Overcompensatory response of a smallmouth bass (*Micropterus dolomieu*) population to harvest: release from competition?

Elise F. Zipkin, Patrick J. Sullivan, Evan G. Cooch, Clifford E. Kraft, Brian J. Shuter, and Brian C. Weidel

Abstract: An intensive seven-year removal of adult, juvenile, and young-of-the-year smallmouth bass (*Micropterus dolomieu*) from a north temperate lake (Little Moose Lake, New York, USA) resulted in an increase in overall population abundance, primarily due to increased abundance of immature individuals. We developed a density-dependent, stage-structured model to examine conditions under which population control through harvest could result in the increase of a targeted species. Parameter values were derived from a 54-year data set collected from another north temperate lake (Lake Opeongo, Ontario, Canada) smallmouth bass population. Sensitivity analyses identified the demographic conditions that could lead to increased abundance in response to harvest. An increase in population abundance with harvest was most likely to occur when either (*i*) per capita recruitment at low levels of spawner abundance was large, juvenile survivorship was high, and maturation of age-4 and older juveniles was moderately high or (*ii*) per capita recruitment at low levels of spawner abundance was slightly lower, yet the maturation rate of age-3 juveniles and adult survivorship were high. Our modeling results together with empirical evidence further demonstrate the importance of overcompensation as a substantial factor to consider in efforts to regulate population abundance through harvest.

Résumé : Des captures intensives pendant sept ans des adultes, des juvéniles et des jeunes de l'année d'achigans à petite bouche (*Micropterus dolomieu*) dans un lac de la région tempérée nord (lac Little Moose, New York, É.-U.) ont eu pour effet un accroissement dans l'abondance globale de la population, principalement à cause d'une augmentation de l'abondance des individus immatures. Nous avons élaboré un modèle dépendant de la densité et structuré en fonction des stades afin d'évaluer les conditions sous lesquelles un contrôle de la population par la récolte peut entraîner une augmentation de l'espèce ciblée. Les valeurs des paramètres ont été tirées d'une banque de données couvrant 54 années et provenant d'une population d'achigans à petite bouche d'un autre lac de la région tempérée nord (lac Opeongo, Ontario, Canada). Des analyses de sensibilité ont permis d'identifier les conditions démographiques qui pourraient mener à une abondance accrue en réaction à la récolte. Une augmentation de l'abondance de la population en réaction à la récolte va plus vraisemblablement se produire quand ou bien (*i*) le recrutement par individu aux faibles densités de reproducteurs est important, la survie des juvéniles est élevée et la maturation des juvéniles d'âge 4 ou plus est modérément élevée ou alors (*ii*) le recrutement par individu aux faibles densités de reproducteurs est un peu plus faible, mais malgré tout le taux de maturation des juvéniles d'âge 3 et la survie des adultes sont élevés. Les résultats de notre modélisation combinés à des données empiriques démontrent de plus l'importance de la surcompensation comme facteur important à considérer lorsqu'on tente de contrôler l'abondance d'une population par des récoltes.

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Introduction

Optimizing resource use and maximizing productivity are common management objectives of harvest, but reducing abundance levels of undesirable species is another objective less frequently considered. Although harvest can be an effective method to control the abundance of nuisance or exotic species (Brooks and Lebreton 2001; Hein et al. 2006), control through harvest is complicated by factors such as demographic structure and density dependence. Individuals of different ages, sizes, or stages contribute disproportionately to future demography of populations due to disparities in survivorship and fecundity. Hauser et al. (2006) demonstrated that in a structured population, it is

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necessary to consider the relative reproductive value of each stage when devising a control harvest strategy. Additionally, the effects of a compensatory mechanism (i.e., density-dependent birth rates, growth rates, or mortality) can complicate efforts to control organisms through harvest (Brooks 2002). Recent studies have focused on optimal strategies to control overabundant populations and have demonstrated the potential for harvest to achieve this objective (Jensen 2000; Frederiksen et al. 2001; Hauser et al. 2007).

