruitment-based management approaches to test for differences in our response variables of interest: NR (lakes with NR only), combination (C; lakes with some NR supplemented with stocking), and stocked-only (ST; lakes with no natural NR that are solely maintained via stocking). Lake-specific walleye recruitment status was designated based on previous age-0 electrofishing surveys and a GLIFWC flowchart that accounts for each lake-specific recruitment history and the most recent fall age-0 walleye survey (Cichosz 2022b; Lawson et al. 2022; Elwer et al. 2023).

Given that the CTWI walleye fishery is a joint fishery (i.e., recreational angling and subsistence tribal harvest; Mrnak et al. 2018), we grouped lakes into two fishery type categories: angling only and angling/tribal harvest combined. Due to the small number of lakes that experienced tribal harvest and not angling ($n = 8$), we did not conduct an analysis on tribal harvest-only lakes. These distinct fisheries are managed differently where the angling fishery is open access with limited regulation of effort, whereas the tribal spear fishery is based on lake-specific harvest quotas (Mrnak et al. 2018).

Production (P), biomass (B), biomass turnover (P/B), yield (Y), and yield over production (Y/P) calculations

Production (P), biomass (B), biomass turnover (P/B), and yield (Y) were calculated for each lake-year combination ($n = 399$) following methods established in Embke et al. (2019). For all analyses, individuals < 5 years old were excluded, as immature walleye of these ages are not reliably vulnerable to capture by fyke nets (Hansen et al. 1991). Production (kg·ha^{-1}·year^{-1}) was estimated for each lake and year combination with available data by applying the instantaneous growth method to fish from all age-classes from age 5 to $a_{\max}$ (maximum age):

$$(1) \qquad P_y = \sum_{a=5}^{a_{\max}} G_{a,y} \bar{B}_{a,y}$$

where a refers to an age class, P_y is the total walleye production for year y (kg·ha^{-1}·year^{-1}), and $G_{a,y}$ is the instantaneous growth rate of cohort aged a in year y. Given we lacked measurements of cohorts in repeated years, we estimated growth rate from consecutive cohorts in the same year (i.e., $\log_e\left(\frac{\text{mean weight at age a+1,y}}{\text{mean weight at age a, y}}\right)$). Mean biomass (kg·ha^{-1}) between consecutive age classes or cohorts ($\bar{B}_{a,y}$) during the year was estimated by substituting age-classes for time.

To estimate loss of biomass due to fishing, we estimated age-specific yield (harvested biomass; kg) for each lake-year with available data ($n = 399$). For tribal yield, the total number of fish harvested was known, but for angling harvest, the total number of fish harvested was projected by WDNR based on creel data. For both harvest types, a subsample of harvested fish was measured for TL. To estimate yield, we randomly sampled with replacement from the available subset of length data for that lake-year combination and then assigned those values as lengths to the unmeasured fish from that same lake-year combination. Once all harvested fish had a corresponding length, we assigned ages and weights to all fish using the age-length keys and length–weight regressions developed through earlier calculations. From this information, we calculated the number of fish harvested for each age class (H_a) as well as mean weight-at-age of harvested fish ($W_{ha,\,a}$; kg), which we used to calculate age-specific tribal and angler biomass harvest ($Y_{t,\,a}$ and $Y_{f,\,a}$; kg):

$$(2) \qquad Y_{t,\,a} \text{ or } Y_{f,\,a} = H_a * W_{ha,\,a}$$

Total annual biomass harvest (Y_y; kg·ha^{-1}) was calculated by summing $Y_{t,a,y}$ and $Y_{f,a,y}$ for each lake. All biomass harvest estimates were divided by lake-specific surface area (kg·ha^{-1}). We evaluated production harvest as biomass harvested relative to production (i.e., Y/P). See Embke et al. (2019) for detailed methods and open-source calculation code available on GitHub (https://github.com/hembke/Production-and-Biomass-Calculation).

Statistical analyses

P, *B*, *P*/*B*, *Y*, and *Y*/*P*

We created relative frequency histograms for P, B, P/B, and Y/P by recruitment designation and used a Shapiro–Wilk test to test for normality. If data were non-normally distributed, values were $\log_{10}$-transformed to achieve normality prior to analysis. Analyses were considered statistically significant at $\alpha = 0.05$. A mixed effects model with Tukey's post hoc test and the Bonferroni correction for multiple comparisons was used to test for statistical differences in mean P, B, P/B, and Y/P among recruitment categories, where P, B, P/B, or Y/P were the response variables, recruitment category was the explanatory variable, and lake and year were random effects. We tested for statistically significant changes over time in P, B, P/B, Y, and Y/P among recruitment categories using mixed effects regression models where P, B, P/B, Y, or Y/P was the response variable, year was the explanatory variable, and lake was a random effect. Given the large number of models, we corrected for multiple comparisons.

Hyperstability

We tested for hyperstability (i.e., relationship between fisher yield and adult walleye production) for each recruitment category (i.e., NR, C, ST) and fishery type (i.e., angling only, angling/tribal harvest combined) using the power function:

$$(3) \qquad Y = qP^b$$

where Y is the respective yield estimate, P is the annual rate of new biomass accumulation, q is a proportionality parameter, and b represents the curvature of the relationship. Hyperstability is evident when $b < 1$, $b = 1$ indicates a proportional relationship, and $b > 1$ indicates hyperdepletion (Feiner et al. 2020; Golden et al. 2022). We created histograms of production values for each recruitment category or fishery type to identify and remove outliers that may have a disproportional influence on the relationship ($n = 1$ lake-year removed from C recruitment category). We tested whether b was significantly <1 for each recruitment category and fishery type using a one-tailed t test.

Lake classification

We classified lakes into management groups of low, moderate, or high vulnerability to harvest based on yield over production (Y/P) and biomass turnover (P/B) dynamics. Vulnerability to harvest should be low when Y/P is <1 and biomass turnover is relatively quick. Conversely, systems with $Y/P > 1$ and slow biomass turnover will likely be more vulnerable to sustained or increased harvest. All systems with $Y/P < 1$ are sustainable by definition and are not production overharvested. Yet, lakes with $Y/P < 1$ and a slow biomass turnover will be at a lower capacity to absorb additional harvest (i.e., more vulnerable). Regardless of biomass turnover, systems with $Y/P > 1$ are being production overharvested.

