

Production rates of walleye and their relationship to exploitation in Escanaba Lake, Wisconsin, 1965–2009

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

Abstract: Understanding variability in fish production, biomass, production/biomass (P/B) ratios, and their relationship to exploitation is central to fisheries sustainability. At Escanaba Lake, Wisconsin, USA, data from a compulsory creel census (1965–2009) were combined with survey data on fish populations to test for empirical relationships between annual production and exploitation rates of walleye (*Sander vitreus*). Empirical estimates of walleye production were relatively high and temporally variable in Escanaba Lake. Annual production, biomass, and P/B ratios ranges were 2.4–11.3 kg·ha⁻¹·year⁻¹, 9.1–49.4 kg·ha⁻¹, and 0.15–0.30 year⁻¹, respectively. Walleye production rates were significantly and positively correlated with adult (i.e., age 3+) walleye density — the core metric used to manage walleye populations in the Ceded Territory of Wisconsin. However, adult walleye density correlated best with ages 4–6 production. Annual exploitation based on the percentage of individuals removed from the population was linearly related to annual exploitation based on the percentage of production removed. On average, 100% of annual production was harvested at ~20% annual exploitation of individuals; thus, higher sustained exploitation rates would deplete walleye biomass in Escanaba Lake over time. A sustainable annual exploitation rate of 20% annually is lower than the 35% limit reference point currently used for walleye management in the Ceded Territory of Wisconsin. Nevertheless, our estimate is strongly concordant with two recent and independent modeling efforts addressing this same topic. We suggest empirical estimates of fish production are a vastly underutilized tool for better understanding sustainable exploitation rates in walleye populations and, likely, fisheries in general.

Résumé : La compréhension des variations de la production, de la biomasse et des rapports production/biomasse (P/B) ainsi que de leur lien avec l'exploitation est essentielle à la durabilité des pêches. Au lac Escanaba, au Wisconsin (États-Unis), des données d'un relevé des prises obligatoire (1965–2009) ont été combinées à des données d'évaluation des populations de poissons afin d'établir s'il y a un lien empirique entre la production annuelle et les taux d'exploitation du doré jaune (*Sander vitreus*). Les estimations empiriques de la production de dorés jaunes étaient relativement élevées et variables dans le temps au lac Escanaba. La production annuelle, la biomasse et les rapports P/B étaient de 2,4–11,3 kg·ha⁻¹·an⁻¹, 9,1–49,4 kg·ha⁻¹ et 0,15–0,30 an⁻¹, respectivement. Les taux de production de dorés jaunes présentaient une corrélation significative positive avec la densité de dorés jaunes adultes (c.-à-d. 3 ans et plus), le principal paramètre utilisé dans la gestion des populations de dorés jaunes dans le Territoire cédé du Wisconsin. Toutefois, la densité des dorés adultes présentait la meilleure corrélation avec la production d'individus âgés de 4 à 6 ans. L'exploitation annuelle basée sur le pourcentage d'individus extraits de la population était linéairement reliée à l'exploitation annuelle basée sur le pourcentage de production extraite. En moyenne, 100 % de la production annuelle était prise à un taux d'exploitation annuelle des individus de ~20 %, de sorte que des taux d'exploitation soutenus plus élevés se traduiraient par une réduction de la biomasse de dorés jaunes avec le temps. Un taux d'exploitation annuel durable de 20 % est plus faible que la limite de référence de 35 % actuellement utilisée pour la gestion du doré jaune dans le Territoire cédé du Wisconsin. Quoi qu'il en soit, notre estimation concorde très bien avec les résultats de deux efforts de modélisation indépendants récents portant sur cette même question. Nous suggérons que les estimations empiriques de la production de poissons constituent un outil largement sous-utilisé pour mieux comprendre les taux d'exploitation durables des populations de dorés jaunes et d'autres pêches en général. [Traduit par la Rédaction]

Introduction

Secondary production, defined as the accumulation of heterotrophic biomass over time (Benke 2010), is a foundational concept in fisheries science (Ricker 1946; Wiley et al. 1984; Beamish 1993; Dolbeth et al. 2012). However, there has been a surprising lack of basic information on how fish production rates vary spatially and temporally (but see Carlander and Payne 1977; Randall et al. 1995; Waters 1999; Valentine-Rose et al. 2011). More importantly, there are large gaps in our understanding of how fisheries production relates to exploitation, even though these relationships are fundamental to sustainable natural resource management (Mosindy et al. 1987; Waters 1992).

The lack of extensive studies on empirical fish production rates likely stems from the sizable effort and monetary expense thought to be required for their calculation (Hanson and Leggett 1982; Poff and Huryn 1998; Lobón-Cerviá 2005). For inland lake fisheries, population estimates are typically required, along with information on growth (length-at-age), representative size structure, and creel data (if a relationship to exploitation is to be tested). Consequently, many fisheries management systems are constructed on component pieces of production (e.g., density, biomass, growth rates, recruitment, fish condition) rather than on production itself (Hilborn and Walters 1992; Goodyear 1993; Mace 1994). Thus, it is assumed that the component pieces inform enough about production dynamics so as to be useful for developing sustainable

Received 27 August 2014. Accepted 24 December 2014.

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fisheries management. However, in many high-profile fisheries, biologists are already collecting all of the necessary data to estimate fish production empirically. Thus, relationships between exploitation and production need not be modeled in complex ways, but rather calculated empirically and evaluated directly. For example, Ricker (1946), and later Waters (1992), contended that simple quantification of the fraction of biomass removed by anglers from the annual production (i.e., the “ecotrophic coefficient”) informed highly useful inland fisheries management endpoints, and these metrics have since been used in a variety of important fisheries management scenarios (Huryn 1996; Lobón-Cerviá 2005; Colvin et al. 2012; Pierce 2012).

