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Life-history plasticity and sustainable exploitation: a theory of growth compensation applied to walleye management

NIGEL P. LESTER,[1,2,5] BRIAN J. SHUTER,[1,2] PAUL VENTURELLI,[3] AND DANIEL NADEAU[4]

[1]*Harkness Laboratory of Fisheries Research, Ontario Ministry of Natural Resources, Peterborough, Ontario K9J 7B8 Canada*
[2]*Ecology and Evolutionary Biology, University of Toronto, Toronto, Ontario M5S 3B2 Canada*
[3]*Department of Fisheries, Wildlife, and Conservation Biology, University of Minnesota, St. Paul, Minnesota 55108 USA*
[4]*Ministère des Ressources Naturelles et de la Faune, Rouyn-Noranda, Quebec J9X 2N9 Canada*

Abstract. A simple population model was developed to evaluate the role of plastic and evolutionary life-history changes on sustainable exploitation rates. Plastic changes are embodied in density-dependent compensatory adjustments to somatic growth rate and larval/juvenile survival, which can compensate for the reductions in reproductive lifetime and mean population fecundity that accompany the higher adult mortality imposed by exploitation. Evolutionary changes are embodied in the selective pressures that higher adult mortality imposes on age at maturity, length at maturity, and reproductive investment. Analytical development, based on a biphasic growth model, led to simple equations that show explicitly how sustainable exploitation rates are bounded by each of these effects. We show that density-dependent growth combined with a fixed length at maturity and fixed reproductive investment can support exploitation-driven mortality that is 80% of the level supported by evolutionary changes in maturation and reproductive investment. Sustainable fishing mortality is proportional to natural mortality (M) times the degree of density-dependent growth, as modified by both the degree of density-dependent early survival and the minimum harvestable length. We applied this model to estimate sustainable exploitation rates for North American walleye populations (*Sander vitreus*). Our analysis of demographic data from walleye populations spread across a broad latitudinal range indicates that density-dependent variation in growth rate can vary by a factor of 2. Implications of this growth response are generally consistent with empirical studies suggesting that optimal fishing mortality is approximately $0.75M$ for teleosts. This approach can be adapted to the management of other species, particularly when significant exploitation is imposed on many, widely distributed, but geographically isolated populations.

Key words: biphasic growth; compensation; degree-days; density dependence; evolution; life history; maturity; natural mortality; plasticity; Sander vitreus; *sustainable exploitation; walleye.*

INTRODUCTION

Sustainable exploitation theory assumes that the removal of biomass from a population triggers density-dependent life-history changes that compensate for the higher mortality imposed by exploitation (Krebs 2001). The extent to which different life-history traits can respond to biomass removal therefore determines maximum population growth rate and, by extension, maximum sustainable exploitation rate. Consequently, sustainable exploitation in practice requires a working knowledge of compensatory life-history changes and their effects on population growth rate (Rose et al. 2001).

Fisheries science has traditionally presented two distinct views of population regulation (Hilborn and Walters 1992), namely, that a reduction in the density of the exploited segment of the population leads to either (1) a density-dependent increase in the rate of production of the exploited segment, or (2) a reduction in egg production that, in turn, leads to a density-dependent increase in larval/juvenile survival. These views are exemplified, respectively, by surplus production (e.g., Graham 1935, Schaefer 1954) and stock-recruitment (e.g., Ricker 1954, Beverton and Holt 1957) models of sustainable exploitation. Both of these views are limited. The surplus production approach does not identify how changes in different life-history traits contribute to the overall increase in net production. On the other hand, the stock recruitment approach assumes that a single life-history trait (i.e., survival in early life) regulates recruitment, thus ignoring the impact of changes in other life-history traits. For example, density-dependent body growth is typically observed in exploited populations (e.g., Beverton and Holt 1957, Rijnsdorp and van Leeuwen 1992, Rochet 1998, Post et al. 1999, Rose et al. 2001, Bjornsson and Steinarsson 2002, Engelhard and Heino 2004, Lobon-Cervia 2007), yet its role in population regulation is rarely quantified. Recent work

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[5] E-mail: nigel.lester@ontario.ca

TABLE 1. Abbreviations and symbols used in this paper.

Abbreviation or symbol	Description
a	constant in the relationship between body length and somatic mass
fec_t, $\mathrm{fec}_{t,\mathrm{M}}$, $\mathrm{fec}_{t,\mathrm{F}}$	relative fecundity (number of eggs/somatic mass) at age t
F, F_{ext}	annual instantaneous fishing mortality rate, subscript “ext” labels extinction
g, g_{M}, g_{F}	index of annual reproductive investment (gonad mass/somatic mass expressed in equivalent energetic units)
h, h_{M}, h_{F}	annual immature growth rate
DD5	annual growing degree-day >5°C
k, k_{M}, k_{F}	von Bertalanffy growth parameter; Brody growth coefficient
L, L_{M}, L_{F}	length at maturity (i.e., length at the onset of investment in reproduction)
l_{c}	minimum length subject to harvest (i.e., size of entry to fishery)
l_0	y-intercept of the immature growth line ($=-h\,\tau$)
l_t, $l_{t,\mathrm{M}}$, $l_{t,\mathrm{F}}$	length at age t
l_∞, $l_{\infty,\mathrm{M}}$, $l_{\infty,\mathrm{F}}$	von Bertalanffy growth parameter; asymptotic length
M	annual instantaneous natural mortality rate of juveniles and adults
R_0, $R_{0,\mathrm{M}}$, $R_{0,\mathrm{F}}$	net reproductive rate of a typical female
s, s_{M}, s_{F}	an early survival parameter that acts as a multiplier of e^{-M}
T, T_{M}, T_{F}	age at maturity (i.e., age at the onset of investment in reproduction)
T	age
t_c	earliest age subject to harvest (i.e., age of entry to fishery)
t_0, $t_{0,\mathrm{M}}$, $t_{0,\mathrm{F}}$	von Bertalanffy growth parameter; hypothetical age at which length is 0
τ, τ_{M}, τ_{F}	biphasic growth parameter; hypothetical age at which length is 0 ($=-l_0/h$)
w_{egg}	wet mass of an average egg
W_t, $W_{t,\mathrm{M}}$, $W_{t,\mathrm{F}}$	somatic mass at age t

Notes: All life-history traits are for females. Subscripts M and F label unexploited and exploited populations, respectively.

suggests that its importance needs to be reconsidered (Lorenzen and Enberg 2002, Bystrom et al. 2004, Rose 2005, de Roos et al. 2007, Lorenzen 2008) since, in fish, it indirectly affects population size via its interaction with maturity and fecundity schedules. A further limitation of both stock recruitment and surplus production theory is that neither approach addresses the long-term evolutionary effects of exploitation on life-history traits; they both view life-history traits as plastic responses to variation in fish density, despite growing evidence that exploitation alters the evolutionary trajectory of relevant life-history traits (e.g., see reviews by Jorgensen et al. [2007], Kuparinen and Merila [2007], and Allendorf and Hard [2009]).

In this paper, we develop a simple, general theory that describes how plasticity in various life-history traits affects the ability of a population to sustain the additional mortality imposed by exploitation. Through this model, we compare the relative influences of density-dependent plasticity in growth and early survival on the levels of exploitation that are sustainable. The most common plastic response is that reduced competition enables faster growth and earlier maturation if maturation size is fixed (Policansky 1993). We assumed this norm of reaction in developing our plastic response model. Phenotypic plasticity allows individuals to respond quickly to changes in the environment and may act as a buffer against selection pressures, thus preventing, or at least slowing down, evolutionary changes (Stearns 1982, Sultan 1987, Ernande et al. 2004). We assessed this buffering capacity by comparing a density-dependent plastic response to an evolutionary response in which age at maturity, size at maturity, and reproductive investment have adapted optimally to changes in mortality rate imposed by exploitation. We demonstrate application of the plastic response model by estimating sustainable exploitation rates for walleye (*Sander vitreus*; see Plate 1) populations throughout North America.

DEVELOPMENT OF THE COMPENSATION MODEL

Here we describe a model for predicting sustainable exploitation from compensatory life-history changes. The logic of our model is as follows. We assumed that: (1) the average female in an equilibrium population exhibits life-history traits that result in the production of exactly one mature daughter over that female's lifetime (i.e., the average female has a net reproductive rate, R_0, of 1); (2) the rate at which this population is being exploited affects some life-history traits; and (3) life-history traits are constrained (by genetics, physiology and climate) to a range of values that together define a threshold rate of exploitation beyond which the population will collapse. If (1) the average female in an exploited population also has $R_0 = 1$; and (2) the female life histories characteristics of both unexploited and exploited populations are known, then it is possible to estimate how much additional exploitation mortality can be imposed on the population before it collapses. Details of this approach are described in this section. The subscripts M and F are used to designate unexploited and exploited conditions, respectively. Table 1 provides a complete list of abbreviations and symbols used in this paper.

For a female in an unexploited population, net reproductive rate is expressed as

$$R_{0,\mathrm{M}} = \sum_{t=T_{\mathrm{M}}+1}^{\infty} s_{\mathrm{M}} \times e^{-Mt} \times \mathrm{fec}_{t,\mathrm{M}} \qquad (1)$$

where T_M is the initial age at maturity, M is a background instantaneous natural mortality rate, s_M is an early-life survival parameter, and $\text{fec}_{t,M}$ is the number of female eggs produced by a female at age t (Lester et al. 2004). Eq. 1 implies that survival from egg to age at maturity is $s_M e^{-MT_M}$, after which annual survival is e^{-M}. The early survival parameter (s_M) accounts for a higher rate of mortality early in life: mortality typically declines rapidly as individuals grow and become less vulnerable to predation (Peterson and Wroblewski 1984, McGurk 1986, Lorenzen 1996).

In an exploited population, net reproductive rate is expressed as

$$R_{0,F} = \sum_{t=T_F+1}^{\infty} s_F \times e^{-Mt} \times \text{fec}_{t,F} \times e^{-F(t-t_c)} \tag{2}$$

where F is instantaneous fishing mortality rate, and t_c is the youngest age subject to harvesting. This equation is identical to Eq. 1, except that it includes an additional term ($e^{-F(t-t_c)}$) that describes the mortality imposed by exploitation. It also acknowledges potential changes in life-history traits by using a different subscript (F instead of M) to label age at maturity (T_F), early survival (s_F) and fecundity ($\text{fec}_{t,F}$).

By comparing Eqs. 1 and 2, we can see that exploitation in the absence of compensatory changes in life-history traits (e.g., maturation, early survival, or fecundity) will lead to a net reproductive rate <1, and eventual population extinction. The degree of compensation dictates the maximum F that can be sustained (i.e., maintain $R_{0,F} \geq 1$). This reference point, F at extinction (F_{ext}), provides a starting point for choosing a safe level of exploitation (Shuter et al. 1998). It can be expressed in terms of an annual percentage exploitation rate, $100(1 - e^{-F_{\text{ext}}})$ or converted to a total mortality rate ($Z_{\text{ext}} = F_{\text{ext}} + M$), which translates to an annual percentage mortality of $100(1 - e^{-Z_{\text{ext}}})$.

Exploitation reduces population biomass and is expected to increase resource availability per capita and, thus, the net rate of energy acquisition for individuals. A density-dependent response in somatic growth rate due to exploitation is a plastic response that potentially affects various life-history traits identified in Eqs. 1 and 2. Faster somatic growth reduces the period during which young fish are especially vulnerable to predation and may increase early survival (i.e., $s_F > s_M$) (e.g., Ricker 1975:281). Faster growth reduces age at maturity ($T_F < T_M$) if length at maturity (L) remains constant (i.e., $L_F = L_M$). Faster growth increases fecundity at age ($\text{fec}_{t,F} > \text{fec}_{t,M}$), if reproductive investment (i.e., gonad mass/somatic mass) remains constant. Each of these changes is compensatory, but our ability to estimate a sustainable level of exploitation requires quantitative assessment of how growth compensation and associated life-history changes translate into net reproductive rate.