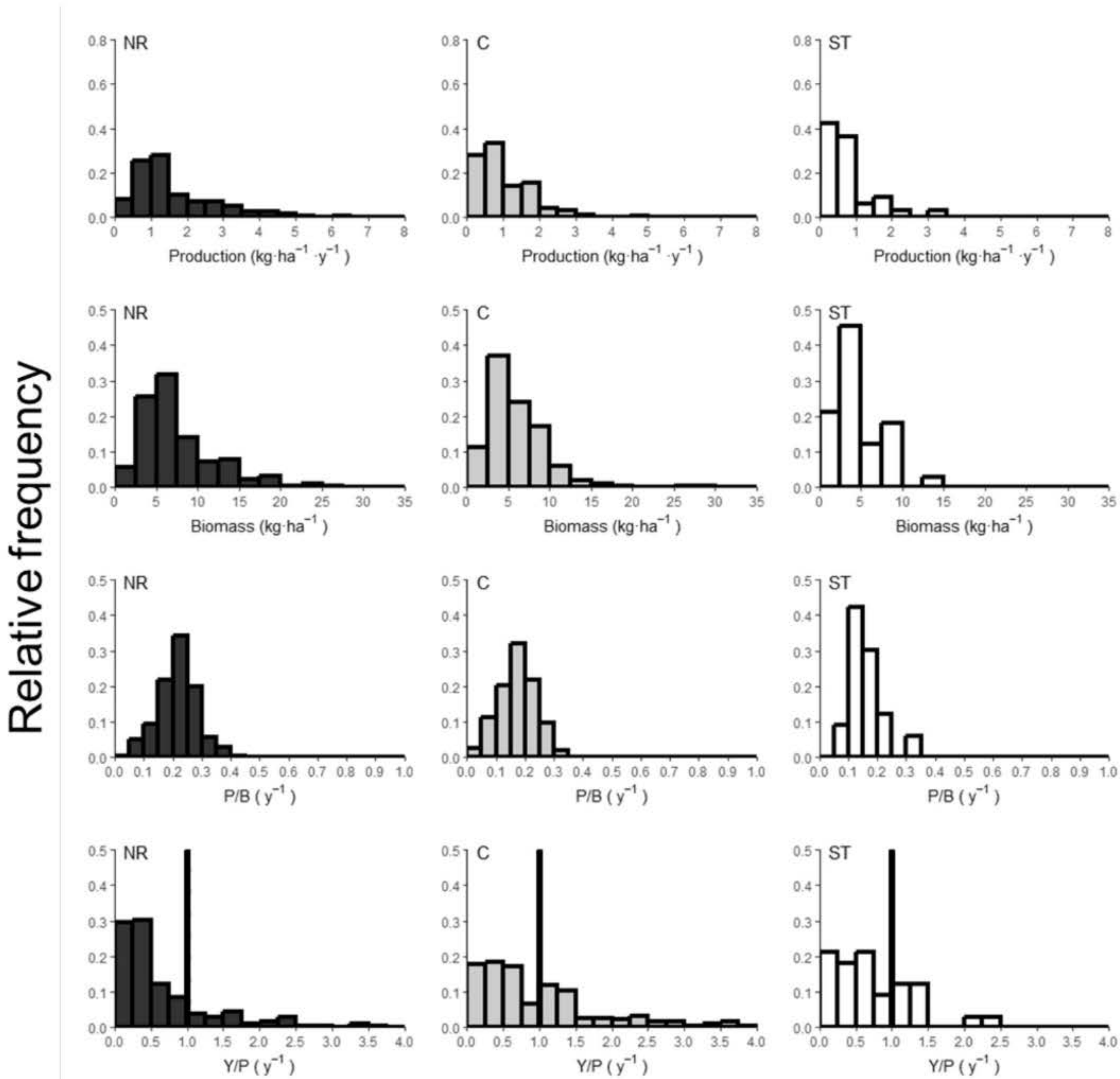
Results

P, *B*, *P*/*B*, *Y*, and *Y*/*P*

Production, B, and Y/P estimates were non-normal in their distribution among recruitment categories with a right-skew, peaks at low values, and long tails (all Shapiro–Wilk test $P < 0.001$; Fig. 2). Production overharvest ($Y/P > 1$) occurred in about 20% (35 out of 179), 41% (76 out of 186) and 30% (10 out of 33) of the lake-years for NR, C, and ST lakes, respectively (Fig. 2). Biomass turnover (P/B) values were normally distributed in NR (Shapiro–Wilk test $P = 0.34$) and C lakes (Shapiro–Wilk test $P = 0.65$) but were non-normally distributed for ST lakes (Shapiro–Wilk test $P = 0.001$; Fig. 2). Across all years, P/B had modal peaks at 0.25, 0.20, and 0.15 for NR, C, and ST recruitment categories, respectively (Fig. 2). Therefore, walleye B is replaced every 4.0, 5.0, and 6.7 years in NR, C, and ST lakes.

Mean walleye P, B, and P/B estimates were significantly greater in NR lakes compared to C and ST lakes (all mixed effects models, Bonferroni $P < 0.01$). There were no differences in mean walleye P, B, or P/B values between C and ST lakes. Mean P (±SE, range) in NR, C, and ST lakes was 1.64 (0.08, 0.15–6.35), 1.06 (0.06, 0.07–8.0), and 0.81 (0.11, 0.21–3.11) kg·ha^{-1}·year^{-1}. Mean B (±SE, range) in NR, C, and ST lakes was 7.64 (0.35, 0.71–26.28), 6.02 (0.27, 1.13–29.91), and 4.78 (0.51, 1.71–14.71) kg·ha^{-1}. Mean P/B (±SE, range) in NR, C, and ST lakes was 0.21 (0.005, 0.04–0.42), 0.17 (0.005, 0.01–