Walleye (*Sander vitreus*) are a large-bodied, piscivorous percid native to the mid- and high latitudes of North America (Carlander 1977; Becker 1983). In Wisconsin and many nearby regions, the native distribution of this species has been obscured by a long and poorly documented stocking history (Becker 1983; Jennings et al. 2005; Dupont et al. 2007). The current distribution of walleye in Wisconsin is “patchy” and, in many cases, remains dependent upon supplemental stockings (Jennings et al. 2005). Walleye are often associated with large rivers and lakes (generally >80 ha with large amounts of open water) that contain adequate spawning habitat (sand, gravel rubble, boulder; Becker 1983) and a robust forage base such as yellow perch (*Perca flavescens*; Maloney and Johnson 1957) and (or) cisco (*Coregonus artedii*; Krueger and Hrabik 2005). The recreational fishery for walleye in northern Wisconsin has been and remains extremely popular. In spring 1985, an off-reservation Chippewa Native American tribal spear fishery for walleye began in the Ceded Territory of Wisconsin (approximately the northern third of Wisconsin; Hansen 1989; Hansen et al. 1991). Tribal harvest of walleye by gill nets has not occurred in the Ceded Territory of Wisconsin. However, in addition to the recreational fishery, walleye stocks were exposed to an additional source of fishing mortality through spearing. To avoid potential overexploitation of walleye stocks, the Wisconsin Department of Natural Resources adopted a conservative management strategy in 1990 and enacted an extensive stock assessment program. The current management system places a harvest quota on individual lakes, based upon adult walleye population estimates (Hansen 1989; Hansen et al. 1991). Adults are typically defined as the fishable portion of the stock and normally correspond to age classes 3 and greater. This convention is based in part on the susceptibility of these size and age classes to sampling and thus the reliability of population estimates via mark and recapture. For up to 2 years after a population estimate is conducted, a limit reference point for harvest in individual lakes is 35% of the adult population (i.e., no more than one occurrence of 35% in 40 lake and year instances) minus error margins to account for variability in population estimates (Hansen et al. 1991). After 2 years, walleye abundance is estimated using a model based on population size and lake area (Nate et al. 2000). Following tribal harvest declaration, a sliding recreational angler bag limit is applied on individual lakes based on the limit reference point. In general, this management system has been effective at maintaining regional walleye density targets (e.g., three adult fish per acre; 1 acre = 0.404 ha) over time. Yet recent data suggest regional trends in declining walleye recruitment, and speculation abounds that harvest could be one factor underlying this factor. Consequently, new methods of modeling sustainable exploitation rates of walleye could be valuable tools for refining walleye conservation management.

Escanaba Lake is a 118 ha lake (mean depth = 4.3 m, maximum depth = 7.9 m) located in Vilas County, Wisconsin, on undeveloped, state-owned land. The watershed is forested, and the lake has an irregular shoreline with several small islands lined with rock-boulder habitat. Fish species present in Escanaba Lake include walleye, yellow perch, largemouth bass (*Micropterus salmoides*), smallmouth bass (*Micropterus dolomieu*), muskellunge (*Esox masquinongy*), northern pike (*Esox lucius*), rock bass (*Ambloplites rupestris*), pump-

kinseed (*Lepomis gibbosus*), bluegill (*Lepomis macrochirus*), black crappie (*Pomoxis nigromaculatus*), and white sucker (*Catostomus commersonii*). To our knowledge, walleye are not thought to have occurred naturally in Escanaba Lake. Rather, walleye were stocked into Escanaba Lake in the 1930s and 1940s and quickly established a sizeable and naturally reproducing population (Kempinger and Carline 1977). Escanaba Lake has not been stocked with any fish since 1945 (Patterson 1953). Currently, largemouth bass and black crappie are rarely observed in Escanaba Lake, and the fish community is dominated by walleye, yellow perch, northern pike, muskellunge, and smallmouth bass.

Studies of walleye and other fishes in Escanaba Lake have been ongoing since 1946 (Patterson 1953), primarily through the longest running compulsory creel census in the world (see Methods for more detail). During 1946–2002, studies of the lake’s walleye fishery focused on understanding effects of liberalized angling regulations, including no bag limits, closed seasons, or minimum length limits. In 2003, all experiments related to liberalized harvest ceased (the walleye regulation changed to a 711 mm minimum length limit and a daily bag limit of one), with the walleye population never collapsing during the liberalized regulations period. Over time, these and related research efforts on Escanaba Lake have served as vital case studies for better understanding management of walleye in Wisconsin and other populations across their native and introduced range (Patterson 1953; Kempinger and Carline 1977; Hansen et al. 1998). Although walleye production rates have been previously calculated for the Escanaba Lake (Kempinger and Carline 1977), little research has focused on understanding temporal variability in walleye production rates and their relationship to exploitation. Understanding how production, biomass, and harvest relate to one another through time could be extremely useful for fisheries managers and scientists, as these metrics provide empirical estimates of how much biomass is available for harvest sustainably in any given year (e.g., annual harvested biomass should not exceed annual biomass production if maintaining biomass over time is a goal of the fishery).

The goals of our study were to (i) empirically estimate annual standing stock biomass (B), secondary production rates (P), and production/biomass (P/B) ratios of walleye in Escanaba Lake for all years in which data were available; (ii) test for statistical relationships between exploitation and production; and (iii) compare current walleye management recommendations with those that might be derived from the analysis of production data. We predicted that walleye biomass and production rates would be variable over time. Therefore, we also predicted that the fraction of biomass available for sustainable harvest would also be variable over time and correspond directly to annual production rates.

Materials and methods

Walleye datasets

Fisheries data are collected on an annual basis for walleye in Escanaba Lake with little deviation in methodology. Adult walleye population estimates (age 3+) are conducted each spring immediately following ice-out. Adult walleye are captured in standard fyke nets (set around the perimeter of the entire lake), and fish are marked by tagging or fin-clipping. Through 2002, all recaptures were made through the creel (see description below) and population estimates calculated using Bailey’s modification of the Peterson estimator. Beginning in 2003, however, recaptures were made shortly after marking using AC electrofishing (this change was due to the high minimum length limit and a corresponding lack of harvested fish), and population estimates were calculated using the Chapman variation of the Peterson method (Chapman 1951). Young-of-year (YOY) walleye population mark-recapture estimates are also conducted each fall using AC electrofishing (three passes) and multiple-census Schnabel models.

Table 1. Example calculation of secondary production for walleye (*Sander vitreus*) in Escanaba Lake, Wisconsin, USA, in 2005.

Age	No.	Total mass (kg)	Mean mass (kg)	B (kg·ha ⁻¹)	$\bar{B}$ (kg·ha ⁻¹)	G	P (kg·ha ⁻¹ ·year ⁻¹)
0	11 984	1 307	0.11	11.02	—	—	—
3*	924	271	0.29	2.28	2.22	0.99	2.19
4	745	325	0.44	2.74	2.51	0.40	1.00
5	29	19	0.64	0.16	1.45	0.39	0.56
6	501	437	0.87	3.69	1.92	0.30	0.59
7	170	188	1.11	1.59	2.64	0.24	0.63
8	108	158	1.46	1.33	1.46	0.28	0.40
9	46	81	1.77	0.69	1.01	0.19	0.19
10	58	121	2.08	1.02	0.85	0.16	0.14
11	79	194	2.46	1.64	1.33	0.17	0.22
12	17	46	2.69	0.39	1.01	0.09	0.09
13	4	13	3.21	0.11	0.25	0.18	0.04
14	4	14	3.38	0.11	0.11	0.05	0.01
15	4	14	3.44	0.12	0.12	0.02	0.00
18*	4	16	3.91	0.13	0.04	0.13	0.01
Total				27.0			6.1

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

*Denotes missing age classes and interpolated production estimates.