However, harvest can lead to unexpected dynamics such as increases in abundance of targeted populations, as has been reported for both plant (Paige 1992; Buckley et al. 2001; Newingham and Callaway 2006) and insect (Nicholson 1957; Cameron and Benton 2004) populations. Within a fisheries context, Matsuda and Abrams (2004) and Abrams and Matsuda (2005) demonstrated the potential for a predator population to increase in abundance with high mortality (such as that caused by harvest), which they referred to as the “hydra effect”. Using theoretical models, their studies demonstrated that harvesting an unstructured predator population can either stabilize or destabilize a population, resulting in either an increase or decrease in population size, a response that varied according to the number of prey species, the interactions of the prey, and the functional response of the predator (Abrams and Vos 2003; Matsuda and Abrams 2004; Abrams and Quince 2005). However, empirical examples of this phenomenon have rarely been described in the fisheries literature (for a discussion of this topic, see Abrams and Matsuda 2005).

In this paper, we link harvest theory to an empirical study of an experimentally overexploited smallmouth bass (*Micropterus dolomieu*) population that has increased in abundance despite — and in response to — seven years of intense harvest. The removal effort has been successful in reducing the overall biomass of bass, primarily through a reduction of adults (>200 mm), subsequently leading to major increases in the abundance of six native fishes (Weidel et al. 2007) and increased piscivory and growth of the lake’s apex fish predator, lake trout (*Salvelinus namaycush*) (Lepak et al. 2006). Yet despite these changes in food web linkages within the study lake, the relative abundances of juvenile bass (<200 mm) have increased throughout the time period of removal (Weidel et al. 2007). Although the overall biomass of smallmouth bass was reduced through the removal, the increase in juveniles has resulted in greater numbers of bass in the lake. This change in demography has important consequences for the continuation of the removal, namely that it may be necessary to continue the intense removal indefinitely to preserve the positive changes observed to date.

We developed a density-dependent stage-structured model to explore the response of the bass population to harvest with two key questions in mind. First, what are the demographic factors that could have led the population to respond to an intensive harvest with an overcompensation in abundance, specifically in young-of-the-year and juveniles? Second, what alternative harvest strategy could be employed to reduce the overcompensatory response of juvenile stages while simultaneously minimizing adult abundance? When determining whether harvest is a viable control option, it is essential to understand the circumstances under which demographic factors can confound control efforts. The model was developed to identify specific life stage factors that may be responsible for the apparent increase in overall abundance of the smallmouth bass population in response to an intense harvest.

Materials and methods

Smallmouth bass in Little Moose Lake

The study population is located in Little Moose Lake (271 ha), an oligotrophic lake in the Adirondack Park of northern New York State (Weidel et al. 2007). Smallmouth bass are not native to the Adirondacks or to many other north temperate lakes where introduced populations have led to declines in native fish abundance (Vander Zanden et al. 1999; Brown et al. 2000; Jackson 2002). As such, smallmouth bass population control is an important management objective for preserving native fish communities in north temperate lakes (Whittier and Kincaid 1999; Vander Zanden et al. 2004). Since their invasion into Little Moose Lake in the late 1940s, smallmouth bass have successfully dominated the littoral fish community in the lake (Brown et al. 2000). To improve conditions for native fishes, a smallmouth bass removal program was initiated in the spring of 2000 using targeted shoreline boat electrofishing. Prior to the removal, bass were surveyed in the springs of 1998 and 1999 to establish baseline levels of relative abundance and preremoval length distributions. From 2000 to 2007, smallmouth bass were collected and removed over the course of several weeks during both the spring and fall. A total of 53 947 smallmouth bass were removed over this time period. Details of the removal and methods are presented in Weidel et al. (2007).

