



# Production dynamics reveal hidden overharvest of inland recreational fisheries

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Recreational fisheries are valued at \$190B globally and constitute the predominant way in which people use wild fish stocks in developed countries, with inland systems contributing the main fraction of recreational fisheries. Although inland recreational fisheries are thought to be highly resilient and self-regulating, the rapid pace of environmental change is increasing the vulnerability of these fisheries to overharvest and collapse. Here we directly evaluate angler harvest relative to the biomass production of individual stocks for a major inland recreational fishery. Using an extensive 28-y dataset of the walleye (*Sander vitreus*) fisheries in northern Wisconsin, United States, we compare empirical biomass harvest (Y) and calculated production (P) and biomass (B) for 390 lake year combinations. Production overharvest occurs when harvest exceeds production in that year. Biomass and biomass turnover (P/B) declined by ~30 and ~20%, respectively, over time, while biomass harvest did not change, causing overharvest to increase. Our analysis revealed that ~40% of populations were production-overharvested, a rate >10× higher than estimates based on population thresholds often used by fisheries managers. Our study highlights the need to adapt harvest to changes in production due to environmental change.

recreational fisheries | freshwaters | production

Recreational fisheries are valued at \$190B globally with nearly 1 billion people participating annually (1), constituting the predominant use of wild fish stocks in developed nations (2, 3). Recreational fisheries offer multiple benefits to diverse user groups (4), while also providing an important connection with nature in an era when people are more urbanized than ever (5, 6). Inland waters are hot spots for recreational fisheries; they are a significant component of these fisheries, despite making up only 0.01% of Earth's total water volume (1, 7, 8).

Inland recreational fisheries are thought to be highly resilient and self-regulating (9), but the rapid pace of environmental change is increasing their vulnerability to overharvest and collapse (10–14). Habitat loss due to climate change and lakeshore residential development in combination with other anthropogenic drivers (e.g., pollution and invasive species introductions) diminish the potential for freshwater ecosystems to support fisheries (14–17). Nonetheless, fishing effort is often constant across a range of fish densities while the contribution to fishing effort from highly skilled anglers may actually increase, thereby increasing total harvest (18, 19). Given these trends, there is an urgent need to understand current and emerging threats to inland recreational fisheries, including the potential for excess harvest (11).

Here we focus on the inland fisheries for walleye (*Sander vitreus*) in northern Wisconsin, United States. Walleye are the most sought-after game fish in north-central North America (20) and support a robust recreational angler and tribal spearing fishery (21). Like many inland fisheries, the Wisconsin fishery is composed of multiple discrete stocks associated with individual lake or river ecosystems. Over the past 2 decades, many walleye stocks have declined, on average by ~36% (Fig. 1B); however, the

cause remains unclear (22–24). Conventional wisdom has been that overharvest is not contributing to walleye declines (25). In the current management regime, a stock is considered overharvested if >35% of the adult population is removed. Using this criterion, a small fraction (<3%) of stocks were overharvested over the past 3 decades (25, 26). There is growing awareness that lakes differ widely in terms of productivity, and stocks may respond heterogeneously to harvest and other anthropogenic influences (24, 27). This heterogeneity highlights the need for a more biologically grounded framework for assessing stock productivity and overharvest.

We extend previous research on production dynamics of inland walleye stocks (24, 28) by directly comparing estimated rates of biomass production and biomass harvest for individual walleye stocks to quantify overharvest. Using a unique and expansive 28-y standardized dataset of a valuable inland fishery, walleye in northern Wisconsin, United States, we compare empirical annual biomass harvest (Y), empirically estimated standing stock biomass (B), production (P; the annual rate of accumulation of new biomass), and biomass turnover rate (P/B) for 390 lake year combinations. We examined the threshold at which annual biomass harvest (Y) exceeded annual production (P) (production overharvest;  $Y/P > 1$ ) such that the stock exhibits depletion, referred to as the ecotrophic coefficient (29–31). We found ~40% of walleye

## Significance

Despite the great economic and cultural importance of inland recreational fisheries, overharvest of inland fish stocks is rarely studied. We compared biomass harvest and biomass production in a unique 28-y, 179-lake dataset of a valuable inland fishery and found ~40% of stocks to be overharvested, a rate >10× higher than population thresholds used to manage these fisheries. This is an empirical example of recreational fisheries overharvest in a declining fishery revealed through a biomass production approach. The high level of production overharvest we found highlights the value of ecosystem approaches to inform recreational fisheries management in an era of rapid environmental change.