All anglers visiting Escanaba Lake are required to obtain a free angling permit at a clerk station located at the only landing on the lake. Following completion of each fishing trip, the catch of each angler is inspected by an on-duty creel clerk. Any walleye harvested are measured, weighed, tags noted, their sex determined, and a scale or fin spine collected for age estimation.

Production calculations

Production rates of walleye in each year were based on the instantaneous growth method:

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

where P is total walleye production (kg·ha⁻¹·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 (kg·ha⁻¹), and i is age class.

This methodology was originally formulated by Ricker (1946) and then independently again by Allen (1949). It has since been applied to a diverse range of taxa, including insects (Benke 1979), mollusks (Negus 1966; Hall et al. 2006), fungi (Suberkropp and Weyers 1996), and plants (Mathews and Westlake 1969). In fishes, the instantaneous growth method typically involves calculation of interval production between age classes (Mann 1971; Kempinger and Carline 1977; Valentine-Rose et al. 2007). Thus, estimates of the size- and age-structure of the fish population in question, as is typically obtained from age and growth surveys, is required (Waters 1977; Kwak and Waters 1997). Total annual production is then calculated as the sum of all age-specific production estimates in a given year (Waters 1977).

Annual population estimates of walleye were converted to age-specific abundance estimates by calculating the proportion of the adult population (from the creel) in each age class. Proportional values were subsequently applied to the population estimate of adults to derive abundance estimates for each age class in each year. Population estimates of YOY walleye from fall electrofishing surveys were used in their raw form. Mean mass-at-age was estimated for each year by calculating the mean mass of walleye in each age class as captured in the creel. In a small number of cases, missing mass data were estimated from total lengths using a length-mass equation. Whereas walleye do not typically enter the creel until ages 2–3, their production was instead interpolated

between ages 0 and 3 (i.e., 3-year production). Biomass in each age class was calculated as the product of the age-specific abundance and mean mass (i.e., $\bar{W}$). Mean biomass ($\bar{B}$) was calculated as mean B between adjacent age classes. Production rates for each age class or time period (e.g., ages 0–3) were calculated using eq. 1 and age-specific production estimates summed to derive total annual production of walleye in Escanaba Lake. We provide an example production calculation for one calendar year of data in Table 1.

As with any method of production estimation, limitations and assumptions are apparent that merit explicit consideration. The instantaneous growth method is ultimately a “snapshot” method of production estimation. This is in contrast with various other forms of production calculation (e.g., the increment summation or size-frequency methods) whereby individual cohorts, along with their growth and mortality, are tracked over the course of months, seasons, or years for biomass gains. Therefore, there will always be error in some components of the instantaneous production estimates. For example, otolith sagittae were not used to estimate walleye age, so the precision of age (and thus production) estimates for older fish may contain some error (e.g., be slightly higher) owing to underestimated age. However, because total production is driven primarily by the abundance of young fish (sensu the Allen curve), variation in total walleye production rates due to age-estimation bias would be extremely low (age-specific production rates in example calculation for an idea of the relative magnitude of production contributions across age classes; Table 1) so long as age-estimation error is low for younger age classes. Ultimately, the instantaneous growth method remains the standard by which production rates are empirically estimated in fish populations because of its simplicity along with the difficulty, workload, and monetary cost of tracking fish cohorts using alternative production estimation methodologies.

Exploitation rate calculations

We calculated exploitation rates of the total number of individuals in the population (E_i) for each year using estimates of walleye harvest from the creel surveys (Larson et al. 1991; Pierce et al. 1995; Isermann and Knight 2005):

$$(2) \quad E_i = \left(\frac{\text{number of adults in the creel}}{\text{number of adults in the population}} \right) \times 100$$

Exploitation can also be expressed in a production context. For example, biomass is a standard convention used in the management of heavily exploited marine fish stocks (Sainsbury et al. 2000; Worm et al. 2009). Ricker (1946) introduced the concept of the “ecotrophic coefficient”, which we hereinafter refer to instead as “production exploitation” or “ E_p ”. If production estimates and creel data are available, annual exploitation can be expressed as a percentage of annual production. Annual E_p was therefore calculated as

$$(3) \quad E_p = \left(\frac{\text{biomass of walleye in the creel}}{\text{total annual production of walleye}} \right) \times 100$$

Although E_i and E_p are likely related, to our knowledge this relationship has never been previously tested. Given that walleye management is based on E_i (Serns and Kempinger 1981; Hansen et al. 1991; Gangl and Pereira 2003), we tested for a relationship between E_i and E_p such that both variables might be understood within the context of one another.

Statistical analyses

Pearson product moment correlations were calculated to relate annual adult walleye density to total annual walleye production and ages 0–3, 4–6, and 7+ production. Series autocorrelation in biomass, production, P/B , harvest, and E_p time series data was evaluated using simple time series analyses. Temporal trends (1965–2009) in biomass, production, and harvested production were first assessed using 8-year moving averages after interpolating gaps, and then autocorrelations were visually inspected using standard correlograms. Statistical significance was tested using Ljung–Box tests. Time series analyses was performed using the SMA function of the TTR package for smoothing trends and the acf and Box.test functions for detecting autocorrelation in R software version 3.0.3 (R Core Team 2014).

Long-term changes in walleye growth rates (an important component metric of production calculations) were also examined. Whereas growth rates (G) are greatest among the youngest ages classes, we focused on evaluating long-term trends in juvenile (ages 0–3) walleye growth. Density-dependent growth was evaluated by linearly regressing juvenile G against annual estimates of YOY and adult walleye density. Long-term changes in G were then evaluated by regressing juvenile G and the residuals of the juvenile G – adult density relationship (to account for potential density-dependent effects) versus year.