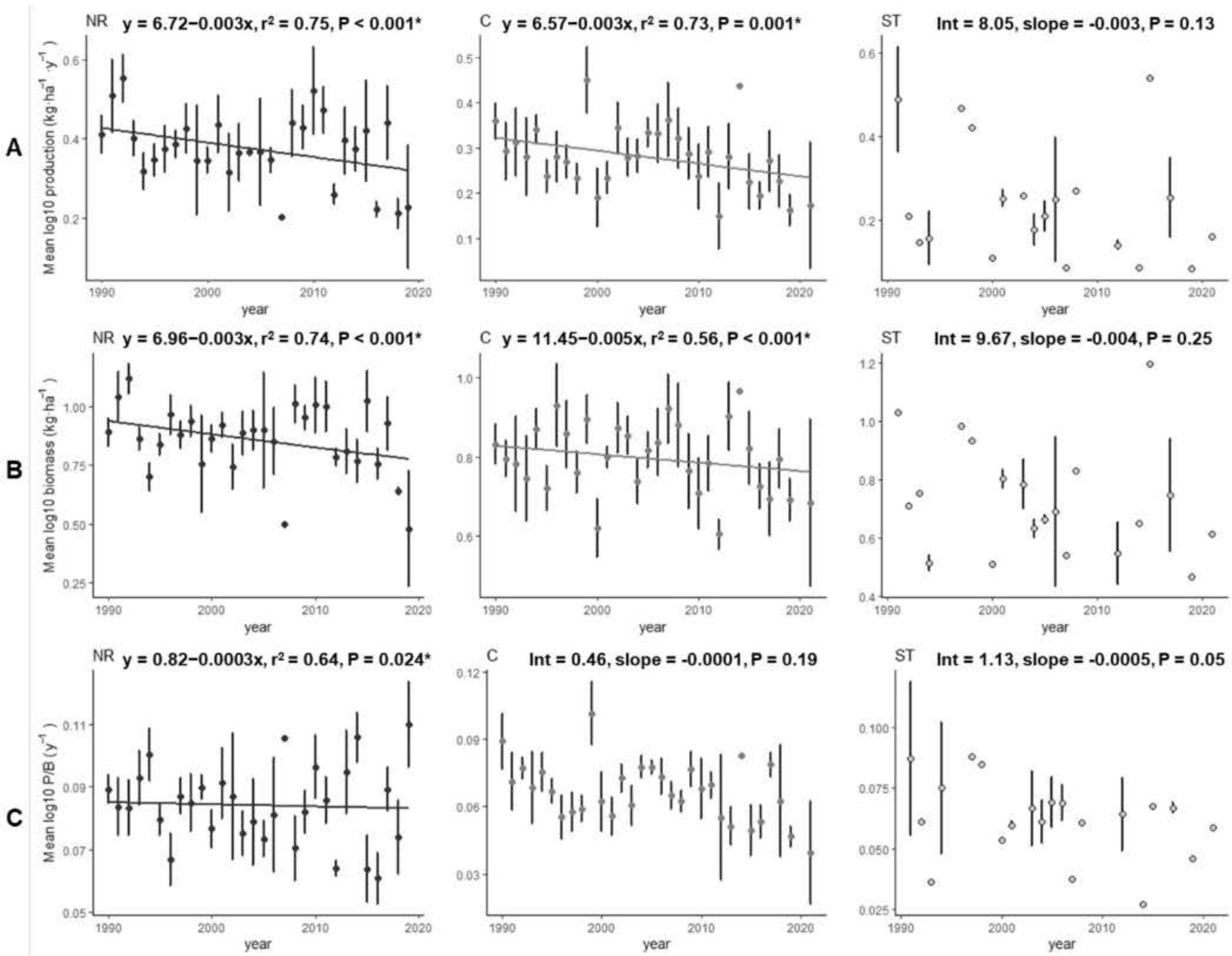
Fig. 2. Relative frequency of walleye (*Sander vitreus*) population characteristics in the Ceded Territories of Wisconsin lakes. First row: production (P; kg·ha^{-1}·year^{-1}). Second row: biomass (kg·ha^{-1}). Third row: biomass turnover (P/B; year^{-1}). Fourth row: yield over production (Y/P; year^{-1}). Recruitment-based management approaches include NR = natural reproduction, C = combination of natural reproduction and stocking, or ST = sustained only by stocking during 1990–2022. Solid lines for the yield over production distributions ($Y/P = 1$) indicates the threshold at which biomass harvest exceeds annual production (production overharvest; $Y/P > 1$).



0.33), and 0.16 (0.01, 0.06–0.34) year^{-1}. There was no difference in mean walleye Y/P between NR and ST and C and ST lakes. Mean Y/P (±SE, range) in NR, C, and ST lakes was 0.66 (0.05, 0.0003–3.54), 1.03 (0.05, 0–7.8), and 0.72 (0.10, 0.03–2.38). Mean walleye Y/P was statistically different between NR and C lakes (Bonferroni $P = 0.007$).

NR lakes exhibited significant decline in walleye P and B over time (mixed effect model $P < 0.001$ and $P = 0.01$, respectively) as did C lakes (both $P < 0.001$; Fig. 3). The slope for P and B over time in ST lakes was not different than zero (Fig. 3). Biomass turnover rate only significantly declined over time in NR lakes ($P = 0.02$) and was not different than zero in C or ST lakes (Fig. 4). Yield did not change over time in NR and ST lakes. In C lakes, Y significantly declined over time ($P = 0.03$; Fig. 4). Across all recruitment categories, there was no change in Y/P over time (Fig. 4).

Fig. 3. Annual mean (±1SE) walleye (*Sander vitreus*) $\log_{10}$-transformed production (*P*; kg·ha^{-1}·year^{-1}; row A), biomass (*b*; kg·ha^{-1}; row B), and biomass turnover (*P/B*; year^{-1}; row C) over time in the Ceded Territories of Wisconsin lakes among recruitment-based management approaches (i.e., NR = natural reproduction, C = combination of natural reproduction and stocking, ST = sustained only by stocking) during 1990–2022. Mixed effects models with significant trends are shown with an equation of the line, r^2, and *P*-value (*P*) above each panel. Mixed effects models with nonsignificant trends are shown with coefficient estimates (Intercept (Int) and slope) and *P*-value above each panel. Best fit regression lines indicate a significant trend (i.e., slope ≠ 0; mixed effect $P < 0.05$).



Hyperstability

Hyperstability in walleye yield rates across a gradient of walleye population productivities were observed across all recruitment categories and fishery types (e.g., angling only or angling/tribal harvest combined; all one-tailed *t* test $P < 0.05$; Table 1; Figs. 5 and 6). Hyperstability in the relationship between *Y* and *P* was similar for NR and C lakes ($b = 0.20$ and $b = 0.22$, respectively) and was most pronounced in ST lakes ($b = 0.17$; Table 1; Fig. 5). Hyperstability was greater for angling only fisheries ($b = 0.17$) than in joint angling and tribal harvest fisheries ($b = 0.23$; Table 1; Fig. 6).

Lake classification

Lakes were classified into management groups of low, moderate, or high vulnerability to harvest based on $Y/P = 1$ (production overharvest) and $P/B = 0.19$ (median biomass turnover rate for dataset; Fig. 7). The upper right quadrant represents productive fisheries with high levels of harvest while the lower right quadrant represents productive fisheries with low levels of harvest (Fig. 7). Low vulnerability to harvest likely occurs when $Y/P < 1$ and $P/B > 0.19$ and was documented for 58%, 28%, and 22% of lake-years for NR, C, and ST recruitment categories, respectively (Fig. 7). High vulnerability to harvest occurs when $Y/P > 1$ and $P/B < 0.19$ and was observed for 11%, 29%, and 24% of lake-years for NR, C, and ST recruitment categories, respectively (Fig. 7). Moderate vulnerability to harvest may occur when $Y/P > 1$ and $P/B > 0.19$ (less frequent) or when $Y/P < 1$ and $P/B < 0.19$ (more frequent; Fig. 7).