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The authors declare no competing interest.

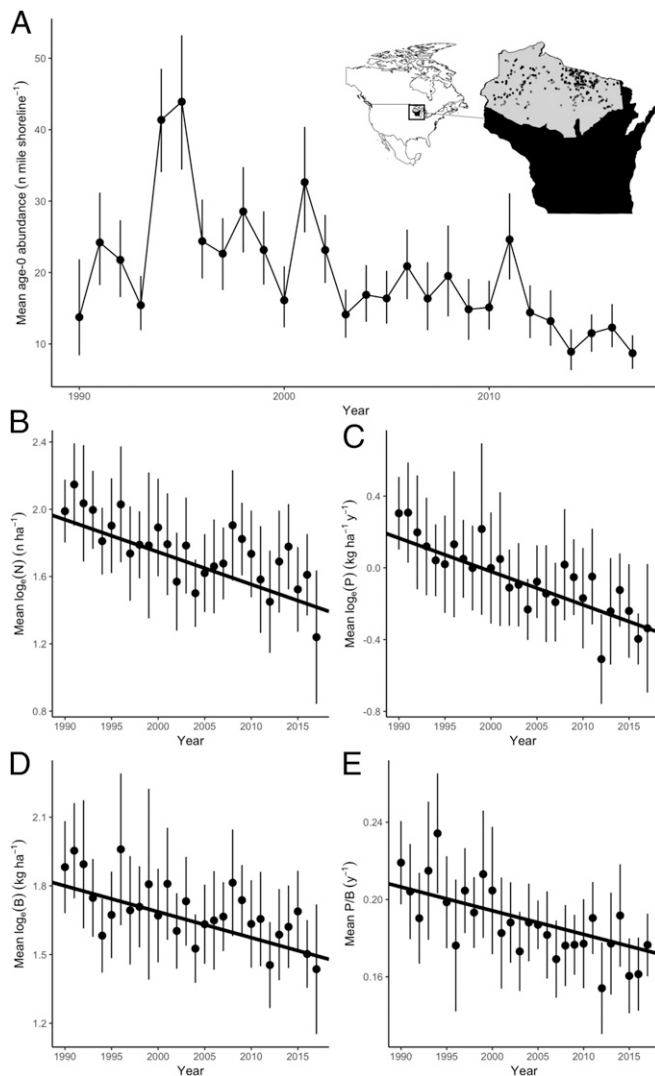
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Data Deposition: All code detailing production and biomass calculations have been deposited on GitHub (<https://github.com/hembke/Production-and-Biomass-Calculation>). All data have been deposited in the Environmental Data Initiative repository (<https://doi.org/10.6073/pasta/611479e438500a56d5085020d3aa16cd>).

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**Fig. 1.** Inset map identifies the location of lake year combinations as black dots used in this analysis in northern Wisconsin, United States, during 1990 to 2017 ( $n = 566$ ). (A–E) Mean  $\pm$  95% confidence intervals for annual walleye (*S. vitreus*) age-0 abundance (number of age-0 individuals per mile shoreline),  $\log_e$ (adult density; N) ( $n \text{ ha}^{-1}$ ),  $\log_e$ (adult production; P) ( $\text{kg ha}^{-1} \text{ y}^{-1}$ ),  $\log_e$ (adult biomass; B) ( $\text{kg ha}^{-1}$ ), and adult biomass turnover rate (P/B) ( $\text{y}^{-1}$ ). Trend lines in B–E correspond to linear mixed effects models.

populations to be production-overharvested, a rate  $>10\times$  higher than current population-based estimates. We suggest that production could be measured along with harvest as a tool to assess the status of walleye populations of this region as well as for other inland fisheries (24, 28). Our study highlights the need for new approaches for managing and adapting harvest to changes in production in the face of global change (6).