Application of the biphasic growth model to net reproductive rate

To explore the consequences of density-dependent growth, one needs a growth model that accommodates a trade-off between growth and reproduction. We employed the biphasic growth model (Lester et al. 2004, Shuter et al. 2005, Quince et al. 2008*a*, *b*) for this purpose. Although the von Bertalanffy (VB) growth equation is widely used to describe the lifetime growth pattern of somatic growth in fishes (e.g., Ricker 1975, Chen et al. 1992) and other organisms that exhibit indeterminate growth, life-history theory suggests that a single equation is incapable of accounting for both pre- and post-maturation growth (e.g., Roff 1983, Charnov 1993, Day and Taylor 1997, Charnov et al. 2001). Building on this concept, Lester et al. (2004) showed that lifetime growth is made up of two phases: a pre-maturation phase that depends solely on the net rate of energy acquisition, and a post-maturation phase that also depends on how much energy is invested in reproduction. The biphasic model showed that when reproductive investment is constant with age, the post-maturation growth phase is described by a VB growth equation.

The simplest biphasic growth model (Lester et al. 2004) assumes that net production is proportional to $W_t^{2/3}$ (where W_t is body mass at age t) and W_t is a cubic function of body length (l_t). These assumptions imply that, prior to maturity, all surplus energy is allocated to somatic growth and length at age (l_t) is therefore a linear function of age as follows:

$$l_t = h(t - \tau) \tag{3}$$

where h is the net rate of energy acquisition expressed in terms of somatic growth rate (i.e., mm/yr), and τ is the theoretical age when length equals zero (i.e., the y-intercept (l_0) equals $-h\tau$). For many fish species, annual investment in reproduction (g = gonad mass/somatic mass) is fairly constant over the reproductive life time of a typical female (Table 1 in Roff 1983). A constant g produces a post-maturation growth curve that is described by a VB growth equation with parameters (l_∞, k, and t_0) that are related to the net rate of energy acquisition (h), age at maturity (T), and reproductive investment (g) (see equations 3.1–3.4 in Lester et al. 2004). That is,

$$l_t = l_\infty\left(1 - e^{-k(t-t_0)}\right) \tag{4}$$

where

$$l_\infty = \frac{3h}{g} \tag{5}$$

$$k = \ln\left(1 + \frac{g}{3}\right) \tag{6}$$

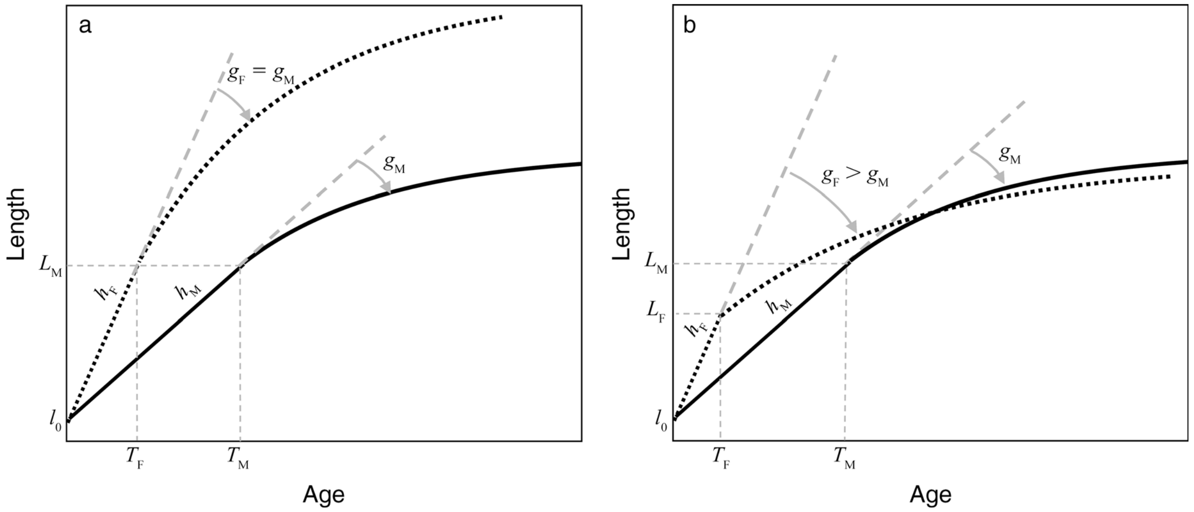

FIG. 1. Two examples of how growth and maturation may respond to exploitation. Solid lines show the unexploited growth pattern, and dotted lines show exploited growth patterns. Age (T) and length (L) at maturity are shown along the axes, with subscripts denoting unexploited (M) and exploited (F) cases. The y-intercept of the immature growth line is shown with l_0. Immature growth is linear and faster under the exploited condition ($h_{\mathrm{F}} > h_{\mathrm{M}}$). Post-maturation growth is slower and asymptotic due to the investment in reproduction (g), represented by the length of the arc connecting the realized growth curve to extrapolated immature growth line. (a) Length at maturity and reproductive investment are fixed at values that are optimal for the unexploited condition (i.e., a plastic response). (b) Length at maturity decreases, and reproductive investment increases, a result expected if the reproductive schedule adapts optimally to the increased mortality imposed by exploitation (i.e., an evolved response). In all cases, asymptotic length equals $3h/g$.

$$t_0 = T + \ln\left(1 - \frac{g(T-\tau)}{3}\right) \Big/ \ln\left(1 + \frac{g}{3}\right). \qquad (7)$$

When a population is subject to exploitation, the average lifetime growth pattern is expected to change (Fig. 1). Immature growth rate is expected to increase in response to an increase in the net rate of energy acquisition, but growth after maturity depends on how reproductive investment responds to the increase in surplus energy. In this paper, we contrast two types of life-history responses, which we label as plastic and evolutionary. The plastic response (Fig. 1a) assumes that length at maturity and reproductive investment do not change (i.e., $L_{\mathrm{F}} = L_{\mathrm{M}}$ and $g_{\mathrm{F}} = g_{\mathrm{M}}$); these traits remain fixed at values that maximize net reproductive rate in an unexploited population (i.e., when adult mortality rate $= M$). Therefore, when growth rate increases (i.e., $h_{\mathrm{F}} > h_{\mathrm{M}}$), age at maturity declines and asymptotic length increases (i.e., $l_{\infty,\mathrm{F}} = 3\ h_{\mathrm{F}}/g_{\mathrm{M}}$). This scenario describes an initial response to exploitation in which all compensation is due to an increase in growth rate and its automatic effect on age at maturity and fecundity at age.

The evolutionary response differs from the plastic response in that it maximizes net reproductive rate through more complex changes in life history. An example of this evolved response to exploitation is illustrated in Fig. 1b, where length at maturity has declined ($L_{\mathrm{F}} < L_{\mathrm{M}}$) and reproductive investment has increased ($g_{\mathrm{F}} > g_{\mathrm{M}}$). These types of changes are predicted by life-history theory (Roff 1992, Stearns 1992) and have been observed in some heavily exploited fish stocks (e.g., Rochet et al. 2000, Rijnsdorp et al. 2005, Jorgensen et al. 2007, van Walraven et al. 2010). As illustrated in Fig. 1b, reduced length at maturity supports earlier maturation, and increased reproductive investment redirects energy that would otherwise support somatic growth. The net effect of this evolved response is a smaller fish that is better adapted to the increase in mortality imposed by exploitation. Thus, an evolved response will support a level of exploitation that is higher than that of a plastic response. "How much higher?" is one question that we address in this paper.

We compared the fitness implications of the plastic and evolved responses by calculating their effects on net reproductive rate. As shown in Box 1, we used the biphasic growth model to expand the net reproductive rate formulae for unexploited (Eq. 1) and exploited (Eq. 2) cases. Given that fecundity is proportional to $gl_t^{\,3}$ and l_t is described by the biphasic model, the resulting formulae (see last row in Box 1) are of the form

$$R_{0,\mathrm{M}} = (Cs_{\mathrm{M}}h_{\mathrm{M}}^3) \times f(M, T_{\mathrm{M}}, g_{\mathrm{M}}) \qquad (8)$$

$$R_{0,\mathrm{F}} = (Cs_{\mathrm{F}}h_{\mathrm{F}}^3 e^{Ft_c}) \times f(M+F, T_{\mathrm{F}}, g_{\mathrm{F}}) \qquad (9)$$

where C combines parameters that are assumed to be constant and the functions $f(M,\ T_{\mathrm{M}},\ g_{\mathrm{M}})$ and $f(M+F,\ T_{\mathrm{F}},\ g_{\mathrm{F}})$ are expressed in the general form

Box 1. Derivation of formulae for net reproductive rate based on a biphasic growth model.

Unexploited population	Exploited population
Given $R_{0,\mathrm{M}} = \sum_{t=T_{\mathrm{M}}+1}^{\infty} s_{\mathrm{M}} \times e^{-Mt} \times \mathrm{fec}_{t,\mathrm{M}}$	Given $R_{0,\mathrm{F}} = \sum_{t=T_{\mathrm{F}}+1}^{\infty} s_F \times e^{-Mt} \times \mathrm{fec}_{t,\mathrm{F}} \times e^{-F(t-t_c)}$
then $R_{0,M} = s \sum_{t=T+1}^{\infty} e^{-Zt} \times \mathrm{fec}_t$	then $R_{0,F} = s \times e^{Ft_c} \sum_{t=T+1}^{\infty} e^{-Zt} \times \mathrm{fec}_t$
where $Z = M$, $s = s_{\mathrm{M}}$, $T = T_{\mathrm{M}}$, $\mathrm{fec}_t = \mathrm{fec}_{t,\mathrm{M}}$.	where $Z = M + F$, $s = s_{\mathrm{F}}$, $T = T_{\mathrm{F}}$, $\mathrm{fec}_t = \mathrm{fec}_{t,\mathrm{F}}$.

In general, $R_0 = s \times e^{Ft_c} \sum_{t=T+1}^{\infty} e^{-Zt} \times \mathrm{fec}_t$.

Given $\mathrm{fec}_t = \dfrac{gW_t}{2w_{\mathrm{egg}}}$ and $W_t = al_t^3$

then $R_0 = \left(\dfrac{ase^{Ft_c}}{2w_{\mathrm{egg}}}\right) \sum_{t=T+1}^{\infty} e^{-Zt} gl_t^3$.

Post-maturation growth is described by a VB function,

$l_t = l_\infty\left(1 - e^{-k(t-t_0)}\right)$, with biphasic model parameters (e.g., Lester et al. 2004) as follows:

$l_\infty = \dfrac{3h}{g}$, $k = \ln\left(1 + \dfrac{g}{3}\right)$, and $t_0 = T + \ln\left(1 - \dfrac{g}{3}(T - \tau)\right) \Big/ \ln\left(1 + \dfrac{g}{3}\right)$.

Substituting for l_t in the R_0 equation gives

$$R_0 = \left(\frac{27ash^3 e^{Ft_c}}{2w_{\mathrm{egg}}}\right) \sum_{t=T+1}^{\infty} e^{-Zt} \left(\frac{1}{g^2}\right) \left(1 - \left(1 - \frac{g(T-\tau)}{3}\right)\left(\frac{3}{3+g}\right)^{t-T}\right)^3$$

which is expressed in the closed form as

$R_0 = (Csh^3 e^{Ft_c}) \times f(Z, T, g)$

where

$$f(Z,T,g) = e^{-ZT}\left(\frac{1}{g^2}\right)\left(\frac{1}{e^Z - 1} + \frac{3\left(g(T-\tau) - 3\right)}{e^Z(3+g) - 3} + \frac{3\left(g(T-\tau) - 3\right)^2}{e^Z(3+g)^2 - 9} + \frac{3\left(g(T-\tau) - 3\right)^3}{e^Z(3+g)^3 - 27}\right)$$

$C = (13.5a/w_{\mathrm{egg}})$

Assigning subscripts for unexploited (M) and exploited (F) states implies:

$R_{0,\mathrm{M}} \;=\; (Cs_{\mathrm{M}}h_{\mathrm{M}}^3) \times f(M, T_{\mathrm{M}}, g_{\mathrm{M}})$ (8)	$R_{0,\mathrm{F}} \;=\; (Cs_{\mathrm{F}}h_{\mathrm{F}}^3 e^{F\,t_c}) \times f\,(M+F, T_{\mathrm{F}}, g_{\mathrm{F}})$ (9)

$$f(Z,T,g) = e^{-ZT}\left(\frac{1}{g^2}\right)\left(\frac{1}{e^Z - 1} + \frac{3\left(g(T-\tau) - 3\right)}{e^Z(3+g) - 3} + \frac{3\left(g(T-\tau) - 3\right)^2}{e^Z(3+g)^2 - 9} + \frac{\left(g(T-\tau) - 3\right)^3}{e^Z(3+g)^3 - 27}\right) \quad (10)$$

where Z refers to total mortality (i.e., $Z = M$ for unexploited, $Z = M + F$ for exploited).