 Can. J. Fish. Aquat. Sci. **81**: 1650–1665 (2024) | dx.doi.org/10.1139/cjfas-2023-0372

Fig. 4. Annual mean (±1SE) walleye (*Sander vitreus*) $\log_{10}$-transformed yield (*Y*; kg·ha^{-1}; row A) and yield over production (*Y/P*; year^{-1}; row B) over time in the Ceded Territories of Wisconsin lakes among recruitment-based management approaches (i.e., NR = natural reproduction, C = combination of natural reproduction and stocking, ST = sustained only by stocking) during 1990–2022. Mixed effects models with significant trends are shown with an equation of the line, r^2, and *P*-value (*P*) above each panel. Mixed effects models with nonsignificant trends are shown with coefficient estimates (Intercept (Int) and slope) and *P*-value above each panel. Best fit regression lines indicate a significant trend (i.e., slope ≠ 0; mixed effect $P < 0.05$).

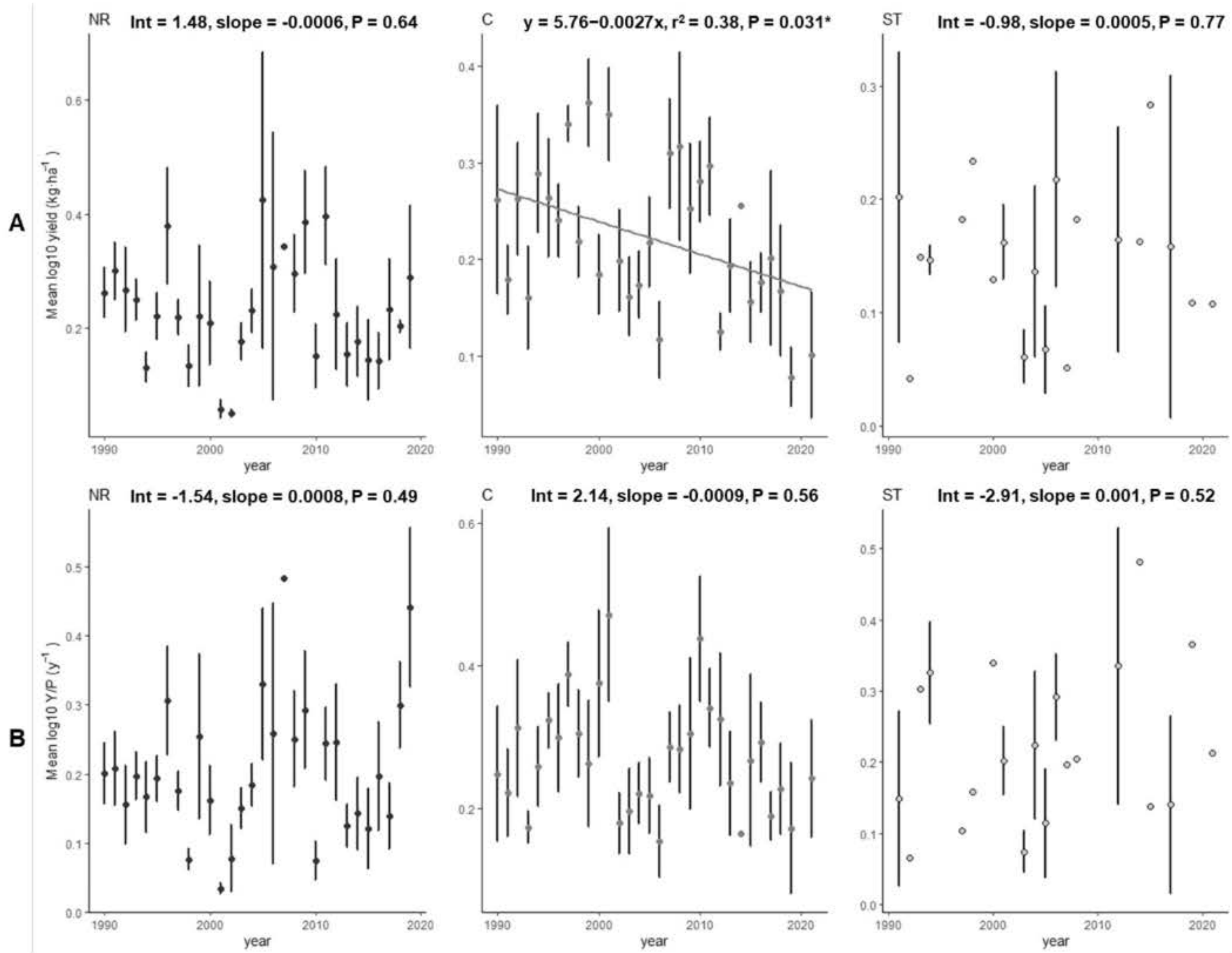
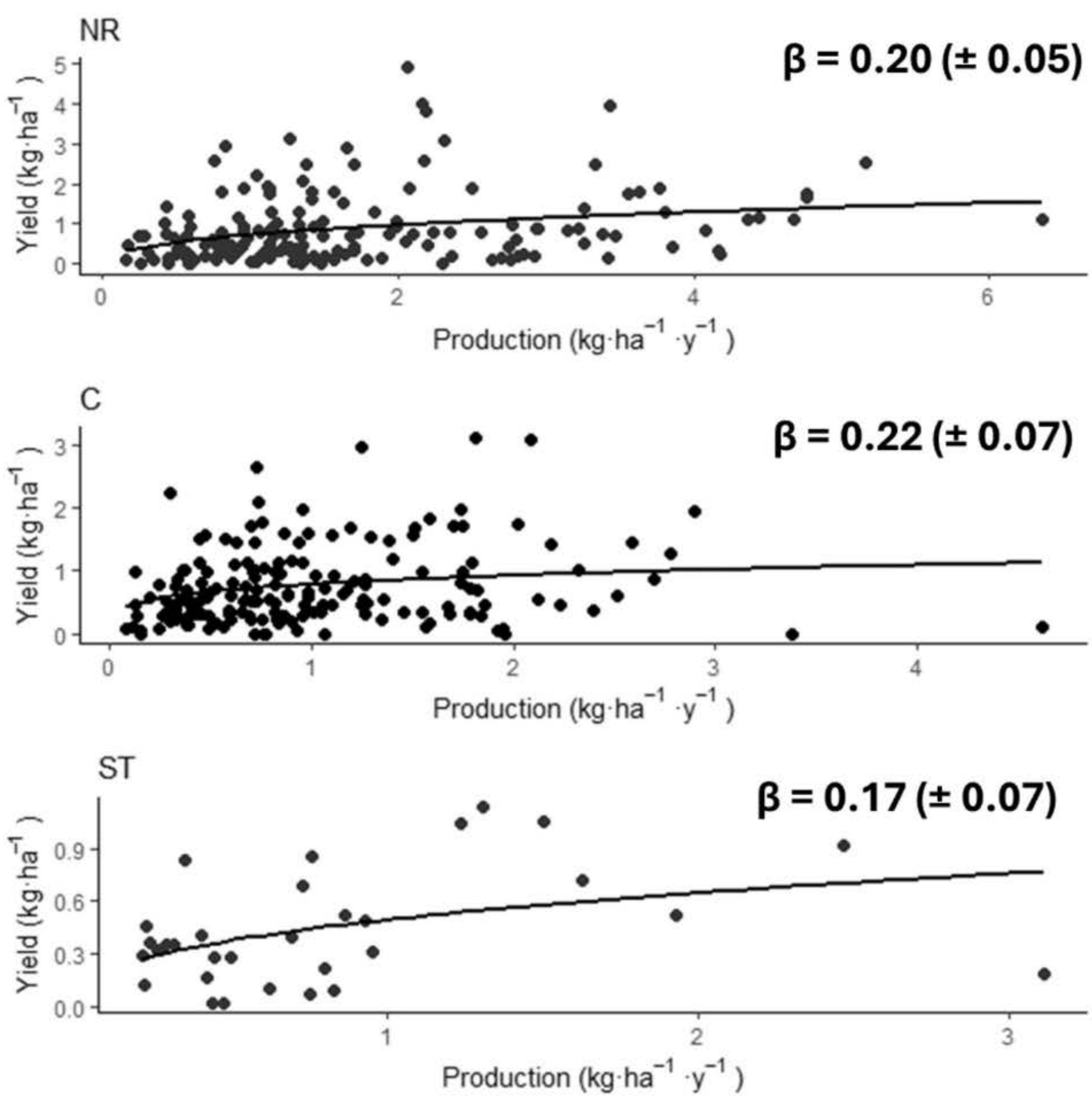