We used electrofishing catch per unit effort (CPUE) data from standard nighttime surveys to examine how the relative abundance of the population has changed over the course of the removal. Although total smallmouth bass biomass has declined (Weidel et al. 2007), CPUE in numbers caught has increased from 1998 to 2007 (Fig. 1). Subdividing the population into length categories illustrates that although the abundance of adults (>200 mm) has declined, the relative abundances of young-of-the-year and yearlings (<100 mm) and older juveniles (100–200 mm) have increased since the onset of the removal (Fig. 2). The intensity of the harvest allowed us to estimate the minimum population abundance at the initiation of the harvest using a cohort analysis applied to the full set of cohorts present in 2000, followed through subsequent years using cohort slicing (Quinn and Deriso 1999). It was not feasible to use a cohort analysis to estimate the total abundance of the population at other times during the removal because it is not possible to accurately determine age from length data for smallmouth bass.

Model development

We developed a population model, using discrete time difference equations, with an annual time step during which smallmouth bass reproduce and are harvested once each year. The smallmouth bass population (N) was divided into four stages: yearlings (Y), age-2 juveniles ($J2$), age-3 and older juveniles ($J3$), and adults (A) (Fig. 3). Juveniles were separated into different stages because survivorship and fe-

Fig. 1. Catch-per-unit-effort (CPUE) in number of smallmouth bass individuals captured (and removed starting in 2000) from Little Moose Lake (per hour of electrofishing run time) from 1998 to 2007. The solid and broken lines show results from spring and fall sampling periods, respectively.

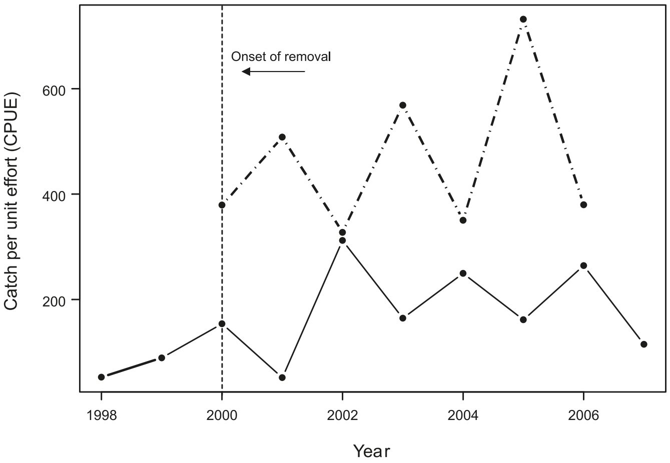
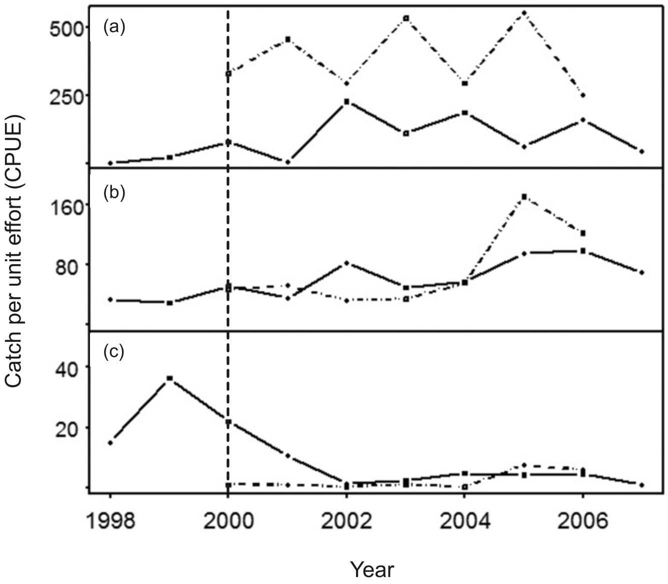