In the R_0 equations (Eqs. 8 and 9), growth rate (h) and early survival (s) appear as multipliers that affect the absolute value of R_0, but not the values of T and g that maximize it. Thus, in a population where equilibrium is maintained by density-dependent effects operating on these multipliers (h and s), selection will produce an evolutionary stable strategy characterized by values of T

and g that maximize $f(Z, T, g)$ (Mylius and Diekmann 1995). Lester et al. (2004) showed that $f(Z, T, g)$ is a convex function of T and g with a single maximum. We will refer to the values of T and g that maximize R_0 as the optimal values for these variables and label them using an * superscript. The optimal values are closely approximated (Lester et al. 2004) by the following empirical functions of Z:

$$g^* \approx 1.18(1 - e^{-Z}) \qquad (11)$$

$$(T^* - \tau) \approx 1.95/(e^{Z} - 1). \qquad (12)$$

In this paper, we use a simpler formula, of similar accuracy, for predicting optimal age at maturity as follows:

$$(T^* - \tau) \approx \frac{2}{Z} - 1 \qquad (13)$$

(for Z in the range [0.05, 1.0], the difference between the exact value of T^* and the value given by Eq. 13 is less than 0.7 years and the proportional difference ranges from 2% to 12%). Given that $L = h(T - \tau)$ from Eq. 3, this simpler formula (Eq. 13) implies the optimal length at maturity is

$$L^* \approx h\left(\frac{2}{Z} - 1\right). \qquad (14)$$

We assume that, under selection, T, L, and g will evolve toward the optimal values given by Eqs. 11, 13, and 14: We refer to this shift in life-history parameters as the evolved response to exploitation. When these equations are used to assign optimal values to T and g in Eq. 10, $f(Z, T^*, g^*)$ is closely approximated by the following empirical function of Z:

$$f(Z, T^*, g^*) \approx e^{-Z\tau}\left(\frac{0.05}{Z^3}\right). \qquad (15)$$

Substituting this optimal form for $f(M, T_{\mathrm{M}}, g_{\mathrm{M}})$ and $f(M + F, T_{\mathrm{F}}, g_{\mathrm{F}})$ in Eqs. 8 and 9 implies

$$R^*_{0,\mathrm{M}} \approx (Cs_{\mathrm{M}}h^3_{\mathrm{M}}) \times e^{-M\tau_M}\left(\frac{0.05}{M^3}\right) \qquad (16)$$

$$R^*_{0,\mathrm{F}} \approx (Cs_{\mathrm{F}}h^3_{\mathrm{F}}e^{Ft_c}) \times e^{-(M+F)\tau_F}\left(\frac{0.05}{(M+F)^3}\right). \qquad (17)$$

Eqs. 16 and 17 describe the net reproductive rate in unexploited and exploited populations, respectively, after life-history traits have evolved to be optimally adapted to the existing total mortality rate. Given $R_0 = 1$ for both equilibrium situations ($Z = M$ and $Z = M + F$), Eqs. 16 and 17 can be equated ($R^*_{0,\mathrm{F}} = R^*_{0,\mathrm{M}} = 1$) to estimate sustainable F for an evolved response.

For a plastic response, the same principles apply, but different conditions apply when calculating $R_{0,\mathrm{F}}$ because life-history traits are not optimized for total mortality rate. Given that length at maturity and reproductive investment are fixed at values adapted to natural mortality rate (M), $R_{0,\mathrm{F}}$ is calculated by Eq. 9 assuming the following:

$$g_{\mathrm{F}} = 1.18(1 - e^{-M})$$

$$T_{\mathrm{F}} = \frac{h_{\mathrm{M}}}{h_{\mathrm{F}}}T_{\mathrm{M}}$$

or, more explicitly,

$$T_{\mathrm{F}} = \frac{h_{\mathrm{M}}}{h_{\mathrm{F}}}\left(\frac{2}{M} - 1\right) + \tau_{\mathrm{F}}.$$

Sustainable F for a plastic response can then be estimated by equating this result with Eq. 16.

Sustainable F assuming an evolved response to exploitation

Equating the optimal expressions for net reproductive rate (Eqs. 16 and 17; with evol for evolved response) implies

$$\left(\frac{M + F}{M}\right)_{\mathrm{evol}} \approx \left(\frac{s_{\mathrm{F}}}{s_{\mathrm{M}}}\right)^{1/3}\left(\frac{h_{\mathrm{F}}}{h_{\mathrm{M}}}\right)e^{Ft_c-(M+F)\tau_{\mathrm{F}}+M\tau_{\mathrm{M}}}. \qquad (18)$$

This equation cannot be solved analytically for F, but an approximate solution is obtained using a Taylor series expansion of the exponential term (see Appendix A) as follows:

$$\left(\frac{F}{M}\right)_{\mathrm{evol}} \approx \frac{\left(\frac{s_{\mathrm{F}}}{s_{\mathrm{M}}}\right)^{1/3}\left(\frac{h_{\mathrm{F}}}{h_{\mathrm{M}}}\right) - 1 - X}{1 - \left(\frac{s_{\mathrm{F}}}{s_{\mathrm{M}}}\right)^{1/3}\left(\frac{2 - M}{3}\right)\left(\frac{l_{\mathrm{c}}}{L_{\mathrm{M}}}\right)} \qquad (19)$$

where l_{c} is the smallest length subject to harvest, and $X = 0$ if the immature growth line passes through the origin ($\tau_{\mathrm{M}} = \tau_{\mathrm{F}} = 0$). Otherwise,

$$X = \left(\frac{s_{\mathrm{F}}}{s_{\mathrm{M}}}\right)^{1/3}\left(\frac{h_{\mathrm{F}}}{h_{\mathrm{M}}} - 1\right)\left(\frac{l_0}{L_{\mathrm{M}}}\right)\left(\frac{2 - M}{3}\right) \qquad (20)$$

where l_0 is the y-intercept of the growth curve (i.e., $l_0 = -h_{\mathrm{M}}/\tau_{\mathrm{M}} = -h_{\mathrm{F}}/\tau_{\mathrm{F}}$). All of these results hold for $l_{\mathrm{c}} \leq L_{\mathrm{F}}$, a constraint imposed by the structure of our model.

We evaluated this approximation of sustainable F/M by comparing predicted values to results obtained using numerical methods (see Appendix A). We estimated maximum sustainable (F/M) for a range of compensation in growth ($h_{\mathrm{F}}/h_{\mathrm{M}}$) and early survival ($s_{\mathrm{F}}/s_{\mathrm{M}}$). Plotting the numeric solution results against values predicted by Eq. 19 (Fig. 2a) indicates that it supplies a very good approximation.

Sustainable F assuming a plastic response to exploitation

To explore a purely plastic response to exploitation, we calculated net reproductive rate when length at maturation and reproductive investment were fixed at values adapted to the natural mortality rate (M). We used numerical methods (see Appendix A) to calculate maximum sustainable F/M for a range of compensation in growth and early survival. We then compared these values of F/M to values obtained assuming an evolved

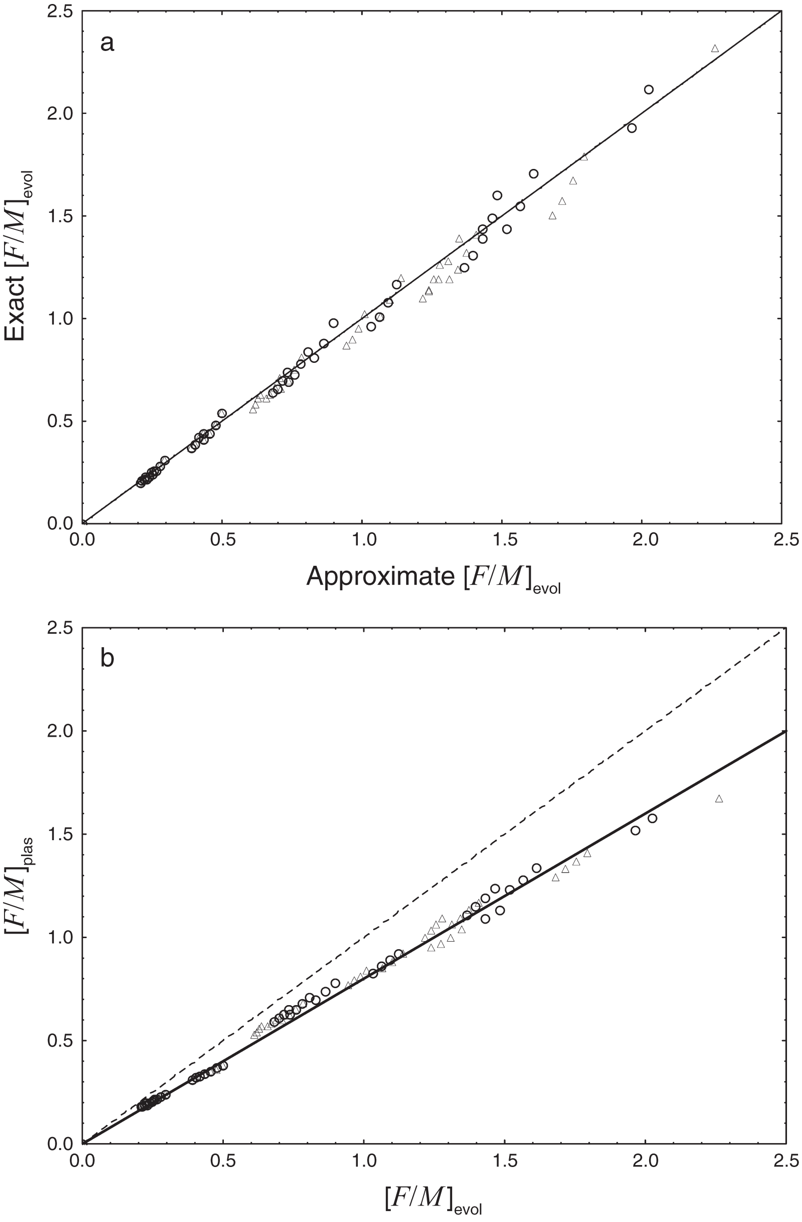

FIG. 2. Evaluation of Eq. 19 for calculating sustainable F/M. (a) Exact values of evolved response F/M ($[F/M]_{\mathrm{evol}}$) obtained by numerical methods are plotted against approximate values predicted by Eq. 19; the solid line is the line of equality. (b) Values of plastic response F/M ($[F/M]_{\mathrm{plas}}$) obtained by numerical methods are plotted against predicted values of $[F/M]_{\mathrm{evol}}$. The dashed line is the line of equality. The solid line is regression through the origin (slope $= 0.8$), indicating that the fishing mortality rate sustained by a plastic response is ~80% of the value sustained by the evolved response. Values were derived from a systematic exploration of the parameter space with the following ranges: growth compensation (1–2), survival compensation (1–2), M (0.1–0.4), l_c/L_M (0.5–1.0), where l_c is harvested length. Symbols indicate different values of l_0 (0 is shown with circles, 80 mm is shown with triangles), the y-intercept of the immature growth line. See Table 1 for clarification of abbreviations.

response (Fig. 2b). These results indicate that a plastic response can support a fishing mortality rate that is ~80% of the value sustained by an evolved response. The evolved response results from selective pressure that shifts length at maturity (L) and reproductive investment (g) toward the values given by Eqs. 14 and 11, respectively. Inspection of Eq. 14 shows that optimal L will be insensitive to changes in total mortality (Z) if increases in mortality are accompanied by compensatory increases in growth rate (h). Thus, density-dependent growth tends to buffer selective pressure for a reduced length at maturity.