Table 1. Nonlinear modeling results testing for hyperstability in the relationship between adult walleye (*Sander vitreus*) yield (kg·ha^{-1}) and adult walleye production (kg·ha^{-1}·year^{-1}) for each recruitment-based management approach (i.e., recruitment category; NR = natural reproduction, C = combination, ST = sustained only by stocking) and fishery type (recreational angling only, angling/tribal harvest combined).

Recruitment category	Fishery type	α (±1SE)	β (±1SE)	df, residual df	*P*-value
NR		0.51 (0.10)	0.20 (0.05)	1, 177	<0.001*
C		0.54 (0.08)	0.22 (0.07)	1, 184	0.001*
ST		0.28 (0.08)	0.17 (0.07)	1, 31	0.03*
	Angling	0.42 (0.10)	0.17 (0.06)	1, 87	0.006*
	Angling/tribal harvest	0.54 (0.07)	0.23 (0.04)	1, 299	<0.001*

Note: Coefficient estimates (±1SE), degrees of freedom (df, residual df), and *P*-values from one-tailed *t* test for $\beta < 1$ are reported. * denotes statistical significance ($P < 0.05$).

Fig. 5. Hyperstable relationships between Ceded Territories of Wisconsin walleye (*Sander vitreus*) yield (Y; kg·ha^{-1}) and production (P; kg·ha^{-1}·year^{-1}) among recruitment-based management approaches (i.e., NR = natural reproduction, C = combination of natural reproduction and stocking, ST = sustained only by stocking) during 1990–2022. Each data point represents a single lake-year estimate. B values (±1SE) from power function analysis reported for each recruitment-based management approach.



Discussion

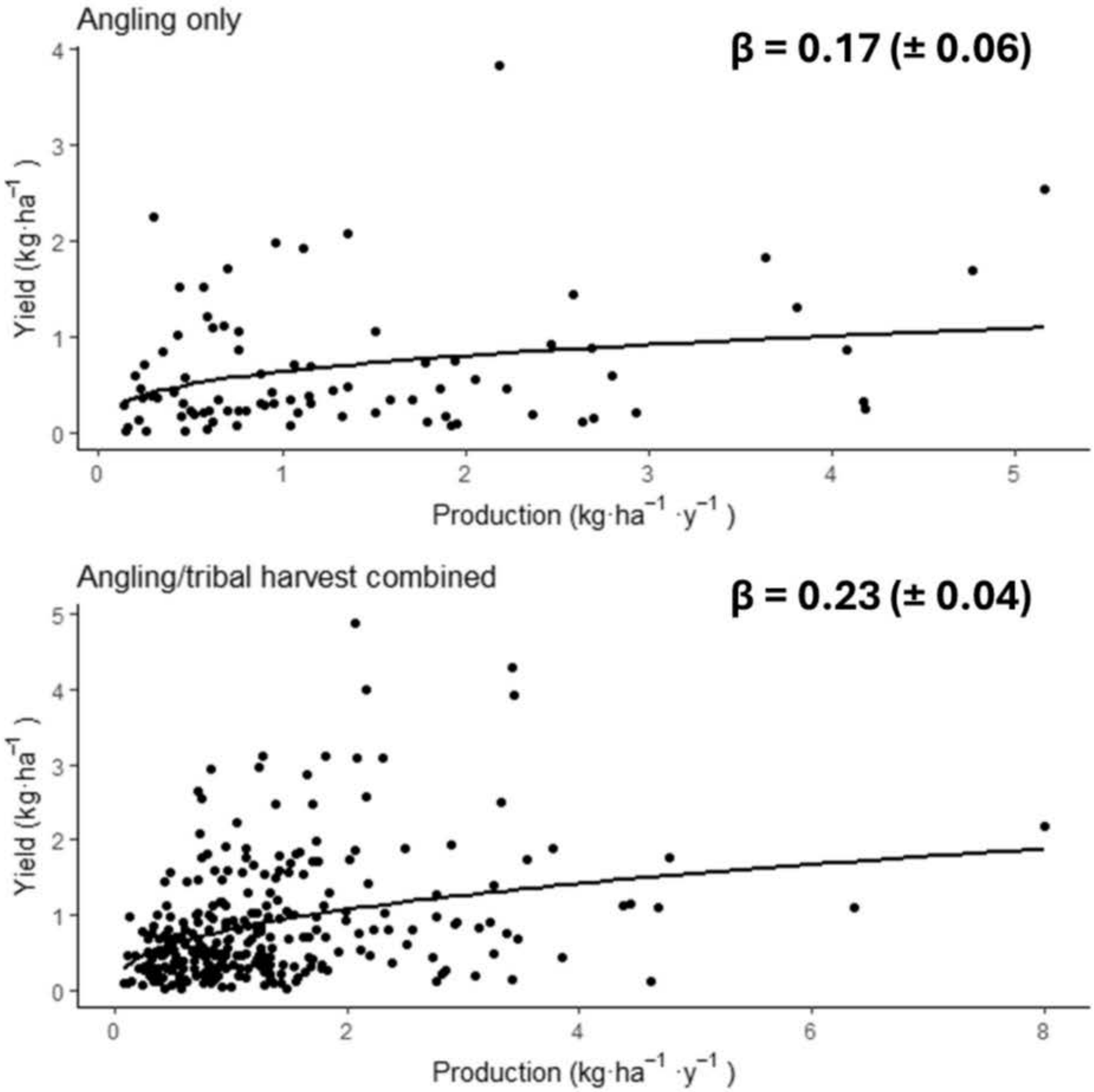
P, B, P/B, Y, and Y/P

Lakes in the CTWI solely supported by NR appear to be the most resilient fisheries and the least vulnerable to harvest. Production and B values were significantly greater in walleye populations solely supported by NR compared to populations supported by a combination of natural reproduction and stocking (C) or sustained only by stocking (ST). Further, NR lakes had the shortest biomass turnover time and least frequent production overharvest (i.e., $Y/P > 1$). Given the decline in NR walleye P, B, and P/B over time and the fact that the proportion of NR lakes is declining (i.e., more lakes transitioning to C or ST; Rypel et al. 2018; Raabe et al. 2020), this is of great management and tribal subsistence concern as formerly more robust walleye populations are now declining.