Fig. 2. Annual catch-per-unit-effort (CPUE) of (*a*) young-of-the-year (in fall) and yearlings (in spring, <100 mm), (*b*) juveniles (100–200 mm), and (*c*) adults (>200 mm). The solid and broken lines show results from spring and fall sampling periods, respectively. The vertical broken line indicates the onset of the removal. Note the differences in scale in the three graphs.



cundity vary as juveniles age (Rose 2005). The annual model cycle assumed that individuals are harvested immediately prior to breeding. We assumed that harvest occurs before breeding because (*i*) the annual spring removal of smallmouth bass is designed to occur prior to breeding in Little Moose Lake and (*ii*) this strategy minimizes the effort necessary for the removal (Doubleday 1975). Natural mortality was assumed to occur subsequent to breeding, followed by maturation to the next stage at the end of the time step. The model counts individuals prior to harvest (i.e., a prebreeding census each spring), which implies that yearlings at time *t* (Y_t) are age-1 and $J2_t$ juveniles are age-2. Individuals in stages *J*3 (immature) and *A* (mature) at time *t* are age-3 and older.

Given our interest in examining how stage-specific harvest affects smallmouth bass population dynamics, we assumed that harvest strategies could be varied to selectively remove differing proportions of each stage. We divided the harvest into three categories: an age-1 harvest (h_y), a harvest of age-2 and older juveniles (h_j), and a harvest of adult fish (h_a). The h_y harvest is applied to age-1 individuals immediately following their first birthday. We assumed that harvest does not occur during the first year of life so that individuals can first be harvested between age-1 and age-2. We combined the harvest of all age-2 and older juveniles, denoted by h_j, because it is impractical to distinguish these two categories in the field. The final harvest category is adult harvest, h_a, which is applied to mature fish. For simplicity, we assumed that harvest strategies remain fixed through time.

Characterizing the stock–recruitment relationship between the number of mature individuals and the number of offspring they produce is a long-standing challenge in the study of fish population dynamics (Ricker 1954; Beverton and Holt 1957; Myers 2001). Available evidence suggests that recruitment to age-1 for smallmouth bass may be overcompensatory (DeAngelis et al. 1991, 1993; Dong and DeAngelis 1998). An overcompensatory density-dependent relationship implies that total recruitment is maximized at an intermediate stock level, beyond which it declines (Quinn and Deriso 1999). We used the Ricker (1954) stock–recruitment function for the yearling stage. The number of yearlings (*Y*) produced in *t* + 1 is dependent on the number of adults in time *t* that are not harvested (1 – h_a):

$$(1) \qquad Y_{t+1} = A_t(1 - h_a)\alpha e^{-\beta A_t(1-h_a)}$$

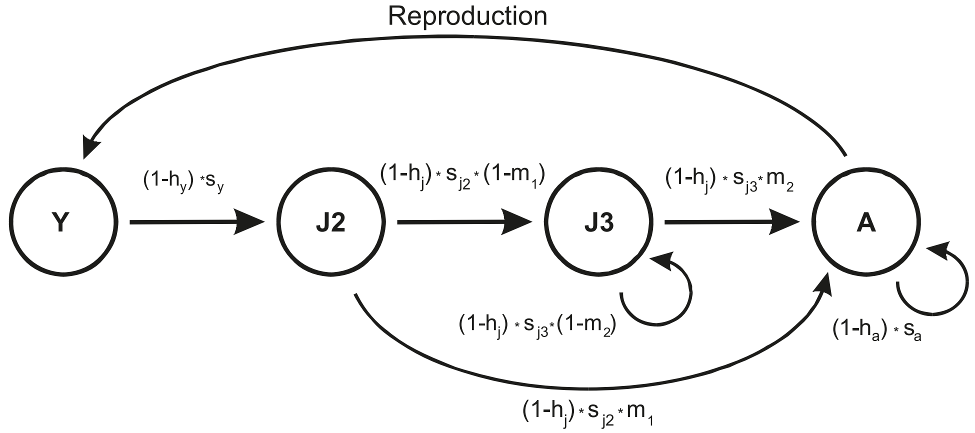
where $\alpha > 0$ and $\beta > 0$ are standard Ricker parameters regulating the maximum number of offspring produced per spawner and the magnitude of the density-dependent effects.