## Results

Age-0 relative abundance as well as adult density (N), P, B, and P/B have significantly declined over the past 28 y (Fig. 1 A–E) in northern Wisconsin walleye populations. Adult ( $\geq 5$  y old,  $>381$  mm) walleye (Fig. 1 B–E) have experienced reductions of  $-36$ ,  $-35$ ,  $-30$ , and  $-19\%$ , respectively (all  $P < 0.001$ ) (24). Water clarity (i.e., Secchi disk transparency), annual growing degree days, and conductivity explained very little of the variance among walleye populations (SI Appendix, Table S1). Declining trends were significant for all metrics (i.e., N, P, B, and P/B) and provided

models of best fit (SI Appendix, Table S1). For example, in 1990, mean P/B was  $0.221 \text{ y}^{-1}$  (biomass replacement time of  $\sim 4.52 \text{ y}$ ) but declined to  $0.174 \text{ y}^{-1}$  (biomass replacement time of  $\sim 5.74 \text{ y}$ ) by 2017. Thus, it takes more than an additional year for an average walleye population to replace its biomass now versus in 1990. Despite P, B, and P/B declines, annual biomass harvest (Y) has not changed significantly over this period (Fig. 2A). Angler harvest has been consistently higher than tribal harvest (Fig. 2A) (32). Over time, tribal harvest has remained relatively constant (Fig. 2A) (32). Relatively constant harvest coupled with declining production could lead to biomass harvest relative to production (Y/P) increasing over time. Overall, our Y/P metric indicated production overharvest in  $\sim 40\%$  of lake year combinations, representing an incidence of production overharvest  $>10$  times higher than current estimates of numerical overharvest (Fig. 2B). Sustained Y/P above 1.0 may deplete biomass in populations where stocking is not able to replace excess biomass harvested (29, 31). When using a more protective Y/P threshold of 0.75, the majority (52%) of populations would be classified as overharvested. The increasing trend in Y/P, although not statistically significant, is not being driven by increased biomass harvest. The combination of dwindling stock biomass (B) and decreasing biomass turnover rates (P/B) has caused similar harvest rates to remove larger proportions of available biomass.

We present modified Kobe plots, a tool commonly used in marine stock assessments (33, 34), to visualize changes in the incidence of production overharvest over time. Traditional Kobe plots track a single population or series of different species through time (34), but we modified this approach as we analyzed all walleye populations as a single fishery and therefore focus on regional temporal trends. When divided into 3 time periods of 9 to 10 y, median Y/P rose from 0.71 to 0.87 over the study period, with most of the change between the first and second decadal periods (Fig. 3). In 9 of 28 study years, biomass harvested exceeded production (i.e.,  $Y/P > 1.0$ ) in more than half of populations (Fig. 2B). Median Y/P exceeded 0.75 in 18 of 28 study years, indicating sustained high levels of production harvest in this fishery.

We quantified the incidence of overharvest in select individual populations with  $>5$  y of data ( $n = 11$ ) (SI Appendix, Figs. S1 and S2). Of these 11 stocks, 2 stocks had median levels of Y/P that exceeded 1.0 and experienced a decline in biomass, while another 4 stocks had median levels of  $Y/P > 1$  (SI Appendix, Fig. S1). Thus, the broad scale pattern of overharvest can also be observed for individual lakes where data are available.