Annual E_p estimates were categorized into five broad exploitation groups parallel to Waters (1992), with categorical values of 0%–24%, 25%–49%, 50%–74%, 75%–99%, and >100%. Significant differences in mean production, biomass, and P/B values among these categories were tested using analysis of variance with Tukey’s post hoc tests. Simple linear and breakpoint regressions were used to test for potential relationships among production, adult density, E_p , and E_i . An $\alpha = 0.05$ was used for all statistical tests.

Results

Annual walleye biomass, production, and P/B ratios were highly variable in Escanaba Lake over time. Total standing stock biomass ranged 9.1–49.4 kg·ha⁻¹, total annual production ranged 2.4–11.3 kg·ha⁻¹·year⁻¹, resulting in P/B ranging 0.15–0.30 (Fig. 1; also see online Supplementary Table S1¹). The lowest two walleye production years were 1995 and 1996, whereas the highest two production years were 1977 and 2001 (Fig. 2; Supplementary Table S1¹). Series autocorrelation was absent from the biomass ($\chi^2 = 33.6$, df = 44, $P = 0.85$), production ($\chi^2 = 58.2$, df = 44, $P = 0.074$), and P/B ($\chi^2 =$

36.3, df = 44, $P = 0.79$) datasets, but not the E_p time series ($\chi^2 = 126.0$, df = 44, $P < 0.001$; Ljung–Box test).

Annual adult densities of walleye in Escanaba Lake were significantly and positively correlated with total annual walleye production (Fig. 2, Pearson $R = 0.33$, $P = 0.04$); however, adult densities correlated best and positively with ages 4–6 walleye production (Pearson $R = 0.75$, $P < 0.0001$). No relationship was observed between adult densities and juvenile (ages 0–3) production (Pearson $R = 0.07$, $P = 0.65$) or production in the older age classes (ages 7+; Pearson $R = -0.11$, $P = 0.50$). In addition, no relationships were observed when evaluating data before 2003 (i.e., the year low walleye harvest was initiated), with the exception that adult densities no longer significantly correlated with total production. Insufficient sample sizes (number of years) were available to appropriately test for these same effects statistically, after 2003. However, correlation strength between adult densities and age 7+ production rates did increase after 2003, while correlation strength between adult densities and ages 0–3 and 4–6 production were reduced.

Juvenile walleye growth was not related to YOY walleye density (linear regression $R^2 = 0.01$, $P = 0.54$). However, juvenile walleye growth was marginally related to adult walleye densities (linear regression, $R^2 = 0.09$, $P = 0.07$). Juvenile walleye growth appeared to have declined over time in Escanaba Lake. After accounting for potential density-dependent effects on growth, the decline in growth over time was stronger and attained statistical significance (linear regression $R^2 = 0.16$, $P = 0.01$).

A significant positive relationship was detected between E_i and E_p (Fig. 3, linear regression $R^2 = 0.62$, $P < 0.0001$). Using this relationship, one can estimate one variable from the other for an average year. For example, an E_p value of 100% (i.e., all of the biomass produced in a single year was harvested) equated on average to an E_i value of 20% in any given year. Furthermore, analysis of 95% confidence intervals from the means of this regression suggest 100% E_p could be consumed at as low as at 17% E_i and at as high as 24% E_i .

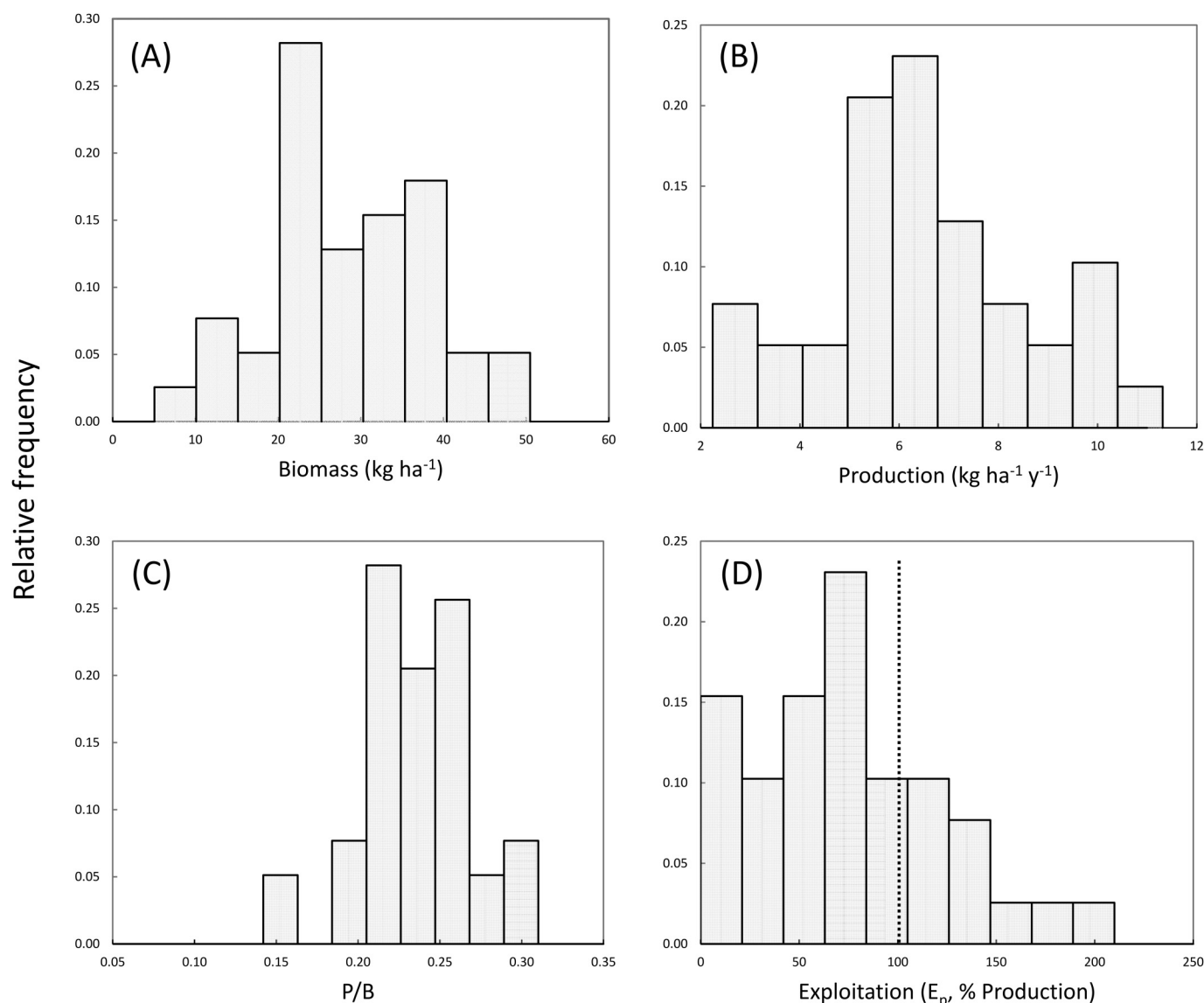
Walleye biomass and production was somewhat compensatory with exploitation. At low to moderate levels of exploitation (E_p class 25%–49%), walleye biomass and production increased relative to zero exploitation (Figs. 4A, 4B). Mean P/B ratios did not vary across exploitation categories (Fig. 4C). A breakpoint regression identified an E_p threshold of 40%, at which total walleye production was maximized. Following this threshold, walleye production declined rapidly with increasing E_p . The four lowest production years all occurred during years in which E_p exceeded 100%. There were no significant relationships between adult density and E_p or E_i . No relationship existed between total walleye production and E_i (linear regression $R^2 = 0.08$, $P = 0.08$). Declining walleye production was highly size- and age-class-specific. There were no relationships between juvenile (ages 0–3) or mid-age (ages 4–6) production and E_p . However, there was a significant negative linear relationship between older walleye production rates (ages 7+) and E_p (linear regression $R^2 = 0.36$, $P < 0.0001$). Thus, increasing exploitation negatively affected production rates, especially in large walleye.