Including 10 years of new data revealed some novel insights between our research and Rypel et al. (2018), but also reaffirmed an ongoing, similar trajectory of decline in productivity of northern Wisconsin walleye populations. Walleye productivity remained highest in lakes solely supported by NR and was right-skewed across all recruitment-based management approaches, indicating that low P and B populations still dominate the landscape (Rypel et al. 2018; Embke

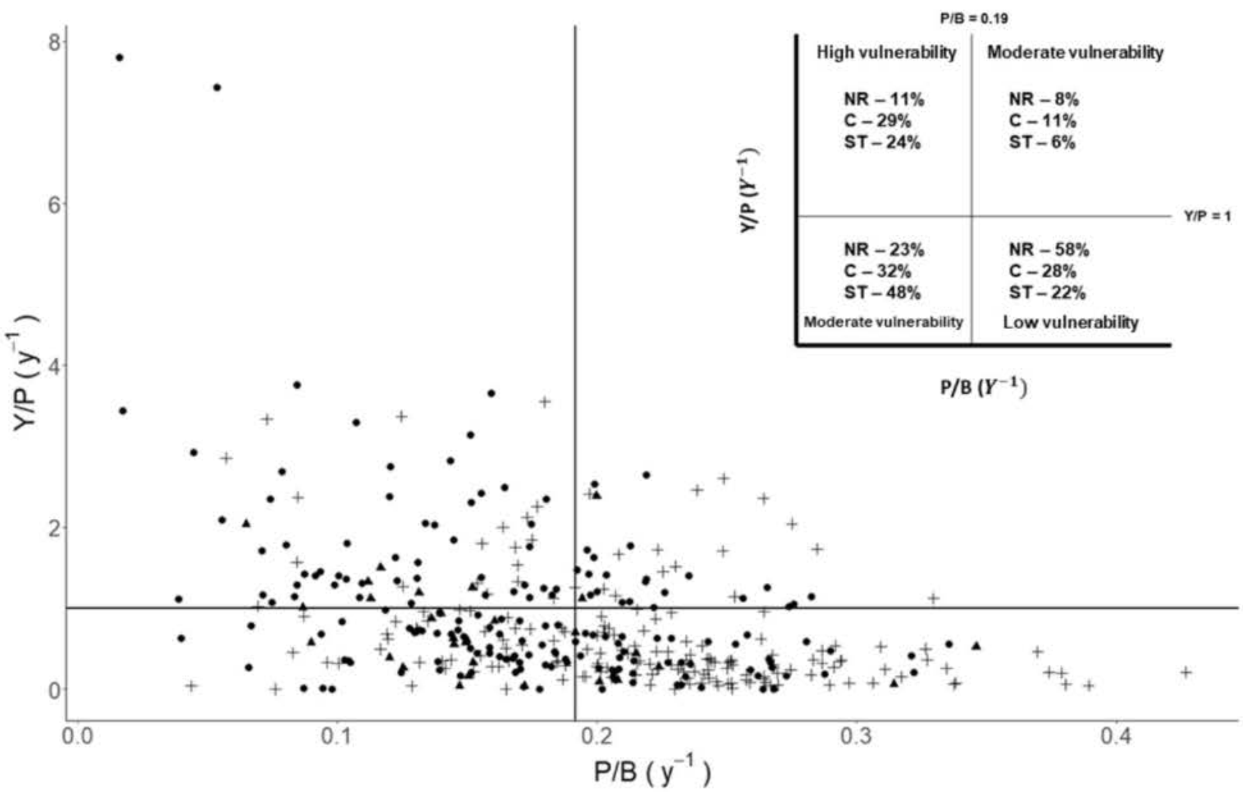
 Can. J. Fish. Aquat. Sci. 81: 1650–1665 (2024) | dx.doi.org/10.1139/cjfas-2023-0372

Fig. 6. Hyperstable relationships between Ceded Territories of Wisconsin walleye (*Sander vitreus*) yield (Y; kg·ha^{-1}) and production (P; kg·ha^{-1}·year^{-1}) between fishery type (i.e., recreational angling only or angling/tribal harvest combined) during 1990–2022. Each data point represents a single lake-year estimate. B values (±1SE) from power function analysis reported for each fisher type.



et al. 2019). Although Rypel et al. (2018) did not find a significant change in NR P or B over time, the nonsignificant negative slopes (i.e., table 3 in Rypel et al. (2018)) were similar to the significant negative slopes reported in this paper, suggesting a similar trajectory of decline. One critical difference between our study and Rypel et al. (2018) was in P/B change over time in naturally reproducing populations. Rypel et al. (2018) reported a significant positive increase in P/B over time, indicating that NR biomass turnover was expected to occur more rapidly in the future (mean NR $P/B = 0.23$, 4.3-year biomass turnover, positive trend). In our study with 10 years of new data, we found a significant negative slope for P/B over time in NR lakes, indicating that biomass turnover is likely to take more time in the future (mean NR $P/B = 0.21$, 4.7-year biomass turnover, negative trend). Further, lakes supported by a combination of natural reproduction and stocking, mean walleye P has decreased by about 58% from 1.34 kg·ha^{-1}·year^{-1} in 1990 to 0.56 kg·ha^{-1}·year^{-1} in 2021 and P/B decreased from about 0.22 year^{-1} (4.5-year biomass turnover) in 1990 to 0.09 year^{-1} in 2021 (11.1-year biomass turnover). Therefore, it currently takes over 6.5 more years to replace C systems walleye biomass now than in 1990, further demonstrating the declining productivity of CTWI walleye populations (Rypel et al. 2018; Embke et al. 2019). Given the decline in lakes categorized as NR and increase in lakes categorized as C (Rypel et al. 2018; Raabe et al. 2020), these CTWI trends are likely linked to regional walleye recruitment declines (Hansen et al. 2017; Zebro et al. 2022; Krabbenhoft et al. 2023). These may suggest

Fig. 7. Walleye (*Sander vitreus*) yield over production (Y/P; year^{-1}) versus biomass turnover (P/B; year^{-1}) for the Ceded Territories of Wisconsin during 1990–2022. Each point represents one lake-year combination with the shape of the point corresponding to recruitment-based management approach (i.e., recruitment category; NR = natural reproduction (+), C = combination of natural reproduction and stocking (•), and ST = sustained only by stocking (▲)). The horizontal solid line establishes the 1.0 harvest threshold where 100% of biomass produced is harvested. The vertical solid line shows the overall median biomass turnover rate for the time series (0.19 year^{-1}). The inset identifies vulnerability to harvest (low, moderate, or high) and the proportional breakdown for each recruitment category as it relates to the Y/P and P/B thresholds.



that habitats and systems that have historically supported greater walleye production and NR are losing their capacity to do so (Rypel et al. 2018; Embke et al. 2019). Multiple mechanisms and hypotheses have been postulated to explain walleye productivity and NR declines including invasive species, climate and habitat changes leading to species interaction shifts, production overharvest, and anthropogenic stressors (Vander Zanden and Olden 2008; Hansen et al. 2015*a*, 2015*c*, 2017; Kelling et al. 2016; Sass et al. 2017, 2021; Rypel et al. 2018; Embke et al. 2019).