Our results imply a plastic response (plas) is predicted by the following equation:

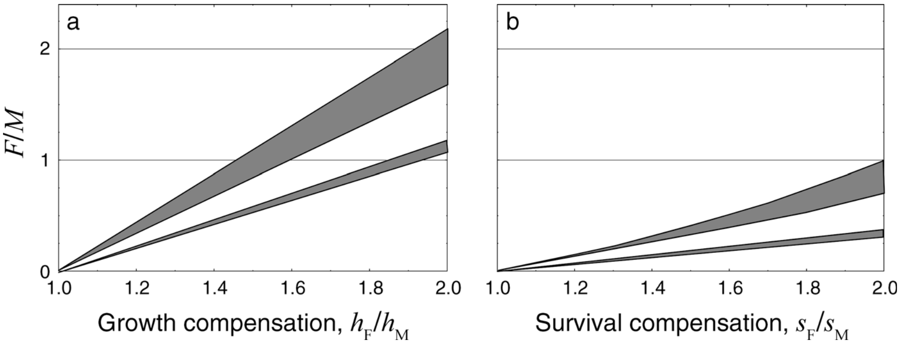

FIG. 3. The effect of compensation in (a) growth (h_F/h_M) and (b) survival (s_F/s_M) on sustainable levels of F/M assuming a plastic response (i.e., L and g are optimally adapted to M). Results are shown for $l_c/L_M = 0.5$ (lower gray wedge) and 1.0 (upper gray wedge). The range in response that characterizes each wedge was generated by varying M between 0.1 (top) and 0.4 (bottom) in Eq. 22, assuming that the immature growth line passes through the origin (i.e., $X = 0$). The x-axes are unitless because compensation is measured as a ratio.

$$\left(\frac{F}{M}\right)_{\text{plas}} \approx 0.80\left(\frac{F}{M}\right)_{\text{evol}}. \tag{21}$$

Substituting Eq. 19 for $(F/M)_{\text{evol}}$ implies

$$\left(\frac{F}{M}\right)_{\text{plas}} \approx 0.80\frac{\left(\frac{s_F}{s_M}\right)^{1/3}\left(\frac{h_F}{h_M}\right) - 1 - X}{1 - \left(\frac{s_F}{s_M}\right)^{1/3}\left(\frac{2-M}{3}\right)\left(\frac{l_c}{L_M}\right)}. \tag{22}$$

The implications of this plastic response are demonstrated in Fig. 3. Sustainable F increases with the degree of compensation in both growth (h_F/h_M) and early survival (s_F/s_M); however, survival compensation is less effective in sustaining exploitation than growth compensation. Sustainable F values also depend on the size at which fish begin to be exploited. Sustainable F increases with l_c because exploitation is increasingly directed at a smaller segment of the population. Because our model applies only when exploitation begins at or before maturity, the highest values of F/M result when harvesting begins at the size of maturity. When this is the case, a twofold increase in growth rate supports $F \approx 2M$. Because exploitation of fish stocks generally begins when fish are nearing their length at maturity (Pauly 1984, Shuter et al. 1998), this example is probably a slight overestimate of the maximum F that could be supported by twofold growth compensation.

APPLICATION OF THE COMPENSATION MODEL TO WALLEYE FISHERIES

In this section, we use the plastic model developed in the previous section to estimate maximum sustainable fishing mortality rate for walleye: a large, predatory fish that is an important recreational and commercial resource throughout much of Canada and the United States. Traditionally (and naturally), sustainable exploitation rate for any species is estimated on a population-by-population basis by observing changes in abundance and life history that are concurrent with changes in exploitation intensity. This approach is impractical when developing management guidelines for resources that are data poor or distributed widely among many populations (e.g., freshwater fish; Shuter et al. 1998, Lester et al. 2003, Hansen et al. 2010).

Our compensation model is ideally suited for managing data-poor or widely distributed resources because it predicts maximum sustainable fishing mortality rate (F_{ext}) from a handful of life-history traits. Given a plastic response (described by Eq. 22), this reference point can be calculated as

$$F_{\text{ext}} \approx 0.80\,M\frac{\left(\frac{s_F}{s_M}\right)_{\text{ext}}^{1/3}\left(\frac{h_F}{h_M}\right)_{\text{ext}} - 1 - X}{1 - \left(\frac{s_F}{s_M}\right)_{\text{ext}}^{1/3}\left(\frac{2-M}{3}\right)\left(\frac{l_c}{L_M}\right)} \tag{23}$$

where

$$X = \left(\frac{s_F}{s_M}\right)_{\text{ext}}^{1/3}\left(\frac{h_F}{h_M} - 1\right)_{\text{ext}}\left(\frac{l_0}{L_M}\right)\left(\frac{2-M}{3}\right). \tag{24}$$

To calculate F_{ext} for any population, one therefore requires estimates of potential compensation in growth $[(h_F/h_M)_{\text{ext}}]$, potential compensation in early survival $[(s_F/s_M)_{\text{ext}}]$, natural mortality rate (M), length at maturity when unexploited (L_M), and minimum harvested length (l_c). If the immature growth line passes through the origin, then $X = 0$; if not, one needs to know its y-intercept (l_0). (Note that because l_0 is typically small relative to L_M, X is also small and produces only a minor adjustment to the estimate of F_{ext} based on $X = 0$). In this section, we show how most of these parameters can be estimated for any walleye population. The one exception is potential compensation in early survival, which is not easily measured. For this parameter, we take a conservative approach by assuming no compensation in early survival.

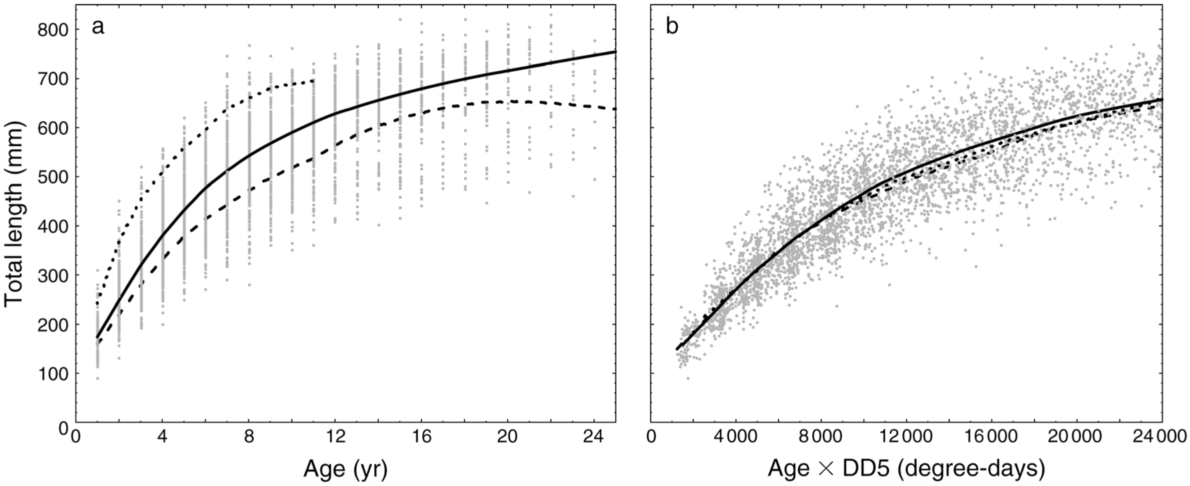

FIG. 4. Variation in female walleye growth. Gray points are mean female total length at age of female cohorts in 425 populations. (a) Mean total length is plotted against calendar age (years). (b) Mean total length is plotted against thermal age (i.e., age × DD5 [degree-days >5°C]). In both graphs, the lines are LOWESS (locally weighted least squares) fits for different climatic groups based on DD5 (dashed is <1500, solid is 1500–2500, and dotted is >2500 degree-days). The three LOWESS lines are not always distinguishable in panel (b) because they sometimes overlap. See Appendix B for data sources.

Sources of data

We estimated walleye parameters using comparative data that were available for populations across a broad climatic gradient. Our data sources included syntheses of walleye data (Colby et al. 1979, Carlander 1997, Zhao et al. 2008), case studies reported in the literature, and survey databases maintained by the provinces of Ontario and Quebec. Our collection included growth data for 425 populations and maturation and mortality data for 92 populations (see Appendix B for details). These populations were distributed from northern Canada to the southern United States, spanning a climatic gradient of 1000 to 4000 degree-days (DD5, degree-days >5°C).

Walleye life-history parameters

The life-history variation of walleye across a broad temperature gradient is well studied (Colby et al. 1979, Colby and Nepszy 1981, Beverton 1987, Baccante and Colby 1996, Quist et al. 2003, 2004, Venturelli at al. 2010*a*, Bozek et al. 2011). These studies demonstrate that walleye grow faster, mature earlier, and die younger in warmer climates, and that there is residual (i.e., temperature independent) variation both among and within populations. Lifetime growth patterns of female walleye are highly variable, but much of this variation is due to the effect of climate (Fig. 4). We applied a thermal age concept (Neuheimer and Taggart 2007, Venturelli et al. 2010*a*) to account for climatic-driven differences in life history. Walleye growth rate is proportional to DD5, and, consequently, a climate effect can be largely extracted by expressing calendar age (years) as thermal age (years × annual DD5). This conversion results in average growth patterns that differ little among climatic zones (Fig. 4b): LOWESS (locally weighted least squares) fits of mean length at thermal age are virtually identical across zones.

We estimated potential growth compensation in walleye populations by focusing on the immature segment of the growth curve (Fig. 5). Previous work has shown that the lifetime growth pattern of walleye is well described by the biphasic growth model (Shuter et al. 2005, Rennie et al. 2008, Bozek et al. 2011). The immature growth rate is therefore a measure of the net rate of energy acquisition, variation in which reflects density-dependent availability of food. As illustrated by the maturity estimates shown in Fig. 5, the minimum thermal age at maturity of walleye is ~6000 degree-days (see also Venturelli et al. 2010*a*). For cohorts younger than this criterion, mean length at thermal age was approximately linear within populations and variation among populations was wedged shaped. Quantile regression (5% and 95%) characterized this wedge as given by $l_t = 80 + ht$, where t is thermal age, and h ranges approximately twofold from 0.0030 to 0.0067 mm/degree-day. We assumed that this wedge described the response of growth to changes in food availability and was therefore an estimate of potential growth compensation within a single population. In other words, we assumed that the slow growth line was characteristic of an unexploited, high-density population (i.e., h_{M}), and that the fast growth line was characteristic of a heavily exploited, low-density population (i.e., h_{F} close to extinction). Under this assumption, the resultant maximum growth compensation $[(h_{\mathrm{F}}/h_{\mathrm{M}})_{\mathrm{ext}}]$ was approximately twofold.

Additional support for twofold growth compensation in walleye comes from Venturelli (2009), who studied changes in growth and maturation within six walleye populations in which there were large changes in abundance (Fig. 5). In all six of these populations, immature growth rate increased as density decreased

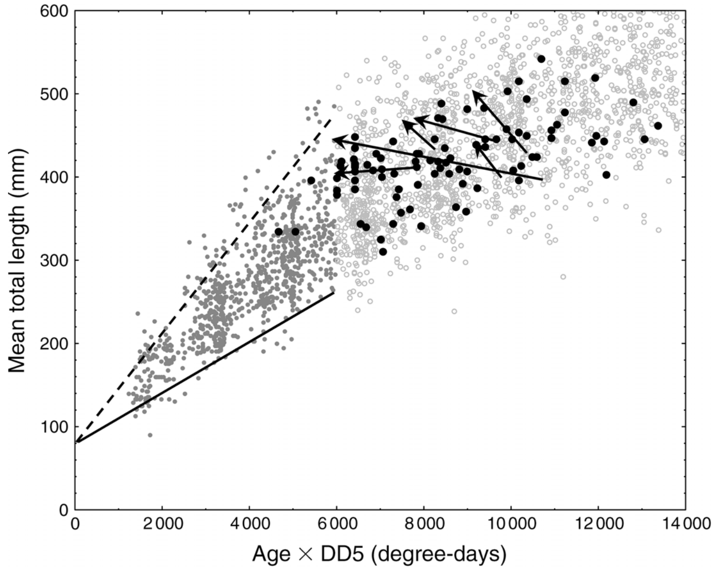

FIG. 5. Walleye growth and maturation. Small gray circles are mean female length at thermal age from 425 populations. For the immature segment of the growth curve (solid gray circles) where thermal age < 6000 degree-days, mean length at thermal age is bounded by 5% and 95% quantile regression lines, implying a common intercept = 80 mm and slopes = 0.0304 and 0.0665 mm/degree-day. Estimates of the slope for 5% and 95% quantiles varied little among climatic zones (5% slope = 0.0338, 0.0323, and 0.0274; 95% slope = 0.073, 0.0656, and 0.0714). Large black circles are size and thermal age at maturity of 92 populations (see Appendix B). Lines with arrows show change in size and age at maturity for six populations in which large changes in walleye abundance have occurred (data from Venturelli [2009]), illustrating that age at maturity is more variable than length at maturity.

and the maximum observed growth compensation was twofold. Venturelli (2009) also showed that age at maturity was more sensitive than length at maturity to changes in growth rate. Based on these observations (summarized in Fig. 5), we assumed that growth rate increases as a result of exploitation, but that length at maturity remains constant. We used the approximate observed mean value ($L_{\mathrm{M}} = 420$) when calculating F_{ext} for walleye. Female length at maturity varies (range = 311–543 mm) among populations, but this variation is not related to climate (Bozek at al. 2011).