Discussion

Long-term studies that empirically estimate production rates in fish populations have been exceptionally rare (Ware and Thomson 1991; Poff and Huryn 1998; Waters 1999). Even fewer studies have had the capability to simultaneously track fish production alongside exploitation to better understand how these two variables interact and vary over time (Mosindy et al. 1987; Waters 1992). As a result, very little is known about how empirical production rates

¹Supplementary data are available with the article through the journal Web site at <http://nrcresearchpress.com/doi/suppl/10.1139/cjfas-2014-0394>.

Fig. 1. Frequency histograms of empirically derived: (A) biomass; (B) production; (C) P/B ; and (D) E_p values for the Escanaba Lake, Wisconsin, walleye (*Sander vitreus*) population, 1965–2009. Dashed vertical line represents 100% exploitation of production.



in fish populations respond to varying exploitation rates, even though this question remains central to fisheries science (Frederick and Peterman 1995; Myers and Worm 2003).

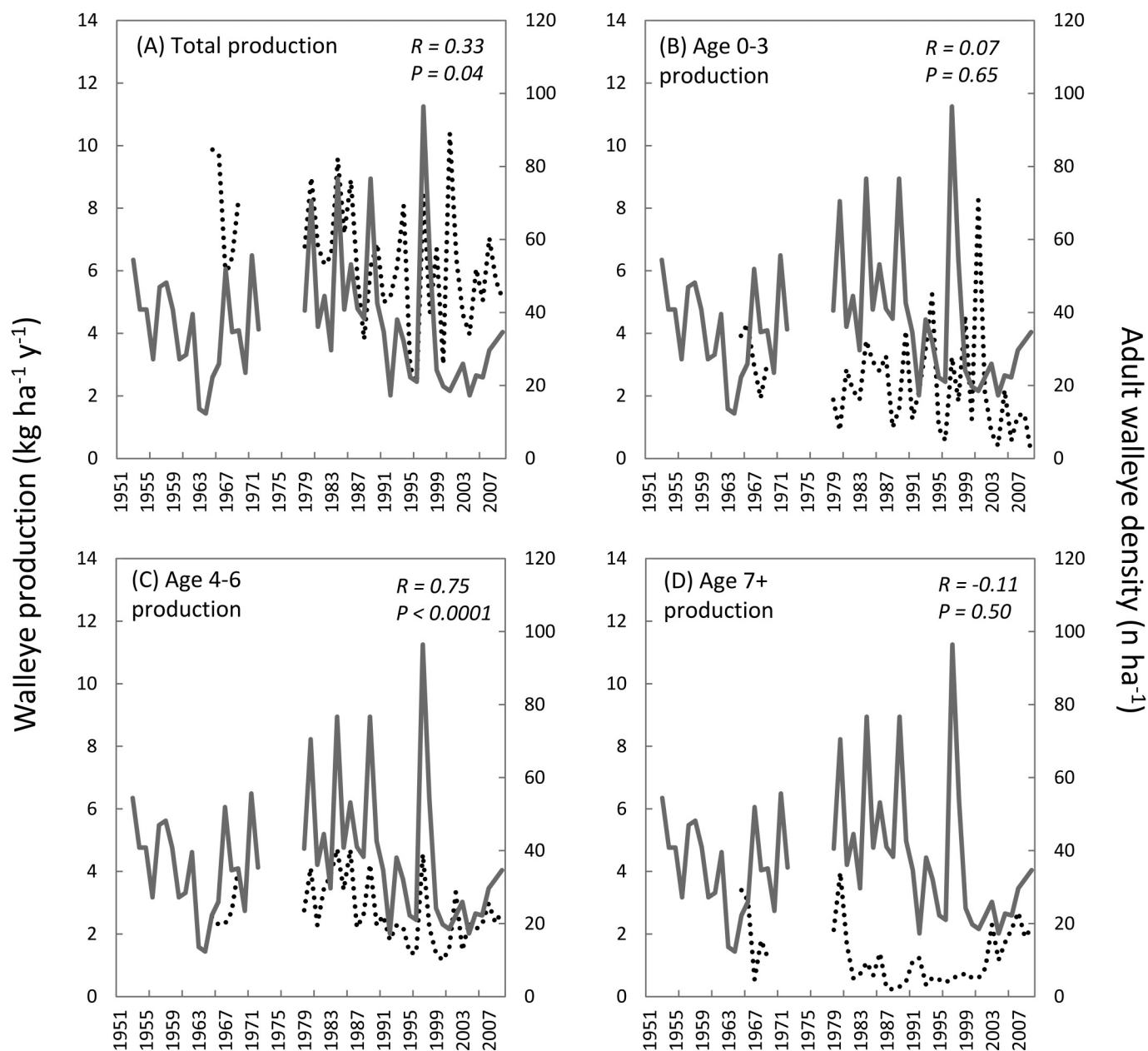
We established relationships between annual production rates of walleye in a north temperate lake and annual exploitation rates by anglers. Our observations covered a 44-year period where production varied by half an order of magnitude and E_p ranged from 0% to >200%. Walleye production was somewhat compensatory at relatively low–moderate levels of exploitation, but declined rapidly with increasing exploitation rates. Adult densities of walleye tracked total annual walleye production; however, adult densities correlated much more strongly with ages 4–6 walleye production. Furthermore, the effect of angling exploitation on production was strongly localized on larger, older walleye.