Production overharvest ($Y/P > 1$) occurred most often in lakes supported by a combination of natural reproduction and stocking (41% of lake-years) followed by ST lakes (30% of lake-years), with NR lakes having the lowest rate of production overharvest (20% of lake-years). Production overharvest in lakes solely supported by stocking was expected as stocking is sometimes conducted to provide opportunities for harvest rather than to reestablish NR. This may also be an effect of anglers targeting lakes that have been stocked whereby they potentially use stocking information as a proxy for population size (Fayram et al. 2006). These results corroborate those in Embke et al. (2019), which reported $Y/P > 1$ for ~40% of all NR and C (combined) walleye lakes in the CTWI. Regardless of the frequency of occurrence, production overharvest is occurring in CTWI walleye populations and may be problematic as sustained $Y/P > 1$ in NR or C lakes may lead to a biomass depletion rate that is insurmountable to overcome with existing management frameworks (i.e., management plans not adjusted for exploitation based on population productivity; Waters 1992; Embke et al. 2019; Elwer et al. 2023). Importantly, Y did not change over time in NR and ST lakes, with a slight decline in Y in C lakes over time, pointing to changes in biomass harvest as a nonsingular driver of production overharvest in CTWI walleye fisheries (Embke et al. 2019). Rather, it appears the joint effects of declining standing stock biomass and decreasing biomass turnover rates are resulting in larger proportions of remaining biomass being harvested (removed) at similar effort levels (i.e., catchability (q) is increasing; Mrnak et al. 2018; Embke et al. 2019).

The CTWI walleye decline is a known issue (Hansen et al. 2015*a*, 2017; Embke et al. 2019), yet a mechanistic understanding for the decline is lacking. Within the current Wisconsin management framework, many alternative management actions exist to potentially increase the productive capacity of these walleye fisheries including key habitat restorations (Sass et al. 2017, 2019, 2023; Raabe et al. 2020;

Krabbenhoft et al. 2023), food web manipulations reducing competitive and predatory pressures on walleye (Sikora et al. 2021, 2022; Embke et al. 2022; Dassow et al. 2023; Mrnak et al. 2023), or reductions or restrictions placed on fisher harvest, particularly as yield approaches production (i.e., management plan adjusts exploitation based on population productivity; Rypel et al. 2018; Embke et al. 2019; Radinger et al. 2023). A novel approach may be needed as declining biomass turnover is indicative of NR declines and the erosion of the productive capacity of these fisheries. The safe-operating space concept (i.e., using actions within managerial control to offset drivers outside of managerial control; Carpenter et al. 2017; Hansen et al. 2019) and the resist–accept–direct climate adaptation framework (Dassow et al. 2022; Feiner et al. 2022*a*) provide two promising ecosystem-based fisheries management approaches that may aid in the conservation of walleye populations. Current CTWI walleye co-management may also consider adjusting exploitation based on individual walleye population productivities as the ability to withstand harvest (P/B) is variable across lakes and recruitment-based management approaches (Fig. 7). Additionally, for the very low Y/P lakes (underexploited), management could aim to increase exploitation in an attempt to take pressure off lakes where $Y/P > 1$.

Hyperstability

The CTWI walleye fishery was repeatedly hyperstable in yield rates across a gradient of population productivities for all recruitment-based management approaches and fishery types (i.e., angling only, angling/tribal harvest combined). Unlike previous research that reported greater hyperstability in recreational angler walleye catch than tribal walleye harvest along an adult walleye density gradient (Mrnak et al. 2018), hyperstability in walleye yield was greatest in angling-only fisheries than ones with both angling and tribal harvest, indicating that anglers may be more efficient at harvesting walleye at low production values. Regardless, CTWI walleye fisheries do not exist in a sustainable feedback loop where fisher yield rates proportionally respond to increases or decreases in walleye production. These hyperstable relationships between walleye yield and production may occur due to fish aggregating behavior (i.e., spawning, optimal habitat; Rose and Kulka 1999; Dassow et al. 2020), angler/tribal harvester behavior, experience, technology, movement (Post et al. 2002; van Poorten et al. 2016; Tidd et al. 2017), or recruitment variability and depensatory population dynamics (Post 2013; Ward et al. 2013; Golden et al. 2022), which are known to exist for CTWI walleye (Sass et al. 2021; Dassow et al. 2023; Krabbenhoft et al. 2023). Due to spawning behavior (Mrnak et al. 2018) and Percidae patch dynamics (Mrnak et al. 2021), walleye often aggregate which may make them more vulnerable to harvest (yield), even at low densities (production values; Ellis and Giles 1965; Mrnak et al. 2018). For example, tribal harvest corresponds with peak walleye spawning aggregations regardless of seasonal lake progression. Depending on ice-off date, walleye may also be vulnerable to recreational angling, which opens on the first Saturday of May. Indeed, this spawning behavior allows for fishers to seek out lakes that provide acceptable harvest rates and avoid lakes where harvest rates are unacceptable, thus alleviating an ecological pressure from that fishery (i.e., fisher harvest). However, this behavior may ultimately homogenize the CTWI fishery landscape and result in systems being driven toward the point of invisible collapse (i.e., by the time yield rates respond to reduced production, fishery may be too far gone for recovery; Post et al. 2002; Ward et al. 2013; Mrnak et al. 2018; Feiner et al. 2020; Golden et al. 2022). The vast number of CTWI walleye lakes likely buffers against an invisible collapse by providing ample local opportunities compared to Alberta Lakes (Post et al. 2002). Importantly, this buffering mechanism would only occur if fishers self-regulate and thus respond to changes in their yield rates (Ward et al. 2013; Mrnak et al. 2018).