We assumed that natural mortality remains constant from year to year for all other stages. Yearlings (*Y*) that survive natural mortality (s_y; survivorship from age-1 to age-2) and are not harvested (1 – h_y) advance to the *J*2 stage:

$$(2) \qquad J2_{t+1} = Y_t(1 - h_y)s_y$$

*J*2 individuals that are not harvested (1 – h_j) survive at a rate of s_{j2} (survivorship from age-2 to age-3). They either remain as juveniles (1 – m_1), advancing into the *J*3 stage, or mature into adulthood at a fixed proportion m_1 (maturation rate of individuals at age-3). The proportion of *J*3 juveniles that survive annually is s_{j3} (annual survivorship of all immature individuals age-3 and older). *J*3 individuals that survive natural and harvest mortality can either remain as juveniles (1 – m_2) or mature into adulthood at a rate of m_2 (maturation rate of immature bass age-4 and older). We assumed that the maturation rates are constant so that a fixed proportion of both *J*2 and *J*3 individuals become adults on an annual basis. The equation for older juveniles is as follows:

Fig. 3. Life cycle diagram for the smallmouth bass population model. The population is divided into four stages: yearling (*Y*), age-2 juveniles (*J*2), age-3 and older juveniles (*J*3), and adults (*A*). The model counts individuals prior to harvest with a prebreeding census each spring. Survivorship, *s*; harvest, *h*; maturation, *m*.



$$(3) \qquad J3_{t+1} = J2_t(1-h_\mathrm{j})s_{\mathrm{j}2}(1-m_1) + J3_t(1-h_\mathrm{j})s_{\mathrm{j}3}(1-m_2)$$

The adult stage (*A*) in time *t* + 1 includes both the *J*2 and *J*3 juveniles from time *t* that survived harvest and natural mortality and matured into adulthood, as well as the adults from time *t* that survive natural mortality, s_a, and were not harvested:

$$(4) \qquad A_{t+1} = J2_t(1-h_\mathrm{j})s_{\mathrm{j}2}m_1 + J3_t(1-h_\mathrm{j})s_{\mathrm{j}3}m_2 + A_t(1-h_\mathrm{a})s_\mathrm{a}$$

Model parameterization

Because of the short length of the time series of data from Little Moose Lake and the intensity of the bass harvest, these data alone were insufficient for estimating the model parameters. Parameter values for the model were instead estimated using data from a smallmouth bass population in Lake Opeongo, a large (5860 ha), oligotrophic lake in Ontario, Canada. Smallmouth bass population information was collected continuously from 1937 through 1990 via creel surveys. Details of the Lake Opeongo data collection process and analysis are presented in Shuter et al. (1987).

We used annual approximations of age-specific abundances and estimates of the proportion of mature individuals at each age (averaged over the time series) to determine values for the parameters in the model. Values for survivorship and maturation were established by averaging annual rates over the 54 years of data collection. The values for s_y (survivorship from age-1 to age-2), $s_{\mathrm{j}2}$ (survivorship from age-2 to age-3), $s_{\mathrm{j}3}$ (average survivorship for older juveniles), and m_1 (maturation rate of age-3 individuals) were taken from Rose (2005), an analysis based on the work of Shuter et al. (1987) in which annual age-specific survivorship for smallmouth bass in Lake Opeongo was averaged over the time series. To determine the annual values for s_a (adult survivorship) and m_2 (maturation of age-4 and older individuals), we first grouped the Lake Opeongo data by our model stages (yearlings, age-2 juveniles, age-3 and older juveniles, and adults) to determine the total number of individuals in each stage in each year. Using the yearly survivorship values and the stage-specific population estimates, we solved eq. 3 for m_2 (assuming that there was no harvest in the population) to estimate annual values and then averaged those estimates to achieve a single parameter value for m_2. We repeated this process for s_a using eq. 4. The Lake Opeongo smallmouth bass abundance estimates included mortality from recreational fishing; any recreational fishing mortality was therefore incorporated into the model as natural mortality.