We estimated natural mortality rate (M) by assuming that length and age at maturity in an unexploited population were optimized to maximize net reproductive rate. Given a biphasic growth model, optimal length at maturity (see Eq. 14) is

$$L_{\mathrm{M}} \approx h_{\mathrm{M}}\left(\frac{2}{M} - 1\right)$$

which re-arranges to

$$M = \frac{2 \times h_{\mathrm{M}}}{L_{\mathrm{M}} + h_{\mathrm{M}}}. \tag{25}$$

Given $h_{\mathrm{M}} = 0.0030$ DD5, then

$$M = \frac{0.06 \times \mathrm{DD5}}{L_{\mathrm{M}} + 0.03 \times \mathrm{DD5}}. \tag{26}$$

Given the mean value of L_{M} (420 mm), Eq. 26 implies that M increases from ~0.13 at the northern boundary of the walleye's range (DD5 = 1000 degree-days) to 0.44 at its approximate southern boundary (DD5 = 4000 degree-days). M is less sensitive to variation in length at maturity than it is to climate. For example, when DD5 = 2000 degree-days, a decrease in L_{M} from 543 to 311 mm (i.e., the observed range) causes M to increase from 0.20 to 0.32 per year.

Empirical estimates of total mortality for unexploited and exploited walleye populations provided strong support for our M model (Fig. 6; see Appendix B for details). For populations in Fig. 5, we used length at maturity and degree days to predict natural mortality rate. We then plotted estimates of total mortality rate against predicted natural mortality. As expected, most total mortality estimates were greater than predicted rates of natural mortality. However, estimated total mortality was approximately equal to predicted natural mortality in 12 lakes in which fishing was illegal or access was limited.

Walleye F at extinction (F_{ext})

Assuming a plastic response to exploitation (Eq. 23), we calculated F_{ext} of walleye over a range of climates (DD5 = 1000–4000 degree-days). These calculations used the following parameter estimates: $(h_{\mathrm{F}}/h_{\mathrm{M}})_{\mathrm{ext}} = 2$, $L_{\mathrm{M}} = 420$ mm, $l_0 = 80$ mm, and M increasing with degree days as specified in Eq. 26. We assumed $(s_{\mathrm{F}}/s_{\mathrm{M}})_{\mathrm{ext}} = 1$ because we could not measure it, and we manipulated minimum harvested length ($l_{\mathrm{c}} = 250$ to L_{M}) to explore the sensitivity of F_{ext} to size restrictions. The lower end of this range matches a value that has been observed in Ontario lakes when size restrictions do not exist

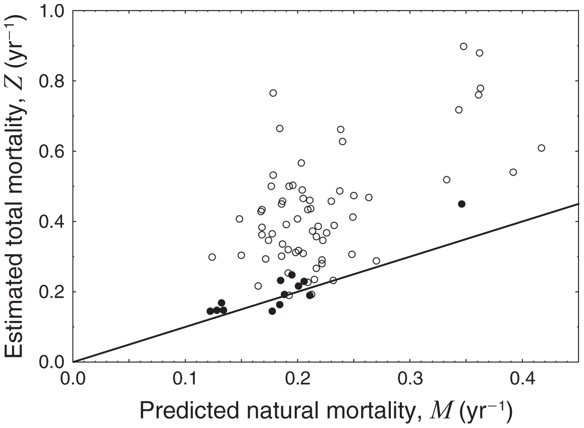

FIG. 6. Estimates of instantaneous total mortality rate (Z) for 71 walleye populations plotted against natural mortality rate (M) predicted from length at maturity and DD5 (Eq. 26). The solid line is the line of equality (i.e., $Z = M$). Solid circles identify 12 populations for which exploitation is known to be very light because the lake is either a sanctuary or in a remote location. Open circles show data from exploited populations. See Appendix B for data sources.

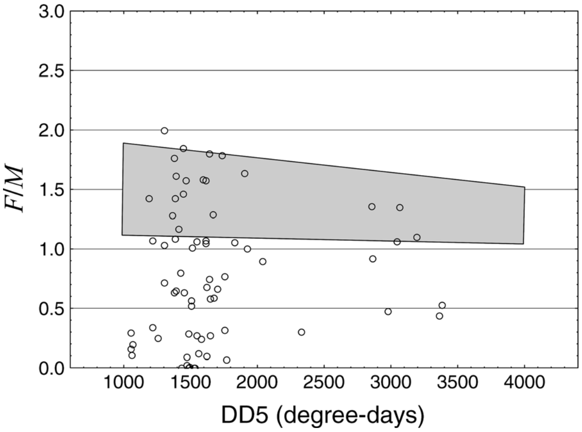

FIG. 8. Estimates of F/M for exploited walleye populations plotted against DD5 (open circles). The shaded area bounds predicted values for F_{ext}/M derived by assuming: twofold compensation in growth, size at maturity (L_{M}) = 420 mm, M estimated from L_{M} and DD5 using Eq. 26, and minimum harvested size (l_{c}) ranging from 250 (lower bound) to 420 mm (upper bound).

(Ontario Ministry of Natural Resources, *unpublished data*).

Model results (Fig. 7) demonstrate that F_{ext} increases with minimum harvested length and degree days. This degree day effect is due to a climate-driven increase in natural mortality rate. The model predicts that F_{ext}/M is approximately equal in all climates. Twofold compensation in growth can support fishing mortality that exceeds natural mortality: F_{ext}/M increases from $\approx$1.1, when $l_{\mathrm{c}} = 250$ mm, to much higher levels as l_{c} approaches length at maturity (Fig. 7b). When $l_{\mathrm{c}} \approx L_{\mathrm{M}}$, F_{ext}/M ranges from 1.8 to 1.5 as DD5 increases from 1000 to 4000 degree-days.

To evaluate the predictions of our model, we compared predicted values of F_{ext} to values of F estimated for the walleye populations in Fig. 6. None of these populations has been identified by local managers as being seriously overexploited. We estimated F by subtracting M from the total mortality estimates shown in Fig. 6. We then plotted the ratio of F/M for each population against DD5 (Fig. 8). Predicted values for F_{ext}/M, derived assuming twofold growth compensation and a range in minimum harvested size ($l_{\mathrm{c}}/L_{\mathrm{M}} =$ 0.6 to 1.0), effectively set an upper bound on the observed F/M ratios. This upper bound indicates that our empirical estimate of potential growth compensation $[(h_{\mathrm{F}}/h_{\mathrm{M}})_{\mathrm{ext}}]$ was large enough to support the observed rates of exploitation in most populations. It is tempting to conclude that exploitation was unsustainable in the one lake in which observed F/M exceeded predicted F_{ext}/M, but it is important to recognize that compensation in early survival $[(s_{\mathrm{F}}/s_{\mathrm{M}})_{\mathrm{ext}}]$ may also play a role. Because concurrent and related compensatory

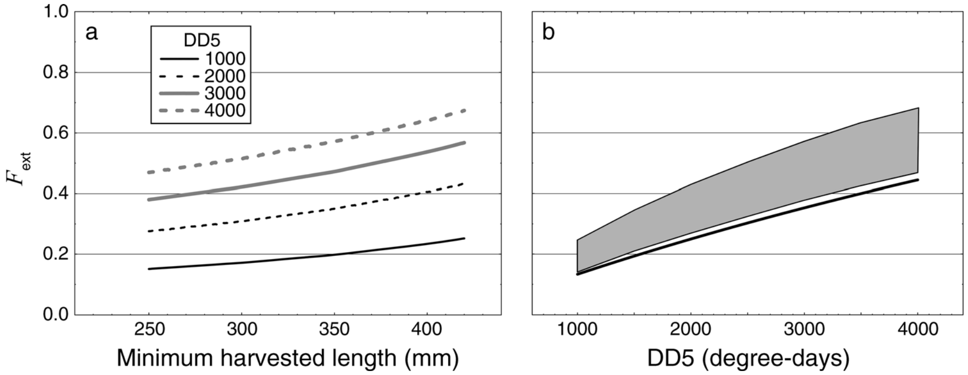

FIG. 7. Predicted values of F at extinction (F_{ext}) over ranges for both minimum harvested length ($l_{\mathrm{c}} = 250$–420) and degree-days (DD5): (a) results plotted against l_{c} for four values of DD5 (1000–4000 degree-days) and (b) results plotted against DD5. The gray wedge in panel (b) shows the increase in F_{ext} that results when l_{c} increases from 250 to 420 mm; the solid line beneath the wedge shows natural mortality. Values were derived from Eq. 23, assuming $(h_{\mathrm{F}}/h_{\mathrm{M}})_{\mathrm{ext}} = 2$, $L_{\mathrm{M}} = 420$ mm, $l_0 = 80$ mm.

changes in both growth and survival are likely (e.g., Post et al. 1999), joint compensatory responses may be involved in sustaining observed levels of exploitation in many of these populations (see the *Discussion*).

Discussion

The initial goal of this research was to examine how density-dependent plasticity in life history supports sustainable exploitation. In modeling this process, it became apparent that the density-dependent effects of exploitation could not be cleanly isolated from evolutionary effects. In specifying a plastic response to exploitation, one must assume reaction norms describing how length at maturity, age at maturity, and reproductive investment change with growth rate. We assumed that length at maturity and reproductive investment were fixed at values adapted to the natural (i.e., unexploited) mortality rate; consequently, age at maturity decreases as growth rate increases (Fig. 1a). We also explored an evolved response to exploitation, in which maturation and reproductive investment adjust to maximize net reproductive rate, given the total mortality imposed by exploitation.

Life-history theory predicts that an increase in mortality rate (e.g., due to exploitation) will select for earlier age at maturity and higher reproductive investment (Roff 1992, Stearns 1992). Earlier age at maturity results from selection for smaller length at maturity or faster growth rate. These evolutionary life-history changes effectively maximize egg production over a shortened life span via a trade-off between reproductive investment and adult size (i.e., individuals mature at a lower age and size, and grow little because of high investment in reproduction; Fig. 1b). In contrast, shorter term, plastic responses to exploitation usually involve an increase in growth rate with relatively little change in length at maturity (Trippel 1995, Rochet 1998, Rochet et al. 2000, Rose et al. 2001, Hsieh et al. 2010), leading indirectly to a lower age at maturity. This plastic response deflates the selective advantage of reduced body size because it moves age at maturity in the same direction as selection, with consequent increases in reproductive life span and reproductive output. Our finding that plasticity approaches evolution in its ability to buffer net reproductive rate against increases in mortality is consistent with work of Kuparinen and Hutchings (2012). It implies that there is strong selective pressure to evolve plasticity in growth rate.

Our analysis suggests that a plastic response can support exploitation-driven mortality that is ~80% of the level supported by evolutionary changes in length at maturity and reproductive investment. It demonstrates the extent to which plasticity can buffer selection pressures that drive evolutionary changes in life-history traits. More importantly, it demonstrates that, while plasticity can be very effective in allowing individuals to respond quickly to exploitation, it cannot eliminate selection for more complex changes in life history. Our model does not address the complexity of life-history evolution that may occur (e.g., de Roos et al. 2006, Dunlop et al. 2007, 2009, Arlinghaus et al. 2009, Matsumura et al. 2011, Jorgensen and Holt 2013). Our plastic response model is designed to predict exploitation levels that are sustainable in the absence of long-term, evolutionary change, thus providing the guidelines that are essential for effective management of exploitation. In one sense, these guidelines are conservative because evolutionary changes may support higher levels of exploitation. In another sense, these guidelines are liberal because lower levels of exploitation may be necessary if it is deemed desirable to avoid long-term evolutionary change.