Hyperstability creates challenges for fisheries management if exploitation rates are not constrained to sustainable levels (Fulton et al. 2011; Ward et al. 2013). Based on our findings, hyperstability in catch and harvest rates across abundance gradients, and yield across a production gradient, appear common for many Wisconsin fisheries (Hansen et al. 2005; Mrnak et al. 2018; Dassow et al. 2020; Feiner et al. 2020; Mosley et al. 2022). Moreover, hyperstable relationships may mask the probability of overfishing (production overharvest) and limit the ability of management intervention to prevent or slow overexploitation when fish population status is evaluated solely on fisheries-dependent data (Carpenter et al. 1994; Fulton et al. 2011; Johnston et al. 2013; Feiner et al. 2020). Observed hyperstability in fisher harvest rates are indicative of consistent exploitation and directed walleye effort across a range of walleye population productivities, despite ample fishing opportunities. Therefore, the hyperstable relationships we identified suggest that fisher behavior may not respond to common management interventions in open access recreational and quota-based subsistence fisheries that do not significantly affect fisher yield rates. Though research indicates that Wisconsin fishers may respond to bag limit changes (i.e., Beard et al. 2003; Rypel et al. 2015), fishers will likely not self-regulate harvest until production significantly declines (if at all), drastically reducing management options for fishery conservation (Allen et al. 2013; Maggs et al. 2016; Feiner et al. 2020). Our results highlight the importance of quantifying relationships between fisher harvest dynamics and walleye production for effective sustainable fisheries management (Beardmore et al. 2011; Post 2013; Mrnak et al. 2018; Feiner et al. 2020; Golden et al. 2022). A better understanding of walleye harvest dynamics is critically needed given that the safe operating space (i.e., Carpenter et al. 2017) of walleye may be compromised by interacting ecological changes resulting in sustained long-term recruitment declines (Hansen et al. 2015*a*, 2015*b*) and continual exploitation (Embke et al. 2020). Based on our findings and using the safe operating space concept, exploitation could be adjusted based on population productivity to offset current challenges faced by walleye that are out of managerial control.

Management implications

Lakes in the CTWI solely supported by NR appear to be the most resilient fish populations and the least vulnerable to harvest. Indeed, walleye lakes with $Y/P < 1$ and $P/B > 0.19$ currently represent sustainable fisheries and are dominated by NR systems (58%; Fig. 7). Yet, all fisheries with $Y/P < 1$ are by definition sustainable. Therefore, walleye lakes with $Y/P < 1$ and $P/B < 0.19$ do represent successful sustainable fisheries, but with a lower potential to absorb increases in harvest. Given that the "low vulnerability to harvest" space is dominated by NR populations, it appears that the current walleye co-management system is almost entirely reliant on consistent NR (Fig. 7). When NR is inconsistent, which has been the case in the CTWI for the last several decades (Krabbenhoft et al. 2023), the current management system has been relatively inflexible to changes in walleye productivity and exploitation. That said, stocking of walleye fingerlings has been used to rehabilitate NR and to increase abundance (albeit with limited success) and in turn, recreational harvest regulations have been adjusted to reduce exploitation and protect longer and older female walleye. Our results showed that the co-management system for CTWI walleye may be improved by adjusting exploitation based on walleye population productivity, which is currently being experimentally tested on Escanaba Lake, Vilas County, WI with an annual harvest quota and compulsory creel census of all anglers and tribal members (see Sass et al. (2022*c*)). Importantly, the infrastructure at the Northern Highland Fishery Research Area (of which Escanaba Lake is a part) allows for this to be easily performed. At the CTWI-level, a compulsory creel survey (paired with annual population estimation) would be challenging and may require substantial changes to the current management framework. Rypel et al. (2018) and Raabe et al. (2020) noted that more lakes are transitioning from NR to C or ST over time. Therefore, NR lakes with $Y/P < 1$ and $P/B > 0.19$ may require the most conservative fisher harvest regulations and greatest monitoring focus to ensure sustainable management where production overharvest remains low and biomass turnover remains high. Alternatively, lakes with $Y/P > 1$ and $P/B < 0.19$ represent the most vulnerable fisheries and pose interesting management questions; should management reduce effort and direct it toward more resilient fisheries or pilot highly conservative (potentially controversial) fisher regulations in an attempt to limit yield and (or) increase P/B?

Northern Wisconsin walleye production is in decline and fisher yield (harvest) is not adjusting to this decline. This means that exploitation has remained consistent over time despite declining walleye productivity (i.e., fishers are harvesting the same size slice (yield) out of an ever-shrinking pie (productivity)). Our results suggest that exploitation may need to decline in the CTWI walleye fishery through compromise among tribal fishers, recreational anglers, and managing agencies to maintain or increase the adaptive capacity of CTWI walleye (i.e., the ability of species to cope with or adjust to ecological change; Thurman et al. 2020). We also highlight that the open-access nature of the recreational angling fishery may be evaluated as a more extreme conservation measure if needed. A limitation or reduction in angler effort could potentially reduce total exploitation, but due to hyperstable relationships, the reduction in effort likely needs to be substantial. Similar to Embke et al. (2019), practitioners may consider a transition away from traditional population estimate-based management regimes (e.g., Hansen et al. 1991; Beard et al. 1997; Cichosz 2022*a*) to one based on holistic ecological principles, fisher dynamics, and empirical data known to be influenced by ecological change. This framework could use walleye production, biomass, and yield estimates to limit annual walleye yield relative to the production capacity of the walleye population (i.e., restrict $Y/P < 1$; Embke et al. 2019). Indeed, production, biomass, and yield are more sensitive to a walleye's ecological environment than simple population estimate-based approaches (Waters 1977; Downing 1984; Kwak and Waters 1997) and may therefore capture critical ecological processes, habitats, and species interaction shifts influencing CTWI walleye. Our productivity approach that acknowledges the socio-ecological system of walleye fisheries and includes fisheries dependent and independent data may represent a more holistic pathway to sustainable fisheries management (Sass et al. 2017; Mrnak et al. 2023; Radinger et al. 2023).

Acknowledgements

We thank the numerous Wisconsin Department of Natural Resources and Great Lakes Indian Fish and Wildlife Commission personnel for the collection and contribution of data used in this research. We specifically thank TA Cichosz for providing the data used in our study. Funding for JTM, MVW, SLS, and GGS was provided by the U.S. Fish and Wildlife Service, Federal Aid in Sportfish Restoration Program and the Wisconsin Department of Natural Resources. Additional funding for JTM was provided by the Tug Juday Memorial Fund, a Juday/Lane Fellowship, the Anna Grant Birge Memorial Fund, and the NSF North Temperate Lakes Long-term Ecological Research Program (grants DEB-0217533 and DEB-1440297). We thank SR Chipps for conducting an internal review of this manuscript for U.S. Geological Survey as well as LW Sikora for constructive feedback. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

Article information

History dates

Received: 15 December 2023
Accepted: 24 July 2024
Accepted manuscript online: 1 August 2024
Version of record online: 8 November 2024

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Data availability

Data available upon request.

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Competing interests

The authors declare there are no competing interests.

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