To parameterize the stock–recruitment relationship, we related the number of mature individuals (*A*) in year *t* to the number of one-year-olds (*Y*) in year *t* + 1 using the Ricker recruitment function. The parameters α and β (see eq. 1) were determined using a nonlinear minimization technique. Additional information on the stock–recruitment relationship in Lake Opeongo can be found in Shuter and Ridgway (2002). The parameter estimates generated from the Lake Opeongo smallmouth bass population are presented in Table 1.

Sensitivity analyses

Our primary interest was to evaluate circumstances under which harvest of one or more stages in a density-dependent population could lead to an increase in overall abundance. To this end, we evaluated the sensitivity of the projected dynamics from our model using two different approaches — an analytical approach and a simulation-based approach; the methodology for the two approaches is discussed below. In both cases, we reduced the parameter state–space (i.e., we nondimensionalized the model) by setting $\beta = 1$, without loss of generality.

Analytical approach

The objective of the analytical approach was to derive the condition under which harvest results in an increase in the total equilibrium population abundance, $\widehat{N}$. The advantage of this approach was that we could explore the equilibrium solution over the entire parameter space. For simplicity and because the current harvest approach consists of removing all captured bass, we considered only the strategy in which all stages are harvested in equal proportions, $h_\mathrm{y} = h_\mathrm{j} = h_\mathrm{a}$, which we denote by *h*.

The first step was to solve for the equilibrium population abundance for each stage in the model (i.e., we set $Y_t = Y_{t+1}$

Table 1. Parameter values estimated from the Lake Opeongo smallmouth bass (*Micropterus dolomieu*) population.

Parameter	Description	Value
α	Ricker parameter — maximum per capita recruitment (without density dependence)	5.503055
β	Ricker parameter — magnitude of density dependence	0.000225
s_y	Proportion of Y that survive (natural mortality) to $J2$	0.74
s_{j2}	Proportion of $J2$ that survive annually	0.74
s_{j3}	Proportion of $J3$ that survive annually	0.61
m_1	Proportion of $J2$ that mature into A	0.0560
m_2	Proportion of $J3$ that mature into A	0.3725
s_a	Proportion of A that survive annually	0.54

and repeat for each stage). The total equilibrium population is the sum of the stages:

$$(5)\qquad \widehat{N} = \widehat{Y} + \widehat{J}1 + \widehat{J}2 + \widehat{A}$$

The interest lies in how the equilibrium population $\widehat{N}$ is affected by a change in harvest. We took the derivative of $\widehat{N}$ with respect to harvest and evaluated the term at $h = 0$. If

$$(6)\qquad \left.\frac{\partial\widehat{N}}{\partial h}\right|_{h=0} > 0$$

then the slope of the equilibrium condition at the origin is increasing with respect to a positive change in harvest. This implies that there exists an $\widehat{N}$ that is greater in the presence of harvest ($h > 0$) than in its absence ($h = 0$). If eq. 6 does not hold, then it is not possible for the population to increase in response to harvest (i.e., the population cannot decrease with small levels of harvest but increase with large levels). The magnitude of the derivative (when positive) provides some information about the harvest intensity that will lead to a population decline (i.e., if the magnitude is small, then the population begins to decline quickly as h is increased).