Our model predicts that the ratio F/M (i.e., sustainable F relative to natural mortality rate) is determined by the compensation in growth (h_F/h_M), the compensation in early survival (s_F/s_M) and the ratio l_c/L_M (i.e., the initial length at harvesting relative to length at maturity). Eq. 22 quantifies the relative sensitivity of F/M to each of these factors (see Fig. 3). It shows that s_F/s_M has less of an effect on F/M than h_F/h_M and that the impact of either or both of these compensatory changes depends on l_c/L_M: sustainable F increases with the minimum length of harvesting.

A useful starting point in choosing an optimal level of fishing is to predict F_{ext}, the minimum fishing mortality rate that would cause population extinction. This reference point is calculated from estimates of maximum compensation in growth [$(h_F/h_M)_{ext}$] and early survival [$(s_F/s_M)_{ext}$]. Estimating potential growth compensation for a population can be a challenge because of confounding effects of temperature, productivity, and food web complexity, and because populations are rarely observed in the unexploited state. We examined variation in growth both within and among walleye populations and concluded that $[h_F/h_M]_{ext} \approx 2$ (Fig. 5). This analysis benefited from the degree-day approach, which is useful for partitioning growth into temperature-dependent and temperature-independent components (Neuheimer and Taggart 2007, Venturelli et al. 2010*a*, Neuheimer and Grønkjær 2012). Growth compensation can also be estimated from laboratory or hatchery studies (e.g., Bjornsson and Steinarsson 2002), field experiments (e.g., Post et al. 1999), archeological data (e.g., Balazik et al. 2010), and density-dependent models of growth (e.g., Walters and Post 1993, Lorenzen and Enberg 2002).

Compensation in early survival is difficult to estimate. A conservative approach assumes no compensation and predicts F_{ext} based on growth compensation alone. The structure of our model suggests that this minimum estimate may offer a close approximation of F_{ext}, because much larger changes in early survival are needed to match the effect of a change in growth. However, it is likely that compensatory increases in growth rate are accompanied by some compensatory increase in early survival via improved competitive

PLATE 1. Walleye caught by a winter angler in Ontario, Canada. Photo credit: Steve Lawrence.

ability and predator avoidance (Miller et al. 1988, Sogard 1997, Post et al. 1999, Cowan et al. 2000, Rose et al. 2001). If early survival increases with growth rate, F_{ext} will be underestimated by this conservative approach. Progress in understanding this linkage can benefit from experimental stocking (e.g., Post et al. 1999), as well as empirical modeling (e.g., McGurk 1986, Lorenzen 1996).

Understanding potential compensation in growth was essential to developing a model to predict natural mortality (M) for walleye. Life-history theory predicts that M can be estimated from age at maturity (T) in an unexploited population (equation 4.5 in Lester et al. 2004), but this approach is a challenge because unexploited T is rarely known. In this paper, we extended the Lester et al. (2004) model to predict M from growth rate and length at maturity in an unexploited population (see Eq. 25). This formulation was more useful for estimating M because the required growth rate could be estimated as the minimum observed growth rate (see Fig. 5) and because length at maturity (L) is relatively insensitive to large changes in walleye abundance (Venturelli et al. 2010*a*). This relative insensitivity of L is predicted by theory (Stearns and Koella 1986) and common among exploited fishes (Trippel 1995, Rochet 1998, Rochet et al. 2000, Rose et al. 2001, Hsieh et al. 2010). Eq. 26 predicts that M in walleye increases from ~0.13 to 0.44 across a climatic gradient of DD5 = 1000 to 4000 degree-days. This trend is likely due to the direct effects of temperature on growth and mortality, as well as the trade-offs that link growth, M, and reproductive investment: walleye at 1000 degree-days grew more slowly, invested less in reproduction, and lived for longer than walleye at 4000 degree-days. Similar effects have been documented in many fish species (e.g., Pauly 1980, Winemiller and Rose 1992, Gislason et al. 2010) and other organisms (McCoy and Gillooly 2008).

The compensation model predicts F_{ext} as a matter of convenience; ideally, F should take some optimal value (F_{opt}) that is less than F_{ext} and maximizes the benefits to a fishery without jeopardizing its sustainability. This F_{opt} is usually specified as the F corresponding to maximum sustainable yield (MSY; e.g., Graham 1935), maximum sustainable rent (e.g., Gordon 1954), maximum discounted yield (e.g., Plourde 1970), maximum discounted rent (e.g., Clark 1973), or some other social optimum (Johnston et al. 2010). Alverson and Pereyra (1969) and Gulland (1970, 1971) originally proposed $F_{\text{opt}} \approx M$, which holds when recruitment is constant (Francis 1974). Given stochastic processes, nonequilibrium, and depensation, $F_{\text{opt}} < M$ is now considered to be a more appropriate (and risk averse) reference point (Patterson 1992, Walters and Martell 2002, Zhou et al. 2012).

Based on our results, we propose $F_{\text{safe}} = 0.5\ F_{\text{ext}}$ as a useful reference point for managing walleye fisheries. Because this reference point corresponds to MSY in a classic surplus production model (Graham 1935, Schaefer 1954), it can be grouped with the various optimally based reference points (F_{opt}). When the minimum harvested size equals the size at maturity and growth compensation is twofold, $F_{\text{ext}} \geq 1.5M$ (Fig. 8) and, hence, $F_{\text{safe}} \approx 0.75\ M$. Thus, our model generally agrees with the rule of thumb that $F_{\text{opt}} \approx M$ (Alverson and Pereyra 1969, Gulland 1970, 1971) and empirical evidence that $F_{\text{opt}}/M = 0.67$–0.87 (Patterson 1992, Zhou et al. 2012), but with the caveats that (1) agreement depends on minimum harvested size relative to size at maturity (l_c/L) and (2) $F_{\text{opt}} \gg 0.5\ M$ must be carefully justified (e.g., Walters and Martell 2002). For walleye, when minimum harvested size is not restricted by regulations, a conservative strategy is to assume that small individuals are exploited, and therefore, set $F_{\text{safe}} < 0.75\ M$. For example, if small individuals were harvested such that $l_c/L = 0.5$, then $F_{\text{safe}} \approx 0.5\,M$. If small individuals are protected from exploitation (e.g., $l_c \geq L$) then $F_{\text{safe}} > 0.75\ M$ may be justified.

The extent to which $F_{\text{safe}}/M \approx 0.75$ is applicable to other species depends mainly on whether $(h_F/h_M)_{\text{ext}} \approx 2$; however, this guideline is easily adapted to other degrees of growth compensation. The literature indicates that growth compensation may be as high as twofold for other species (e.g., Atlantic cod [*Gadus morhua*; Bjornsson and Steinarsson 2002], Atlantic herring [*Clupea harengus*; Engelhard and Heino 2004], brown trout [*Salmo trutta*; Lobon-Cervia 2007], and rainbow trout [*Oncorhynchus mykiss*; Post et al. 1999]). However, we can calculate F_{safe} for any value of $(h_F/h_M)_{\text{ext}}$ because F_{safe} is roughly proportional to the relative increase in growth rate:

$$F_{\text{safe}}/M \approx 0.75\Big((h_F/h_M)_{\text{ext}} - 1\Big). \tag{27}$$

For example, if $(h_F/h_M)_{\text{ext}} = 1.5$ for yellow perch (*Perca flavescens*; Pierce et al. 2006), then $F_{\text{safe}}/M \approx 0.38$. This method of estimating F_{safe} is conservative because it relies solely on estimates of growth compensation and ignores a potential increase in early survival.

Our purpose in this paper was twofold: to (1) build a general framework for exploring the effects of compensation on life-history changes and population dynamics, and (2) use this framework to explore the influence of the two most commonly discussed types of compensation (growth and early survival). Our compensation model was able to predict sustainable rates of exploitation because it is based on the biphasic growth model, which accounts for the trade-off between somatic growth and reproductive investment (Lester et al. 2004). We used the simplest form of the biphasic model because it provides a close approximation of the trade-off between growth and reproduction and is effective at accounting for inter-population variation in walleye life histories (Shuter et al. 2005). Our efforts were rewarded by some relatively simple solutions that describe the role of different compensatory life-history changes in supporting exploitation. These solutions are useful for generating "rules of thumb" that predict safe rates of exploitation when appropriate population and harvest data are lacking; for example, in data-poor fisheries or when the number of populations in a region exceeds the capacity to monitor them.

In future extensions of this work, it would be informative to examine the influence of other factors such as compensation in adult natural mortality (Hansen et al. 2011, Jorgensen and Holt 2013), maternal effects, and stochastic variation in population parameters (Lande et al. 1997, Lillegård et al. 2005). It is possible to develop more complex compensation models by incorporating more general biphasic growth models that relax certain assumptions. For example, Quince et al. (2008*a*, *b*) showed that size-dependent maternal effects could be incorporated by relaxing the assumption that reproductive investment (g) is constant with size. In some species, older larger females produce a higher quality egg-enhancing survival during the embryonic and larval stages (e.g., Longhurst 2002, Berkeley et al. 2004, Hsieh et al. 2010, Venturelli et al. 2010*b*). This condition would offset the benefit of increasing minimum length at harvesting as predicted in the current model. Such refinements to the compensation model may provide more nuanced results but will not change the way that life-history traits interact to affect compensation. Therefore, we view the simplest form of the compensation model (Eq. 22) as a general framework for exploring the effects of compensatory life-history changes on population dynamics and sustainable levels of exploitation.

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Supplemental Material

Appendix A

Formulae for estimating sustainable fishing mortality (*Ecological Archives* A024-002-A1).

Appendix B

Documentation of walleye data (*Ecological Archives* A024-002-A2).

Appendix A. Formulae for Estimating Sustainble Fishing Mortality

Evolved response: Length/age at maturity and reproductive investment are optimal

Table A1 shows the theory for estimating sustainable fishing mortality when the life history response is optimal (i.e., evolved). In this case, length (L_F) and age (T_F) at maturity, as well as reproductive investment (g_F), are optimally adapted to total mortality rate ($Z = M+F$). Derivations shown in Table A1 supplied the following equation for estimating sustainable F/M:

$$\left(\frac{s_F}{s_M}\right)\left(\frac{h_F}{h_M}\right)^3\left(\frac{f_1\,(M+F)}{f_1\,(M)}\right) e^{\frac{F\,l_c}{h_F}+M\,l_0\left(\frac{1}{h_F}-\frac{1}{h_M}\right)} = 1 \tag{A.1}$$

An approximate analytical solution of this equation is available because the function $f_1(Z)$ is closely approximated by the following empirical function:

$$f_1\,(Z) \approx \frac{0.05}{Z^3} \tag{A.2}$$

Substituting for $f_1(M)$ and $f_1(M+F)$ in equation (A.1) gives

$$\left(\frac{M+F}{M}\right)^3 \approx \left(\frac{s_F}{s_M}\right)\left(\frac{h_F}{h_M}\right)^3 e^{\frac{F\,l_c}{h_F}+M\,l_0\left(\frac{1}{h_F}-\frac{1}{h_M}\right)}\ , \tag{A.3}$$

which reduces to

$$\frac{F}{M} \approx \left(\frac{s_F}{s_M}\right)^{1/3}\left(\frac{h_F}{h_M}\right) e^{\frac{F\,l_c}{3\,h_F}+\frac{M\,l_0}{3}\left(\frac{1}{h_F}-\frac{1}{h_M}\right)} - 1\ . \tag{A.4}$$

Because $e^{\frac{F\,l_c}{3\,h_F}+\frac{M\,l_0}{3}\left(\frac{1}{h_F}-\frac{1}{h_M}\right)}$ is a small number, it can be approximated by a Taylor Series expansion as $1+\frac{F\,l_c}{3\,h_F}+\frac{M\,l_0}{3}\left(\frac{1}{h_F}-\frac{1}{h_M}\right)$. Equation (A.4) then becomes

$$\frac{F}{M} \approx \left(\frac{s_F}{s_M}\right)^{1/3} \left(\frac{h_F}{h_M}\right) \left(1 + \frac{F\,l_c}{3\,h_F} + \frac{M\,l_0}{3}\left(\frac{1}{h_F} - \frac{1}{h_M}\right)\right) - 1\,, \tag{A.5}$$

a form that can be solved for *F/M*, as shown below.