Escanaba Lake appears to have the capacity to produce high standing crops of walleye biomass at relatively fast rates compared with other populations and ecosystems (Table 2). For example, maximum biomass observed in Oneida Lake, New York, was only 61% that of Escanaba Lake (Colby et al. 1979). Walleye biomass in Escanaba Lake could be >20× higher than southern USA reservoirs in Kentucky, Tennessee, and Alabama (Brown 1962; Fitz and

Holbrook 1978; Kinman 1990). Production rates of Escanaba Lake walleye were also in some cases higher than rates observed in a Canadian lake (Mosindy et al. 1987); however, production rates in both systems appeared to overlap to a large degree. These comparative results imply that Escanaba Lake possesses the right set of environmental conditions that make it highly conducive to walleye production. We speculate that this productivity may be related to an abundance of high-quality habitat (i.e., islands, boulders, gravel, sand); food web structure and function, including a robust forage base (yellow perch); undeveloped shorelines; and general remoteness.

It is not surprising that adult walleye densities were significantly correlated with total annual production rates and that this correlation was weak compared with that between adult densities and mid-age walleye production. Fish densities are a major factor driving variability in production rates via the biomass coefficient; thus, when densities are high, production should also be high. However, adult densities do not always reflect variability in the size- and age-structure of populations (i.e., for adult densities, an adult is an adult, regardless of size). Thus, at the same adult density, a population could be composed of many small and young

Fig. 2. Comparison of trends in various walleye (*Sander vitreus*) production classes, including (A) total production, (B) ages 0–3 production, (C) ages 4–6 production, and (D) ages 7+ production in Escanaba Lake, Wisconsin, 1965–2009. In all panels, annual production rates (dashed black lines) are plotted against adult densities (solid gray lines), and correlation coefficients represent Pearson product moment correlations between production and density data.

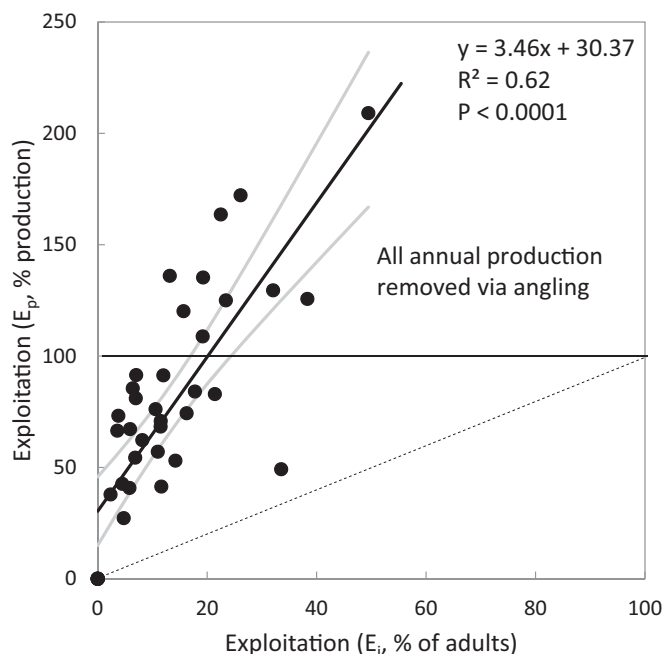


fish, many large old fish, or a diverse mixture of size and age classes. Yet in each of these scenarios, biomass and production could vary substantially even though adult density would remain the same. The stronger correlation observed between adult density and ages 4–6 production reflects the reality that younger fish usually comprise larger fractions of adult walleye densities. Thus, it is logical that weak correlations might exist between adult densities and juvenile or older walleye production.

Changes in growth rate over time were also integrated into the production calculations. Growth rates of fishes are frequently variable and scale-dependent (Conover and Present 1990; Rypel 2009, 2012), changing in response to myriad abiotic and biotic drivers (Houlihan et al. 1992; Sass and Kitchell 2005; Black 2009; Rypel 2011; Richard and Rypel 2013). Secondary production calculations integrate growth and mathematically represents half of

the structural formula of production (i.e., $P = G\bar{B}$). Again, adult densities (and even size-structure in this case) could theoretically remain unchanged over time while production changes significantly if growth alone varied. Escanaba Lake walleye growth has changed (declined) over time. The mechanisms underlying this pattern remain unclear and are beyond the scope of this study. However, one plausible hypothesis might be that changes in walleye density over time, and thus density-dependent growth, underlie the major temporal shift in walleye growth (Fox and Flowers 1990; Walters and Post 1993; Trudel et al. 2010). Indeed, Escanaba walleye growth (ages 0–3) did appear to be related to adult density (juvenile walleye growth was higher when adult density was lower). Yet, even after accounting for density-dependent effects on growth, declines in walleye growth over time were still present and were stronger and more significant. Our results suggest that

Fig. 3. Statistical relationship between annual estimates of E_p and E_i for walleye (*Sander vitreus*) from Escanaba Lake, Wisconsin, 1965–2009. Gray lines represent 95% confidence intervals from mean regression line. The solid horizontal line represents the mean E_i value (20%) at which 100% of annual production is removed via angling. The diagonal dashed line represents a 1:1 fit.