The evaluation of the symbolic derivative of $\widehat{N}$ at $h = 0$ is not easily interpretable as the expression is complicated and seven parameters are included in the model ($\beta = 1$ in the nondimensional model). To better comprehend how various parameter combinations affect whether or not harvest leads to an increase in $\widehat{N}$, we repeatedly drew parameter estimates from a distribution of values and evaluated the sign of the derivative of $\widehat{N}$ at $h = 0$. We assumed that each of the survivorship and maturation parameters were beta-distributed with means equivalent to the values in Table 1. It was not possible to determine the potential variation around the survivorship parameter estimates because the yearly stage-specific abundances were frequently estimated through back calculations (Shuter et al. 1987). We set the standard deviations on the survivorship and maturation parameters reasonably high, from 0.05 to 0.09, to encapsulate potential variability. For each of these parameters, the distribution was dome-shaped with a peak at its estimated mean.

We reviewed previous studies that synthesized the spawner–recruit relationship across many species (Myers et al. 1999; Myers 2001; MacKenzie et al. 2003) to determine a potential range for the parameter α, the maximum number of recruits per spawner at low population densities. (None of the studies included estimates of a stock–recruitment relationship for smallmouth bass.) In 57 species examined by Myers et al. (1999), the annual number of spawners produced per spawner at low abundance (i.e., recruits that survive to maturity) ranged from 0.1 to 15.3 (with one outlier at 113.3), and the lifetime maximum reproductive rate (in spawners produced per spawner) ranged from 1.4 to 74.6 (same outlier at 123.5). Because we were interested in the number of age-1 individuals produced per spawner and not the number that survive to maturity, we examined a wide range for the parameter α ($1 \leq \alpha \leq 50$) to explore all potential dynamics in response to harvest.

To determine the population's sensitivity in response to harvest to changes in the parameter α, we evaluated the derivative of $\widehat{N}$ 10 000 times as each of the maturation and survivorship parameter values were randomly drawn from their potential distribution while holding α constant. We repeated this procedure for values of α from 1 to 50 by increments of 5. To determine sensitivities for the survivorship and maturation parameters, we varied each parameter individually through its potential range (from 0 to 1 by increments of 0.1) and evaluated the derivative of $\widehat{N}$ 10 000 times, where all other parameters were drawn from their unique beta distributions. In these cases, we again held α constant and repeated the process for several values of α.

Simulation-based approach

The numerical simulation-based sensitivity analysis was used to explore how changes in individual parameters affected whether the equilibrium population increased or decreased under various harvest strategies (with all other parameters held constant at their estimated values). The advantage of the simulation-based approach was that it allowed us to explore a larger variety of harvest strategies than was possible using the analytical approach alone. In addition, we used the numerical approach to determine the magnitude of the population increase in response to harvest (when it occurred) and the harvest level that maximized abundance.

We varied each of the individual parameters through their range of potential values while holding the remaining parameters constant at their estimated values. The survivorship and maturation parameters ($s_y, s_{j2}, s_{j3}, s_a, m_1, m_2$) have a potential range from 0 to 1 (i.e., 0%–100% survivorship and 0%–100% maturity) and were varied by increments of 0.1. The parameter α was again varied from 1 to 50 by increments of 5. We examined how individual parameter values affected the equilibrium population abundance under four harvest strategies. The scenarios were as follows: (*i*) harvest of age-1 bass only (h_y varies, $h_j = h_a = 0$); (*ii*) harvest of age-2 and older juvenile bass only (h_j varies, $h_y = h_a = 0$); (*iii*) harvest of adults only (h_a varies, $h_y = h_j = 0$); and (*iv*) harvest of all stages proportional to their relative abundance ($h_y = h_j = h_a$ and all vary). We chose to examine these four harvest strategies because they represent end points on the spectrum of potential approaches to harvest and combinations of these strategies produce results that are simple summations of each strategy on its own. Additionally, these harvest strategies can be practically applied in the field by comparison with strategies designed to remove specific proportions of each stage. For each of the harvest strategies, we varied every parameter individually through its potential range and observed whether or not the equilibrium population abundance was larger in the presence of harvest or in its absence, while holding all other parameter values constant.