To simplify matters, we first show the solution for $l_0 = 0$ (i.e., immature growth line passes through the origin). In this case, (A.5) becomes

$$\frac{F}{M} \approx \left(\frac{s_F}{s_M}\right)^{1/3} \left(\frac{h_F}{h_M}\right) \left(1 + \frac{F\,l_c}{3\,h_F}\right) - 1$$

which expands to

$$F \approx M \left(\frac{s_F}{s_M}\right)^{1/3} \left(\frac{h_F}{h_M}\right) + F \left(\frac{s_F}{s_M}\right)^{1/3} \left(\frac{M\,l_c}{3\,h_M}\right) - M$$

and then to

$$F \left(1 - \left(\frac{s_F}{s_M}\right)^{1/3} \left(\frac{M\,l_c}{3\,h_M}\right)\right) \approx M \left(\frac{s_F}{s_M}\right)^{1/3} \left(\frac{h_F}{h_M}\right) - M\,,$$

implying

$$\frac{F}{M} \approx \frac{\left(\frac{s_F}{s_M}\right)^{1/3} \left(\frac{h_F}{h_M}\right) - 1}{1 - \left(\frac{s_F}{s_M}\right)^{1/3} \frac{M\,l_c}{3\,h_M}}\,. \tag{A.6}$$

This form can be re-arranged so that l_c is expressed relative to length at maturity in an unexploited population (L_M). Given that optimal length at maturity (equation 14) is $L_M = h_M \left(\frac{2}{M} - 1\right)$, it follows that $h_M = \frac{L_M\,M}{(2 - M)}$. Substituting for h_M in (A.6) gives

$$\frac{F}{M} \approx \frac{\left(\frac{s_F}{s_M}\right)^{1/3}\left(\frac{h_F}{h_M}\right) - 1}{1 - \left(\frac{s_F}{s_M}\right)^{1/3}\left(\frac{2-M}{3}\right)\left(\frac{l_c}{L_M}\right)} . \tag{A.7}$$

Equation (A.7) is the solution when the immature growth line passes through the origin. When this is not the case, the solution includes an additional term (X) that accommodates $l_0 \neq 0$. The general solution, appropriately labeled as an evolved response, is:

$$\left(\frac{F}{M}\right)_{evolved} \approx \frac{\left(\frac{s_F}{s_M}\right)^{1/3}\left(\frac{h_F}{h_M}\right) - 1 - X}{1 - \left(\frac{s_F}{s_M}\right)_{ext}^{1/3}\left(\frac{2-M}{3}\right)\left(\frac{l_c}{L_M}\right)} , \tag{A.8}$$

where

$$X = \left(\frac{s_F}{s_M}\right)^{1/3}\left(\frac{h_F}{h_M} - 1\right)\left(\frac{l_0}{L_M}\right)\left(\frac{2-M}{3}\right). \tag{A.9}$$

We evaluated equation (A.8) by comparing predicted values of F/M to results obtained by numerical analysis of equation (A.1). Values of $(F/M)_{evolved}$ shown in Figure 2a (in main text) were obtained by assigning the following ranges to each variable: M = 0.1 to 0.4; h_F/h_M = 1 to 2; s_F/s_M = 1 to 2; l_c = 200 to 400 mm; L_M = 400 mm; l_0 = 0 and 80 mm. Results shown in Figure 2a demonstrate that equation (A.8) supplies a very good approximation of the exact value for sustainable F/M given by equation (A.1).

Plastic response: Length at maturity and reproductive investment are fixed

Table A2 shows the theory for estimating sustainable fishing mortality when a plastic life history response occurs. In this case, length at maturity and reproductive investment are fixed at values that are optimal for natural mortality rate (*M*). Derivations shown in Table A2 supplied the following equation for estimating sustainable *F/M*:

$$\left(\frac{s_F}{s_M}\right)\left(\frac{h_F}{h_M}\right)^3\left(\frac{f_2\left(Z,M,h_M,h_F\right)}{f_1\left(M\right)}\right)e^{\frac{F\,l_c}{h_F}+M\,l_0\left(\frac{1}{h_F}-\frac{1}{h_M}\right)}=1 \qquad \text{(A.12)}$$

Compared to the equation for an evolved response (A.1), the only difference is that $f_2(Z, M, h_M, h_F)$ substitutes for $f_1(M+F)$. For an evolved response, mortality rate alone dictates the value of the f_1 function, but for a plastic response the comparable function (f_2) also depends on the change in growth rate.

We used numerical analysis of equation (A.12) to estimate sustainable *F/M* for a plastic reponse and compared these results to values obtained from an evolved response (see Figure 2b in main text). The results demonstrate that a fixed *L* and *g* support exploitation mortality that is ~80% of the level supported when these parameters are optimized for total mortality.

TABLE A1. Derivation of the formula for estimating sustainable fishing mortality, assuming an evolved life history response.

<table>
<tr><th>Unexploited Population</th><th>Exploited Population
(Evolved response)</th></tr>
<tr><td>Given $R_{0,M} = \left(C\, s_M\, h_M^3\right) f(M, T_M, g_M)$
then $R_{0,M} = \left(C\, s\, h^3\right) f(Z, T, g)$
where $Z = M$, $T = T_M$, and $g = g_M$</td><td>Given $R_{0,F} = \left(C\, s_F\, h_F^3\, e^{F t_c}\right) f(M + F, T_F, g_F)$
then $R_{0,F} = \left(C\, s\, h^3\, e^{F t_c}\right) f(Z, T, g)$
where $Z = M+F$, $T = T_F$, and $g = g_F$</td></tr>
<tr><td colspan="2">and $f(Z,T,g) = e^{-ZT}\left(\frac{1}{g^2}\right)\left(\frac{1}{e^Z - 1} + \frac{3(g(T-\tau)-3)}{e^Z(3+g)-3} + \frac{3(g(T-\tau)-3)^2}{e^Z(3+g)^2-9} + \frac{3(g(T-\tau)-3)^3}{e^Z(3+g)^3-27}\right)$ (eq. 10)
Given optimal values of T and g (eq. 11 and 13)
then $f(Z, T^*, g^*) = e^{-Z\tau}\, f_1(Z)$
where $f_1(Z) = \left(\frac{e^{Z-2}}{x^2}\right)\left(\frac{1}{e^Z - 1} + \frac{3(xy-3)}{e^Z(3+x)-3} + \frac{3(xy-3)^2}{e^Z(3+x)^2-9} + \frac{3(xy-3)^3}{e^Z(3+x)^3-27}\right),$
$x = 1.18\left(1 - e^{-Z}\right)$ and $y = \frac{2}{Z} - 1.$</td></tr>
<tr><td>Substituting $f(Z, T^*, g^*)$ into $R_{0,M}$ gives:
$R_{0,M}^* = \left(C\, s_M\, h_M^3\right) e^{-M\tau_M}\, f_1(M)$</td><td>Substituting $f(Z, T^*, g^*)$ into $R_{0,F}$ gives:
$R_{0,F}^* = \left(C\, s_F\, h_F^3\, e^{F t_c}\right) e^{-(M+F)\tau_F}\, f_1(M+F)$</td></tr>
<tr><td colspan="2">Equating $R_{0,F}^* = R_{0,M}^* = 1$ gives:
$\left(\frac{s_F}{s_M}\right)\left(\frac{h_F}{h_M}\right)^3\left(\frac{f_1(M+F)}{f_1(M)}\right)\left(\frac{e^{F t_c - (M+F)\tau_F}}{e^{-M\tau_M}}\right) = 1$
Given $\tau_M = \frac{-l_0}{h_M}$, $\tau_F = \frac{-l_0}{h_F}$, and $t_c = \frac{l_c - l_0}{h_F}$,
then $\left(\frac{s_F}{s_M}\right)\left(\frac{h_F}{h_M}\right)^3\left(\frac{f_1(M+F)}{f_1(M)}\right) e^{\frac{F l_c}{h_F} + M l_0\left(\frac{1}{h_F} - \frac{1}{h_M}\right)} = 1$ (A1)</td></tr>
</table>

TABLE A2. Derivation of the formula for estimating sustainable fishing mortality, assuming a plastic life history response.

Exploited Population

(Plastic response)

Given $R_{0,F} = \left(C\, s_F\, h_F^3\, e^{F\,t_c}\right) f(M+F, T_F, g_F)$

then $R_{0,F} = \left(C\, s\, h^3\, e^{F\,t_c}\right) f(Z, T, g)$

where $Z = M{+}F$, $T = T_F$, and $g = g_F$

and $f(Z,T,g) = e^{-ZT}\left(\frac{1}{g^2}\right)\left(\frac{1}{e^Z - 1} + \frac{3(g(T-\tau)-3)}{e^Z(3+g)-3} + \frac{3(g(T-\tau)-3)^2}{e^Z(3+g)^2-9} + \frac{3(g(T-\tau)-3)^3}{e^Z(3+g)^3-27}\right)$ (eq. 10)

Given that g and L are optimal for natural mortality rate

$g = 1.18\left(1-e^{-M}\right)$ and $T = \frac{h_M}{h_F} T_M$ or, more generally, $T = \frac{h_M}{h_F}\left(\frac{2}{M}-1\right) + \tau_F$

Then $f(Z,T,g) = e^{-Z\tau}\; f_2\left(Z, M, h_M, h_F\right)$

where $f_2\left(Z,M,h_M,h_F\right) = e^{-Zy}\left(\frac{1}{x^2}\right)\left(\frac{1}{e^Z-1} + \frac{3(xy-3)}{e^Z(3+x)-3} + \frac{3(xy-3)^2}{e^Z(3+x)^2-9} + \frac{3(xy-3)^3}{e^Z(3+x)^3-27}\right)$,

$x = 1.18\left(1-e^{-M}\right)$ and $y = \left(\frac{h_M}{h_F}\right)\left(\frac{2}{M} - 1\right)$.

Substituting $f(Z, T, g)$ into $R_{0,F}$ gives:

$$R_{0,F} = \left(C\, s_F\, h_F^3\, e^{F\,t_c}\right) e^{-(M+F)\tau_F}\; f_2\left(Z, M, h_M, h_F\right)$$

Given the equation for $R^*_{0,M}$ in Table A1, then equating $R_{0,F} = R^*_{0,M} = 1$ gives:

$$\left(\frac{s_F}{s_M}\right)\left(\frac{h_F}{h_M}\right)^3\left(\frac{f_2\left(Z,M,h_M,h_F\right)}{f_1\left(M\right)}\right)\left(\frac{e^{F\,t_c - (M+F)\tau_F}}{e^{-M\,\tau_M}}\right) = 1\,.$$

Given $\tau_M = \frac{-l_0}{h_M}$, $\tau_F = \frac{-l_0}{h_F}$, and $t_c = \frac{l_c - l_0}{h_F}$,

then

$$\left(\frac{s_F}{s_M}\right)\left(\frac{h_F}{h_M}\right)^3\left(\frac{f_2\left(Z,M,h_M,h_F\right)}{f_1\left(M\right)}\right) e^{\frac{F\,l_c}{h_F} + M\,l_0\left(\frac{1}{h_F}-\frac{1}{h_M}\right)} = 1 \qquad \text{(A12)}$$

Appendix B. Documentation of Walleye Data

Data in Figure 3

Walleye growth shown in Figure 3 contains mean length at age estimates of female walleye in 425 water bodies. The sources of data are:

- walleye synopses by Carlander (1997) and Colby et al. (1979);
- walleye survey databases maintained by the provinces of Ontario and Québec in Canada.

Zhou et al. (2008) provided a useful compilation of the Carlander data and supplied estimates of degree days for each water body. The data spanned a range in DD5 (Growing degree days above 5 ºC) of 1000 – 4633 ºC-day. The breakdown of data is as follows:

Source	Number of populations	Range in *DD5* (ºC-day)
Ontario	345	1097 - 2117
Quebec	49	1000 - 1886
Other	31	1557- 4633
Total	425	1000 - 4633

All data from Ontario and Quebec were obtained using a standard survey method, known as Fall Walleye Index Fishing (FWIN). FWIN is a depth-stratified survey conducted during the fall using a standard multi-mesh gillnet (stretch mesh sizes = 1”, 1.5”, 2”, 2.5”, 3”, 4”, 5” and 6”) (Morgan 2002). Fish processing reports sex, maturity, total length and collects otoliths to assign fish age.