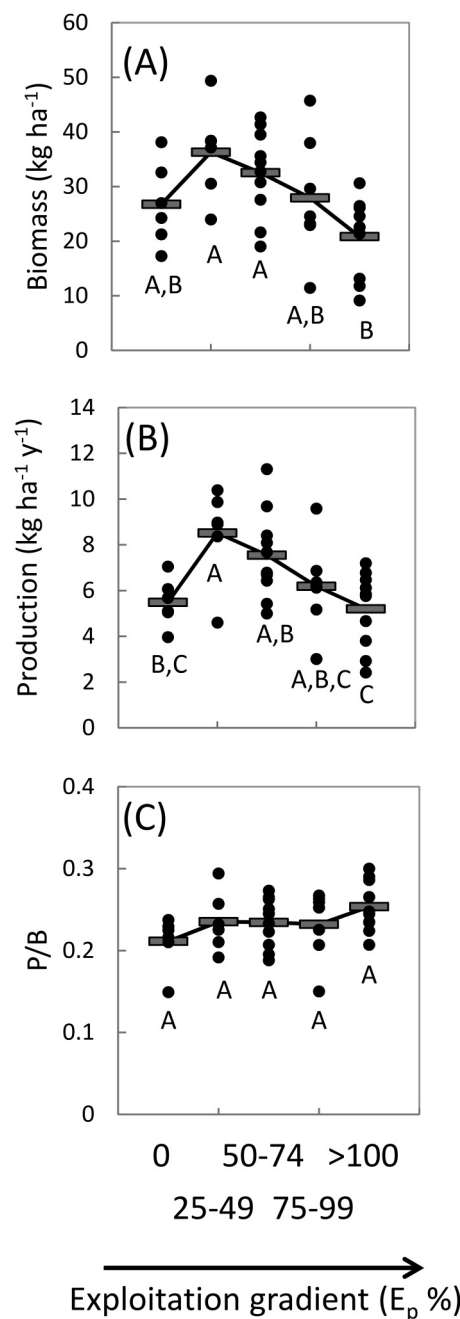


growth rates of walleye in Escanaba Lake have declined over time independent of any density-dependent effects. Alternative explanations for this pattern might involve temperature change (Hokanson and Koenst 1986; Quist et al. 2003), prey base decline (Hartman and Margraf 1992), and (or) genetic or nongenetic parental effects as a result of size-dependent exploitation and selection by anglers (Dutil and Brander 2003; Venturelli et al. 2010). Future research is needed to better understand potential mechanisms underlying this pattern in Escanaba Lake and perhaps other ecosystems.

The significant relationship observed between E_i and E_p (Fig. 4) is a key finding that has important implications for walleye fisheries management. Major differences exist in the calculation of these two variables that likely account for the remaining unexplained variation in this relationship. Most importantly, E_p integrates information on the size- and age-structure, growth rates, and biomass of walleye harvested, while E_i does not. Furthermore, E_i can mathematically never be >100% and can only be high when harvest numbers are high. In contrast, E_p values can frequently be >100% (reflecting the reality that surplus production from previous years can be harvested), and these high values could be achieved in a variety of ways. For example, high E_p can result from harvest of many smaller fish, harvest of a moderate or high amount of very large fish, through a combination of both, or by declines in total annual production rates independent of any harvest changes.

An E_p threshold value of 100% should be considered a highly relevant benchmark for fisheries management. This value clearly and mathematically expresses the point at which more biomass is being removed annually than the population is producing. Thus, sustained E_p values >100% should deplete the standing stock biomass of walleye in Escanaba Lake over time. For example, in 1988, E_p exceeded 200%, indicating that >2 years worth of walleye biomass production had been removed from the lake over the course of a single year of angling. This year corresponded with a high E_i

Fig. 4. Annual values of (A) biomass, (B) production, and (C) P/B in five categories representing an observable gradient of annual walleye (*Sander vitreus*) exploitation in Escanaba Lake, Wisconsin. Exploitation categories were based on those outlined in Waters (1992). Bars represent mean values for each category, and letters denote means that did not statistically differ (Tukey's $P > 0.05$).



rate of 50%, but also a low rate of production (1988 was the fourth lowest year of walleye production on record in Escanaba Lake). Increased exploitation will directly reduce production rates, especially of older fish, thereby indirectly inflating E_p . However, production rates independent of harvest effects (e.g., due to climate; Beamish 1993) could also strongly influence E_p by modifying natural production variability and thus also the proportion of annual production available for sustainable harvest (Dutil et al. 1999; Dutil and Brander 2003; Kjesbu et al. 2014). Collectively, our results suggest potential for adaptive management of walleye

Table 2. Comparison of biomass and production estimates for other North American walleye (*Sander vitreus*) populations.

Population	Detail	B (kg·ha ⁻¹)	P (kg·ha ⁻¹ ·year ⁻¹)	Source
Escanaba Lake, Wis.	39-year period	9.1–49.4	2.4–11.3	This study
Savanne Lake, Ont.	Adult P		6.7–8.2	Mosindy et al. 1987
Hoover Reservoir, Ohio	6-year period		1.3–4.0	Momot et al. 1977
Clear Lake, Ind.	26-year period, adult P	10.4	0.5–3.0	McCann 1960; Carlander and Payne 1977
Big Crooked Lake, Wis.	4-year period	16.8–48.5		Serns and Kendall 1978
Storm Lake, Ind.	Adult P	37.0		Rose 1950
Oneida Lake, N.Y.	Age 3+ P	18.5–30.6		Colby et al. 1979
Mable Lake, Minn.	“Reclaimed lake” after 4 years	8.2–14.0		Johnson and Osborn 1977
Big Butternut Lake, Wis.	Adult P	11.9		Colby et al. 1979
Sauvane Lake, Ont.	Adult P	11.2		Colby et al. 1979
West Blue Lake, Man.		6.7		Colby et al. 1979
Dexter Lake, Ont.	Adult P	4.9		Colby et al. 1979
Burnt Camp Lake, Minn.	Rotenone survey	2.8		Colby et al. 1979
Cumberland Reservoir, Ky.	1980–1985	0.9–2.5		Kinman 1990
Alabama	Seven lakes	1.0–2.1		Brown 1962
Norris Reservoir, Tenn.	1960–1975	0.7–0.8		Fitz and Holbrook 1978

Note: Values are sorted first from highest to lowest of maximum production and then from highest to lowest in maximum biomass. B = annual biomass, P = annual secondary production rates.

exploitation. For example, exploitation might be modified so as to coincide with fluctuations in productivity such that harvest could be expanded during productive periods, but decreased during less productive periods. Variability in walleye productivity (and thus sustainable exploitation) is exemplified by the confidence intervals surrounding the relationship between E_p and E_i (i.e., it is likely that sustainable walleye harvest in Escanaba Lake could range from 17% to 24% E_i depending on the prevailing productivity conditions). Nonetheless, analysis of production and E_p allows a context through which walleye “pulse fishing” (Reid and Momot 1985) scenarios might be explored in the future. For example, high or low total or size-specific production years might be determined following spring fyke netting surveys. Harvest could then be theoretically adjusted upwards or downwards such that 100% E_p is not exceeded. Production values, as in Escanaba Lake, would likely fluctuate substantially over time, thereby allowing for periods of higher or lower harvest possibilities depending on productivity conditions.