## Discussion

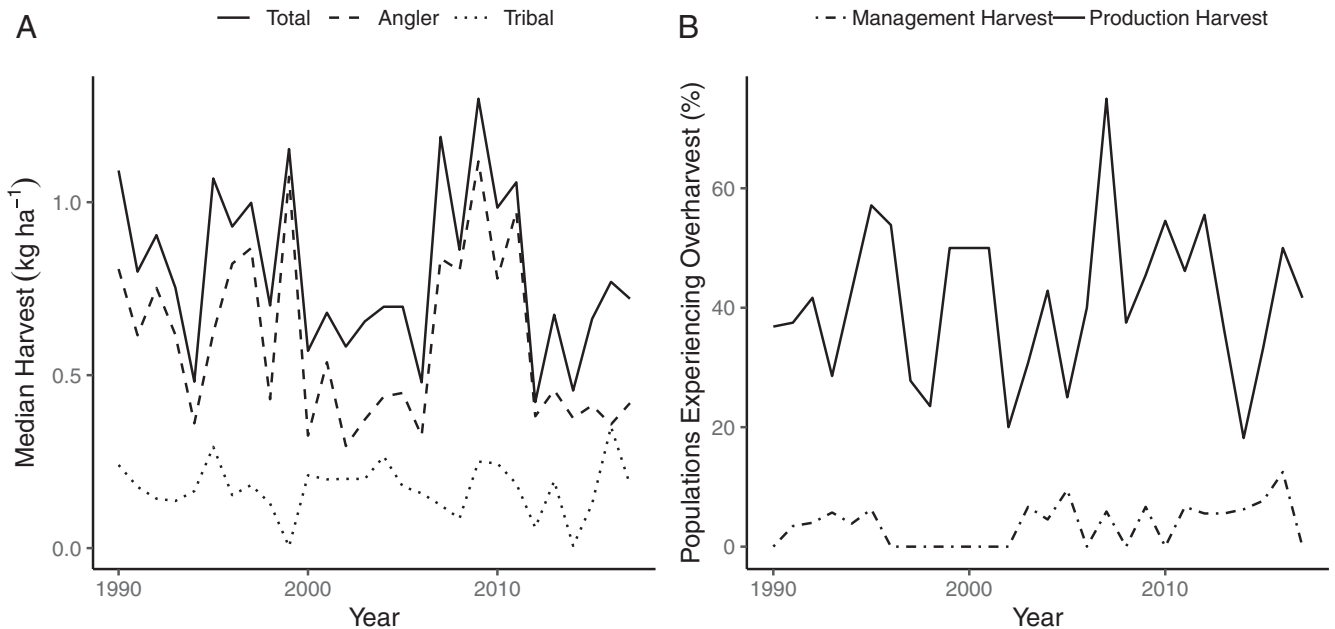
We found high rates of production overharvest when we compared harvest and production in an inland walleye fishery. Specifically, biomass harvest exceeded biomass production  $\sim 40\%$  of the time among our 390 walleye harvest and production estimates over a 28-y period, an overharvest rate  $>10\times$  higher than estimates based on population harvest. While we found that overharvest has been frequent throughout this period, several observations were particularly revealing. First, walleye numerical abundance, biomass, and production all exhibited declines over this period, reflecting previously described regional walleye population declines (24, 35). Meanwhile, walleye biomass harvest has remained constant. Constant harvest on a diminishing resource has led to frequent production overharvest through time due to removal of an ever-increasing proportion of available biomass. Finally, walleye biomass turnover rates (P/B) have also shown marked declines. Not only are walleye populations declining, but the rate at which walleye biomass is being replaced has also declined over the study period. On average, it now takes more than 1 y longer for the existing walleye biomass pool to fully replace itself. This decline in biomass turnover (P/B) is especially concerning as it is reflective of natural recruitment declines and thus the loss of productive capacity of this fishery.

Our analysis revealed high rates of walleye production overharvest, a pattern undetected in the fisheries management framework used over the past 30 y. In the current management framework, the management goal aims to ensure that no more than 35% of the total adult walleye population is harvested more than 1 time in 40 (25, 36). Because this 35% numerical limit reference point is rarely exceeded [ $\sim 3\%$  exceedance over 28 y (25, 26)] and average exploitation rates during the study period were  $\sim 15\%$  (32), the widely held view is that stock overharvest is minimal (25, 32). The fact that these 2 approaches generate such strongly contrasting conclusions regarding the extent of overharvest in this declining fishery warrants a more careful comparison of approaches and interpretation of existing data and analyses. It is important to recognize that population and biomass-based approaches have limitations; thus, we recommend using both in concert to manage this fishery. First, by only considering fish abundance and despite safety factors to account for numerical uncertainty, the current management approach does not account for the contributions of fish of different ages and sizes to future production. In contrast, assessing walleye populations in terms of biomass and production accounts for the relative contribution of individual age classes to growth. Second, a 35% numerical limit reference point to all populations does not recognize that stocks differ inherently in their productivity and capacity to withstand harvest (24, 37). Recent inclusion of lake-specific mixed effects models for setting safe harvest levels has attempted to address this shortcoming. P/B values were highly variable among stocks, ranging from  $\sim 0.02$  to 0.46. P/B is closely correlated with natural mortality rates and therefore approximates the proportion of stock biomass that can be harvested without depleting the population (38). Thus, depending on the stock, anywhere from 2 to 46% of walleye biomass can be sustainably harvested. The fact that P/B varies so widely highlights the difficulty of applying a single exploitation limit for all stocks. Finally, our results indicate that a 35% reference point for population harvest is not protective of many stocks (despite average exploitation rates of  $\sim 15\%$ ). While population and biomass limits are not interchangeable, annual removal of 35% of either the adult population or standing biomass