Data in Figure 4

Figure 4 includes a subset of growth data shown in Figure 3, as well as estimates of length and age at maturity for female walleye in 92 populations. The maturity data are shown in Table B1. The table includes estimates of age and size at maturity, as well as size at spawning. Populations reported for Ontario and Quebec were surveyed using the FWIN method and female attributes were determined directly using only female data (*n*=67). Data from other locations were extracted from the literature (*n*=25). Methods of calculating statistics shown in Table B1 are described below.

(i) Maturity Estimates

For Ontario and Quebec populations, we estimated length and age at 50% mature by probit analysis of the frequency distribution of immature and mature fish. Estimates are reported for 67 well-sampled populations (i.e., n > 100 fish). Because sampling was conducted at the end of the annual growing season and walleye spawn in the spring, the assessed age was rounded up (i.e., minimum age = 1 year) and maturity estimates were treated as estimates of the age and size of spawning (T_{spawn} and L_{spawn}). Age at maturity (i.e., age when egg production begins) was calculated as

$$T = T_{spawn} - 1. \tag{B.1}$$

Size of maturity (i.e., length at start of the year when egg production begins) was estimated as follows:

$$L = \frac{L_{spawn}}{1 + {}^{p}\!/_{T}} \tag{B.2}$$

where $p = 0.285 + 0.36 e^{-0.23\,T}$ (B.3)

This formulation accounts for the fact the decline in growth rate after maturation depends on the reproductive investment (i.e., egg production). It was determined empirically by assuming the biphasic growth model and simulating growth for a range of mortality rates ($M = 0.1$ to 0.4).

In addition to the Ontario and Quebec data, we obtained maturity estimates for 25 populations from data reported in the published literature. These reports typically documented age and size of initial spawning (not maturing) and, in most cases, they did not distinguish by sex. To estimate female maturity from the combined-sex estimates, we derived the following conversion formulae using data from populations where sex-specific estimates were available:

$$T_{spawn\_female} = 1.175 + 0.98\ T_{spawn\_combined} \quad (n=53,\ R^2=0.96,\ SE = 0.48) \tag{B.4}$$

$$L_{spawn\_female} = 20.5 + 1.05\ L_{spawn\_combined} \quad (n=57,\ R^2=0.82,\ SE = 20.7) \tag{B.5}$$

These calculations were performed for 20 populations lacking sex-specific data, after which equations B.1 and B.2 were used to convert estimates of size/age at spawning to size/age at maturity (i.e., one year earlier).

(ii) Mortality Estimates

Natural mortality predictions were calculated from degree days and length at maturity by applying equation 26: $M = \dfrac{0.06\ DD5}{L_M + 0.03\,DD5}$.

For Ontario and Quebec populations, total mortality rate was estimated from age composition using the Robson-Chapman method (Robson and Chapman 1959) and a minimum age of 5 years. For other populations, mortality rate was extracted from the published literature and always based on assessment of age structures.

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TABLE B1. Walleye maturation and mortality rate for 92 water bodies. Exploitation status identifies sanctuary (S) and remote (R) water bodies (where exploitation is known to be light). Length measurements are total length. Sources are: 1. Fall Walleye Index Netting data from Ontario; 2. Fall Walleye Index Netting data from Quebec; 3. Colby and Nepszy 1981; 4. Gangl and Pereira 2003; 5. Quist et al. 2003, 2004; 6. Kocovsky and Carline 2001.

Degree-Days > 5ºC	Water body name	Prov. or State	Exploitation Status	Female Age at 50% maturity (years)	Female length at 50% maturity (mm)	Female length at 50% spawning (mm)	Natural mortality (M, /yr)	Total mortality (Z, /yr)	Number of fish sampled	Female maximum length (mm)	Maximum age (y)	Source
1052	Lac Le Cordier	QC	R	12.4	446	457	0.13	0.17	690	598	30	2
1054	Lac Weakwaten	QC	R	12.7	462	473	0.13	0.15	544	693	31	2
1057	Lac Sans Nom (Stvi-03)	QC	R	11.5	443	455	0.13	0.15	253	570	28	2
1065	Lac Regnault	QC	R	12.0	491	503	0.12	0.15	922	613	31	2
1187	Lac Chibougamau	QC		9.0	543	562	0.12	0.30	734	740	29	2
1217	Lac Duparquet	QC		6.0	345	366	0.19	0.26	986	686	23	2
1217	Lac Preissac	QC		6.0	376	399	0.18	0.37	2097	715	24	2
1253	Lac Malartic	QC		5.6	311	332	0.22	0.27	759	455	19	2
1299	West Kabenung Lake	ON		4.6	399	434	0.18	0.53	252	716	24	1
1299	Lac Dasserat	QC		5.2	416	448	0.17	0.29	578	745	26	2
1303	Makokibatan Lake	ON		7.2	483	507	0.15	0.31	198	740	26	1
1335	Miminiska Lake	ON	R	7.7	412	431	0.18	0.15	188	568	25	1
1364	Wabatongushi Lake	ON		6.9	446	469	0.17	0.38	495	732	20	1
1367	Dog Lake	ON		4.8	459	497	0.16	0.22	221	777	24	1
1375	Nagagami Lake	ON		7.4	516	541	0.15	0.41	294	771	22	1
1375	Lac Des Quinze	QC		5.1	325	350	0.23	0.37	1575	676	22	2
1383	Garnham Lake	ON		5.3	405	435	0.19	0.45	274	775	19	1
1385	Lac Temiscamingue	QC		5.4	357	383	0.21	0.44	582	700	27	2

1387	Fushimi Lake	ON		6.4	392	415	0.19	0.50	370	717	20	1
1392	Lac Opasatica	QC		4.7	344	374	0.22	0.36	625	715	28	2
1412	Missinaibi Lake	ON		7.8	463	484	0.17	0.36	194	711	19	1
1421	Kapkichi Lake	ON		7.2	414	435	0.19	0.34	239	633	20	1
1431	Whitewater Lake	ON		8.5	404	420	0.19	0.19	299	688	25	1
1445	Lac Kipawa	QC		4.4	422	462	0.19	0.46	2145	730	19	2
1445	Lac Mitchinamecus	QC		7.6	448	469	0.18	0.50	1145	775	21	2
1448	Smoothrock Lake	ON		7.2	425	445	0.19	0.30	332	736	19	1
1464	Ivanhoe Lake	ON		6.1	482	512	0.17	0.43	228	790	20	1
1469	Savanne Lake	ON	S	6.9	396	417	0.20	0.22	718	517	17	1
1473	Lake St. Joseph	ON	R	7.2	425	446	0.19	0.19	1019	614	27	1
1483	Henderson Lake	ON	S	4.1	379	419	0.21	0.19	118	662	22	1
1487	Lac Cabonga	QC	R	4.1	415	458	0.19	0.25	979	758	22	2
1494	Red Lake	ON		5.3	342	367	0.23	0.23	848	726	28	1
1503	Wakami Lake	ON		3.6	396	445	0.20	0.31	681	741	20	1
1507	Wenebegon Lake	ON		5.1	362	390	0.22	0.35	265	750	20	1
1511	Lac Des Mille Lacs	ON		7.4	478	500	0.17	0.35	1592	712	26	1
1525	Kebskwasheshi Lake	ON		3.9	385	427	0.21	0.19	218	714	22	1
1533	Trout Lake	ON	R	6.6	455	480	0.18	0.17	298	647	24	1
1544	Lake Abitibi	ON		7.7	441	461	0.19	0.39	588	805	23	1
1545	Little Trout Lake	ON	R	7.1	456	479	0.18	0.23	234	666	24	1
1557	Longlegged Lake	ON		5.1	401	432	0.21	0.23	251	624	23	1
1557	Churchill Lake	ON	R	6.5	408	431	0.21	0.23	341	550	20	1
1582	Lac Nominingue	QC		3.2	335	383	0.25	0.31	508	681	20	2
1589	Round Lake	ON		7.5	519	544	0.17	0.43	806	759	22	1
1613	Pelican Lake	ON		6.0	447	475	0.20	0.50	286	612	15	1
1613	Abram Lake	ON		5.8	437	466	0.20	0.41	179	612	15	1
1614	Botsford Lake	ON		5.5	410	439	0.21	0.44	256	622	25	1
1617	Minnitaki Lake	ON		6.1	458	486	0.19	0.32	620	689	21	1
1621	Lac Seul	ON		5.3	405	435	0.21	0.24	2199	720	28	1
1636	Sandford Lake	ON		5.2	435	468	0.20	0.57	210	720	25	1
1638	Wabigoon Lake	ON		5.1	412	444	0.21	0.37	259	742	26	1
1641	Lac Desjardins	QC		6.0	504	535	0.18	0.77	915	820	19	2

1644	Pekagoning Lake	ON		4.4	420	460	0.21	0.46	566	736	22	1
1646	Eagle Lake	ON		3.9	396	440	0.22	0.28	694	740	26	1
1648	Finlayson Lake	ON		6.3	450	476	0.20	0.31	208	700	20	1
1664	Lac La Garde	QC		6.2	494	523	0.18	0.67	932	830	22	2
1666	Otukamamoan Lake	ON		5.5	439	470	0.20	0.47	394	683	19	1
1671	Winnipeg River	ON		7.1	450	472	0.20	0.32	996	729	25	1
1672	East Vermillion Lake	MN		4.9	421	456	0.21					4
1672	West Vermillion Lake	MN		4.6	463	504	0.20					4
1691	Lake of the Woods	ON		5.9	447	475	0.20	0.49		760	19	1
1701	Lake Timiskaming	ON		5.3	359	386	0.25	0.42	232	677	24	1
1719	Kanetogama Lake	MN		4.1	410	453	0.22					4
1719	Rainy Lake	MN		4.1	400	442	0.23					4
1736	Lake Nipissing	ON		4.3	385	423	0.24	0.66	2497	694	17	1
1744	Upper Red Lake (1990s)	MN		3.5	420	473	0.22					4
1751	French River	ON		4.5	429	468	0.22	0.39	2191	725	21	1
1757	Pickerel River	ON		4.0	423	468	0.22	0.29	248	721	16	1
1765	Lake of the Woods	MN		4.8	471	511	0.20					4
1770	Mindemoya Lake	ON		3.8	341	380	0.27	0.29	524	640	19	1
1801	Upper Red Lake (1980s)	MN		3.8	409	456	0.23					4
1804	Ottawa-Holden Lake	ON		4.3	413	452	0.23	0.39		739	18	1
1828	Lac Aux Sangsues	QC		4.9	408	441	0.24	0.49	1216	770	22	2
1870	Mille Lacs	MN		3.9	443	492	0.22					4
1900	Escanaba Lake	WI		4.4	419	459	0.24	0.63		488	7	3
1918	Winnibigoshish Lake	MN		3.6	428	481	0.24					4
1924	Leech Lake	MN		4.3	446	489	0.23	0.46				4
1955	Ottawa-Allumette Lake	ON		4.7	387	420	0.26	0.47		606	16	1
2036	Rice Lake	ON		3.9	428	476	0.25	0.47	618	689	13	1
2123	Lake Winnebago	WI		3.7	391	438	0.28			536	8	3
2327	Pymatuning Reservoir	PA	S	2.0	334	420	0.35	0.45		625	10	6
2400	Pool 2	MN		4.7	516	561	0.24					4
2857	Kirwin Reservoir	KA		2.0	407	512	0.35	0.90	202	601	5	5
2862	Lovewell Reservoir	KA		2.0	415	521	0.34	0.72	770	642	8	5
2973	Webster Reservoir	KA		2.0	448	563	0.33	0.52	155	666	7	5

3046	Cedar Bluff Reservoir	KA	2.0	412	518	0.36	0.78	354	673	7	5
3061	Glen Elder Reservoir	KA	2.0	417	523	0.36	0.88	1882	702	8	5
3194	Wilson Reservoir	KA	2.0	435	547	0.36	0.76	309	652	8	5
3358	Marion Reservoir	KA	2.0	414	520	0.39	0.54	747	624	8	5
3378	Cheney Reservoir	KA	2.0	385	484	0.42	0.61	307	617	8	5
3502	Center Hill Reservoir	TN	2.2	419	513	0.40			715	8	3
3600	Current River	MO	2.4	364	438	0.46			704	9	3
3690	Lake Meredith	TX	2.3	423	513	0.42			563	7	3