Walleye production was somewhat compensatory, but only at low-moderate levels of exploitation. The highest mean biomass and production rates were observed at levels of E_p between 25% and 49% and declined sequentially by category thereafter. Furthermore, the second lowest mean rate of walleye production occurred in the 0% E_p category. This effect likely originated from (i) density-dependent effects on recruitment, growth, and mortality (Serns 1982; Fox and Flowers 1990; Hansen et al. 1998) and (ii) the period of 0% exploitation directly following a lengthy period of very high harvest from which biomass and production was likely recovering (Myers and Worm 2005). Interestingly, P/B ratios were statistically invariant across exploitation categories. Thus, walleye biomass in Escanaba Lake will likely require similar amounts of time to turn over (~3–7 years) irrespective of exploitation rates.

Management implications for Ceded Territory walleye populations

In Escanaba Lake, walleye biomass and production were variable over time, but were high relative to published data on other walleye populations (Table 2). The elevated capacity of Escanaba Lake to produce walleye biomass is plausibly related to the high environmental character of this lake (e.g., high availability of preferred habitats, forage base, undeveloped shoreline, remoteness). Therefore, the response of walleye production to exploitation in this lake is probably most accurately viewed from the standpoint of a “best case scenario”, particularly for northern Wisconsin. Other walleye populations (especially those subjected to myriad stresses or those that are less productive) may respond very differ-

ently to exploitation than the population did in Escanaba Lake. For example, even though a previous biomass estimate from nearby Big Crooked Lake suggested a similarly high productive capacity for walleye (Serns and Kendall 1978), preliminary analysis of walleye biomass from a large number of Wisconsin lakes indicates that the productive capacity for walleye in some lakes can apparently also be quite low (D. Goto, unpublished data). Furthermore, effects of catch and release mortality on production were not examined in this study and would likely only further reduce the amount of biomass available for sustainable harvest by anglers, especially if catch and release mortality is localized on larger biomass-rich individuals.

Management of walleye across the Ceded Territory of Wisconsin is currently based on an approach using safety factors, wherein the risk of exceeding 35% E_i is estimated to be less than 1 in 40 (Hansen et al. 1991). The 35% E_i limit reference point was originally derived from analysis of Escanaba Lake walleye exploitation creel data (i.e., a 40-year average of E_i). However, our analysis revealed that when $E_i = 35\%$, this translates to an E_p value of ~137% or ~1.4 years of total biomass production. If this exploitation rate were to be sustained, it would likely deplete standing stock walleye biomass relatively quickly. For walleye in Escanaba Lake, 100% E_p is typically achieved at ~20% annual E_i . Interestingly, this result is surprisingly congruent with a recent analysis of walleye sustainable exploitation rates based on growing degree-days and life-history variants across the species range (Lester et al. 2014). For example, Lester et al. (2014) suggested that sustainable walleye exploitation (E_i), based on walleye life-history characteristics and their relationship to growing degree-days should be ~20% in northern Wisconsin. These results also align with another independent age-structured population model of walleye sustainable exploitation across the Ceded Territory of Wisconsin, which again similarly suggested about 20% E_i as a threshold for walleye sustainability in a region-wide population model (I. Tsehay, B. Roth, and G. Sass, unpublished data). Across all Ceded Territory lakes in Wisconsin during 1995–2009, mean E_i was 13%. For Escanaba Lake, this would translate to an E_p value of about 74%. Thus in many respects, the current management system is in fact providing exploitation rates that regularly fall below the 20% value outlined here for Escanaba Lake, albeit with occasional years of exceedance. However, it is unclear the extent to which walleye production in other populations is similar or different compared with Escanaba Lake. Therefore, understanding production rate dynamics in other Wisconsin walleye populations is likely a critically important future research topic.

Empirically quantifying the productive capacity of walleye populations appears to be a highly promising and integrative tool for better understanding walleye ecology in lake ecosystems, including how humans might be interacting with these fisheries. We speculate that the main reason why similar studies have not been conducted is due to the perception by biologists that obtaining the data required to empirically estimate production is so costly and time-consuming. Indeed, the core datasets of the Wisconsin Department of Natural Resources, Escanaba Lake Research Station contain some of the premiere information in the world on walleye biology, including species response to various regulatory initiatives. Thus, the calculation and study of long-term production rates in this ecosystem were long overdue. However, the basic empirical components to estimate fish production and E_p are likely collected much more frequently than often realized by fisheries scientists, especially in more high-profile fisheries. For example, all of the necessary data needed to empirically calculate production rates for other walleye populations (population estimates, growth, creel information) are legally required components of annual Ceded Territory of Wisconsin walleye fishery monitoring protocols. Thus, the potential to expand this analysis in an analogous way spatially and temporally across the regional landscape is high.

Even though walleye production, biomass, and P/B estimates were not serially correlated, E_p was serially correlated. That harvest and production from one year could affect either or both variables in the following year is a result that is both intuitive and important. For example, if E_p exceeded 100% in any given year, this would reduce both density and standing biomass. Since walleye densities and production rates are positively related, this harvest effect could tend to reduce production, making it even more likely for 100% E_p exceedance in the following year. Hypothetical situations like these highlight the dynamic and interactive relationships often present between production and exploitation. Furthermore, it uncovers a potential interdependency between both variables when each year's production and harvest estimates are tabulated and considered independently. We suggest that future studies on empirical production rates of exploited fish stocks consider such effects and develop explicit methodologies for quantifying the effects and risks associated with such interdependencies.

Production and harvest rates are both quantified on annual time scales; thus, E_p clearly quantifies the amount of heterotrophic biomass removed by anglers relative to what is produced each year. Simple yet highly relevant exploitation thresholds like 100% E_p deserve consideration for incorporation in future management of walleye and other fisheries. Walleye densities in Escanaba Lake did not respond in any clear way to exploitation (expressed as either E_i or E_p), yet production rates did. Therefore, production may be a more direct metric for tracking and managing walleye populations, including understanding the response of populations to exploitation.

Acknowledgements

We thank a large number of biologists, technicians, research scientists, and anglers dating back to the 1960s who have contributed in substantial ways to the data collection, study, and experimentation on the Escanaba Lake fishery. We also thank the following individuals who provided prereviews and contributed towards improving the concepts and analyses in this paper, especially Dan Isermann, Michael Hansen, Ron Bruch, Joe Hennessy, Tom Cichosz, Steve Hewett, Gretchen Hansen, and Mike Staggs. Support for this study was provided by the Wisconsin Department of Natural Resources – Bureau of Science Services, Federal Aid in Sport Fish Restoration (Project F-95-P, study SSDI).

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