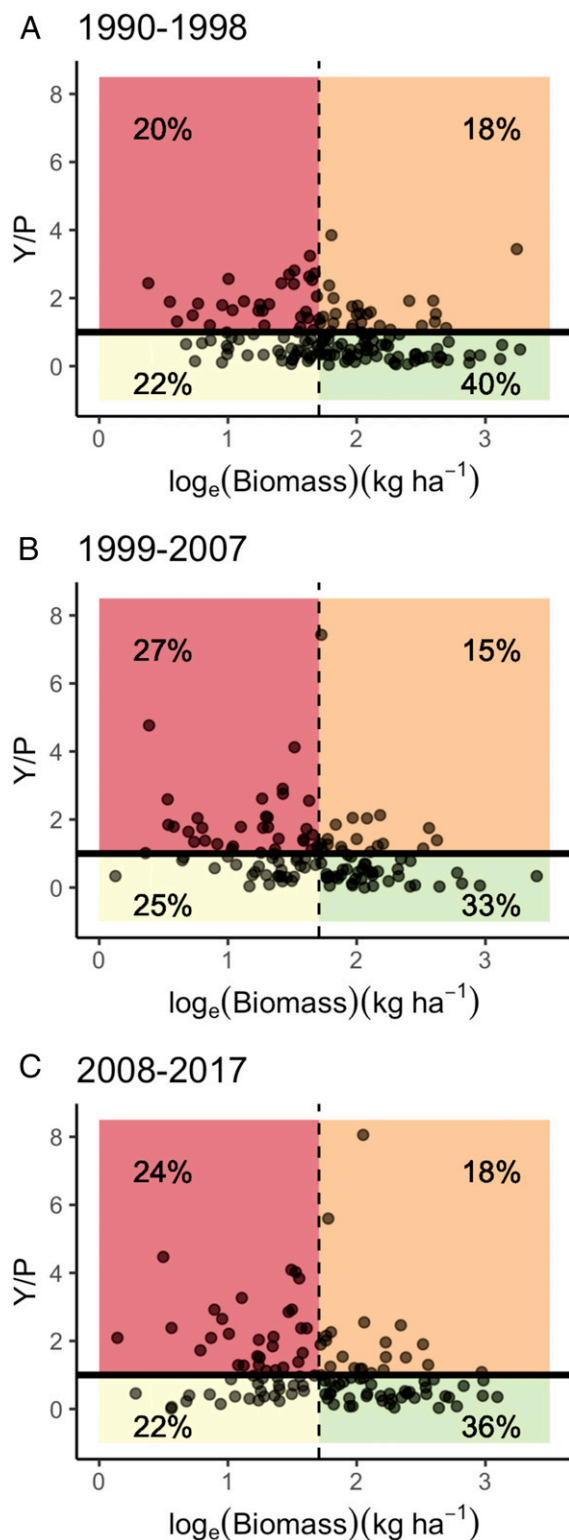
would likely deplete any walleye stock. We found that only a very small fraction of stocks had P/B values exceeding 0.35 or 0.15 ( $\sim 3$  and 71%, respectively) and could thus sustain these levels of production exploitation.

In light of the limitations of the current and biomass-based management regimes described above, our analysis provides an expanded management framework based on broader ecosystem principles and informed by empirical data collected by fishery biologists. In this framework, production, biomass, and P/B would be estimated, and management would aim to limit annual harvest so as to not exceed the estimated productive capacity of the stock. Ideally, such an approach would use a target  $Y/P < 1.0$  (say 0.8) to be protective of walleye stocks in light of estimation error and biological variability. While the vast majority of Wisconsin's  $\sim 900$  walleye stocks are not assessed in a given year, the broad findings of our study provide vital information on walleye populations and productivity that are useful for management. Key features of such a fisheries management regime are reliance on biomass in addition to abundance and that harvest limits are biologically grounded to better reflect heterogeneity in stock productivity. Under such a management regime, harvest limits would likely be lower for most walleye stocks but may increase for others (37). Balancing population and production parameters may improve overall stock management, not only in cases where harvest might be reduced but also in cases where a certain level of production overharvest may be desirable to reduce density and increase growth of individual fish to better achieve management objectives (39). Given that walleye stocks have undergone widespread declines (22–24) and that our assessment reveals that walleye stocks have been production-overharvested, we find that overharvest has contributed in part to the observed walleye declines. A production analysis using the same data adds new dimensions to existing management approaches to protect this valuable fishery.

Dwindling turnover rates (P/B) indicate an alarming trend in the productivity of these walleye populations. Due to slower biomass growth, it now takes an additional year for a given biomass to replace itself due to reduced production. There are multiple



**Fig. 2.** Panels correspond to walleye (*S. vitreus*) populations in Northern Wisconsin, United States, during 1990 to 2017 with harvest data ( $n = 390$ ). (A) Median biomass harvest ( $Y$ ) ( $\text{kg ha}^{-1}$ ) according to harvest type. (B) The percentage of populations considered overharvested annually according to production computations (solid line) as well as management agency harvest computations of walleye exploitation rates exceeding 35% of the adult population in a given lake year (dot-dashed line).



**Fig. 3.** Modified Kobe plots for 3 time periods (9- to 10-y intervals) of walleye (*S. vitreus*) Y/P (% production) relative to  $\log_e$ -transformed biomass ( $\text{kg ha}^{-1}$ ) for each population with harvest data ( $n = 390$ ) for northern Wisconsin, United States, populations during 1990 to 2017. *A* shows populations from 1990 to 1998, *B* shows populations from 1999 to 2007, and *C* illustrates populations from 2008 to 2017. Each point represents 1 lake year combination. Production (P) was measured immediately following spring ice-out, and harvest (Y) was measured for the year following the P estimation. The horizontal solid line establishes the 1.0 harvest threshold, at which 100% of biomass produced is harvested. The vertical dashed line shows the overall

potential reasons for the declining turnover rates (P/B) observed in this fishery resulting from declining natural recruitment (Fig. 14), including reduced habitat because of lakeshore development or climate change (23), invasive species introductions (40), and biotic interactions with increasing warm-water species (22), as well as harvest. In contrast to many documented cases of overfishing found to be due to rising harvest levels, the overharvest we found was due to a combination of declining populations (i.e., declining N, P, and B) and declining turnover (P/B, reflective of true declines in productivity) combined with unchanging harvest trends. Constant harvest as a proportion of a population does not necessarily result in sustainable exploitation, especially if underlying size structure, growth, and recruitment dynamics are shifting. We found that constant harvest of declining stocks led to production overharvest. Given the prolonged production overharvest we identified, harvest is part of a complex of factors that decrease the biomass available for removal. In the face of global environmental changes that impact freshwater ecosystems (41), it is imperative to understand trends in productivity such that conservation and management actions can be implemented swiftly if needed (42, 43).

Our findings have broad implications for recreational fisheries and natural resource management. Large-scale trends in climate or other factors may gradually undermine productivity in uncertain ways beyond the control of local managers. Carpenter et al. (27) developed a safe operating space (SOS) framework that described how manageable and external factors interacted to affect the sustainability of a fishery. When viewed through this paradigm, our findings indicate an empirical example of constant harvest coupled with reduced productivity driven by changes in other factors such as habitat, climate, and biotic interactions (27, 44, 45) pushing a fishery outside of the bounds of the SOS. Local managers must compensate for unmanageable variables by adjusting the factors that directly influence growth and biomass of managed stocks, such as harvest and stocking in the case of walleye (28, 46, 47). Our production-based empirical approach, the SOS framework, and the existing numerical management system could be used to develop more robust management approaches capable of identifying management thresholds in the face of interacting population drivers.

The pattern of production overharvest we found is rarely assessed and may be widespread, particularly for harvest-oriented inland recreational fisheries. Early work by Post et al. (11) suggested that hidden collapse of recreational fisheries may be widespread. Over time, the weight of scientific evidence has supported this perspective (14, 48, 49). Management systems will need to adopt conservation measures to address the call for better governance of recreational fisheries (6, 50). There are many instances where fisheries are declining or have already collapsed, yet management systems may be relying on misleading metrics to evaluate fisheries currently considered sustainable due to hyperstability in catch rates, among other factors (18, 19, 51–53). Production-based metrics provide a system-specific measure of the productive capacity of a population to inform its harvest potential, adding to numerical assessment approaches. For many high-profile recreational fisheries, especially in developed countries, the data necessary to calculate these metrics are already being collected and should be leveraged to their full potential. Furthermore, in fisheries without the necessary data, production can be estimated from biomass using production–biomass relationships (28, 54) and potentially

median biomass level for the region over the entire time period. Points in the red indicate populations where production overharvest is occurring and biomass is low; points in the orange indicate populations where production overharvest is occurring but biomass is high. Points in the green indicate populations where production overharvest does not exceed 1.0 and biomass is high. Points in the yellow indicate populations where production overharvest does not exceed 1.0 but biomass is low. The percentage of populations in each quadrant is shown for each time period.

metabolic theory (55). Although data may never be available for all ecosystems, the merits of production raise a global question as to how to best assess data-poor fisheries and underscore the need to develop a more thorough understanding of surrogates for inland fish production in relation to harvest. Incorporating production with other methods, such as Bayesian hierarchical models, could provide an opportunity to apply knowledge from well-studied populations to data-poor scenarios. Such insights would identify the limits to harvest and help inform strategies for strengthening the management of recreational fisheries.

There is growing recognition of the globally important role of inland recreational fisheries (6). Not only do these fisheries contribute significantly to overall fisheries harvest, but they are a disproportionate economic contributor, while also providing multiple important ecosystem services and improving human well-being (6). Unfortunately, inland waters are subject to accelerating and often interacting anthropogenic impacts (15, 56), all of which can adversely affect fisheries (14, 17). Our study adds to this understanding by revealing widespread and persistent stock overharvest in a valuable and declining recreational walleye fishery using production dynamics. While the walleye decline cannot be fully attributed to fishing pressure, we conclude that the lack of management adaptation to productivity shifts has likely intensified the declines. When viewed in relation to biomass harvested, these metrics offer an assessment of freshwater fish population status founded in biomass flow dynamics that establishes system-specific harvest thresholds based on local productivity. While overharvest almost certainly interacts with other drivers in this regional fishery decline, our results highlight the urgent need for improved governance, assessment, and regulation of recreational fisheries in the face of rapid environmental change (6).

## Methods Summary

**Walleye Data Collection.** Walleye in Wisconsin have been jointly managed by the Wisconsin Department of Natural Resources (WDNR) and the Great Lakes Indian Fish and Wildlife Commission since reinstatement of tribal spearing rights in 1985 (36). This management strategy has involved an annual rotating stratified randomized sampling design to assess walleye populations in lakes in the Ceded Territory (approximately the northern third of Wisconsin; refs. 36 and 57). Over the last ~28 y, population-specific data have been collected for ~900 walleye lakes, including demographic information (i.e., length, weight, sex, and age), growth, size structure, and adult population estimates. Additionally, to obtain an index of walleye recruitment, age-0 walleye were collected from surveys conducted on all lakes where a population estimate was performed. Further information on these surveys can be found in *SI Appendix*. In addition, angler and tribal harvest data are available, including the actual or estimated number of fish harvested as well as a large subset of length measurements of harvested fish.

**Production Calculations.** We calculated production using the instantaneous growth method, an application of a standard model of secondary production for age-structured populations (29, 31, 58, 59). This method measures the production of new biomass from somatic growth and how that production is affected by recruitment and mortality. This metric is distinct from surplus production which specifically accounts for biomass gains from recruitment and losses from mortality in addition to the gains from somatic growth. We show in the supporting information that somatic growth production (i.e., the production estimated in this study) is a suitable and more readily measured proxy for surplus production for walleye in this region (*SI Appendix*, Figs. S5 and S6).

Production was calculated for each lake and year combination with available data ( $n = 566$ ) by applying the instantaneous growth method to fish from all age classes from age 5 to  $a_{max}$  (maximum age) (28, 29, 31, 58):

$$P_y = \sum_{a=5}^{a_{max}} G_{a,y} \bar{B}_{a,y}, \quad [1]$$

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

cohort during the year, also estimated by substituting age classes for time). A detailed description and example calculation of these estimates can be found in *SI Appendix*, Fig. S3 and Tables S3 and S4. For all analyses, we did not include individuals <5 y old, as immature walleye of these sizes are not reliably vulnerable to capture by fyke nets (36).

**Biomass Harvest Calculations.** To calculate loss of biomass due to fishing imposed on northern Wisconsin walleye populations, we estimated age-specific harvest (harvested biomass) for each fishery in each lake year with available data ( $n = 390$ ). For tribal harvest, the total number of fish harvested is known, but for angling harvest, the total number of fish harvested is projected by WDNR based on creel data. WDNR designates adult fish as all fish  $\geq 381$  mm and all sexable fish <381 mm; therefore, we removed individuals <381 mm to maintain comparability between harvest and production estimates. These angler harvest estimates likely underestimate the number of adult fish harvested as they do not include sexable individuals <381 mm.

For both harvest types, a subsample of individual lengths of harvested fish was collected. To estimate angler harvest, for unmeasured fish in a lake year, 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. If the lake year combination had no lengths available (number of lake years = 2), we extrapolated length data from the nearest year from the same lake. According to management regulations for the tribal fishery, all harvested fish 508 mm or larger must be measured; therefore, measured fish represent large individuals, and unmeasured individuals are known to be <508 mm. Thus, to estimate tribal harvest, we randomly assigned lengths to unmeasured fish between 381 mm and 483 mm as this corresponds to the most likely adult size range for these individuals. 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 production 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 ( $W_{h,a}$ ; kg), which we used to calculate age-specific tribal and angler biomass harvest ( $Y_{t,a}$  and  $Y_{f,a}$ ; kg):

$$Y_{t,a} \text{ or } Y_{f,a} = H_a * W_{h,a}. \quad [2]$$

Total annual biomass harvest ( $Y_y$ ;  $\text{kg ha}^{-1}$ ) 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 ( $\text{kg ha}^{-1}$ ). We evaluated harvest as biomass harvested relative to production as this represents the ecotrophic coefficient, i.e.,  $Y/P$  (29, 31).

**Statistical Analyses.** We ran Shapiro–Wilk tests to determine whether distributions for  $P$ ,  $B$ ,  $P/B$ ,  $Y$ , and  $Y/P$  were normal. Based on findings,  $P$ ,  $B$ ,  $Y$ , and  $Y/P$  were  $\log_e$ -transformed prior to analysis to meet assumptions of normality. We developed mixed-effect regression models to test for temporal trends in  $P$ ,  $B$ , and  $P/B$ . For each model, the estimated metric [i.e.,  $\log_e(N)$ ,  $\log_e(P)$ ,  $\log_e(B)$ , and  $P/B$ ] was the dependent variable, year (centered around the mean) was an independent variable, and lake was a random effect. The additional covariates of conductivity, water clarity (i.e., Secchi disk transparency), and annual growing degree days (base temperature of 0 °C) were further assessed (*SI Appendix*, Table S1). Models of best fit were first selected based on Akaike information criterion (AIC). If there was no difference between AIC values, model of best fit was selected based on variance explained. For each model, we calculated percent change over time based on model predictions in 1990 and 2017. Temporal yield and  $Y/P$  trends were also assessed but were not significant. We used an  $\alpha = 0.05$  for all statistical analyses. All calculations and statistical analyses were performed in R version 3.4.3 (60). All code detailing production and biomass calculations is open source and freely available on GitHub (<https://github.com/hembke/Production-and-Biomass-Calculation>). All data have been deposited in the publically-available Environmental Data Initiative repository and can be accessed at <https://doi.org/10.6073/pasta/611479e438500a56d508502d3aa16cd>.

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