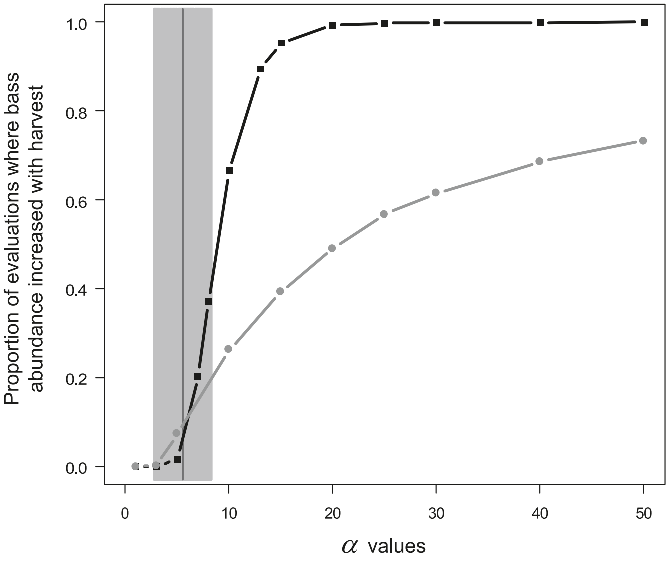
Results

Sensitivity analysis — analytical approach

The solution to eq. 6 confirmed that even though the yearling and juvenile stages could increase with harvest (which could lead to an increase in the abundance of $\widehat{N}$), the adult population could not increase under a harvest strategy in which the stages were harvested in equal proportions, using any combination of parameter values. The results of the analytical sensitivity analysis demonstrated that the parameter α is key to determining the influence of harvest on smallmouth bass population dynamics. We evaluated the proportion of times out of 10 000 trials that the total equilibrium population $\widehat{N}$ increased with harvest for values of α ranging from 1 to 50 when all other values were randomly selected from their unique beta distributions (Fig. 4). When α was between 1 and 3, the derivative of $\widehat{N}$ at $h = 0$ was never positive and was positive in less than 2% of the trials for $\alpha = 5$. As the value of α increased, this percentage rapidly increased; at $\alpha = 15$, more than 95% of the simulations resulted in an increase in $\widehat{N}$ with harvest. Because of the uncertainty surrounding the variance estimates on each of the survivorship and maturation parameters, we repeated simulations for the α values using a uniform distribution for all other parameters across their potential range (from 0 to 1). Under this naïve scenario, we found the same trend in α; the proportion of simulations that resulted in an increase in $\widehat{N}$ with harvest ranged from 0% to 73% as α was varied from 1 to 50 (Fig. 4).

Because of the large influence of the parameter α on the model dynamics, we examined the sensitivities of the survivorship and maturation parameters while holding α constant at several values. The maturation parameters were opposite in their sensitivities to harvest with respect to values of α (Fig. 5). When α was low ($\alpha \leq 5$), the response of the population to harvest was more sensitive to changes in m_1 than when α was high ($\alpha \geq 10$). For $\alpha = 5$, the value of m_1 had a large effect on whether harvest led to an increase in $\widehat{N}$. As α was increased, harvest frequently led to an increase in $\widehat{N}$ regardless of the value of m_1. The reverse was true for m_2. For $\alpha = 5$, harvest rarely resulted in an increase in $\widehat{N}$, even as the value of m_2 approached 100%. For values of $\alpha \geq 10$, small increases in the value of m_2 above zero had a large effect on the response of the population to harvest. The population was similarly less sensitive to changes in the survivorship parameters s_y, s_{j2}, and s_{j3} at $\alpha = 5$ compared with at $\alpha \geq 10$ (Fig. 5). The value of adult annual survivorship, s_a, was more important at values of $\alpha \leq 15$ and became less so as the value of α increased. At $\alpha = 5$, a relatively small change in value of s_a from 0.6 to 0.9 led the population to an increase in its equilibrium abundance with harvest from less than 1% of the evaluations to greater than 99% of the evaluations.

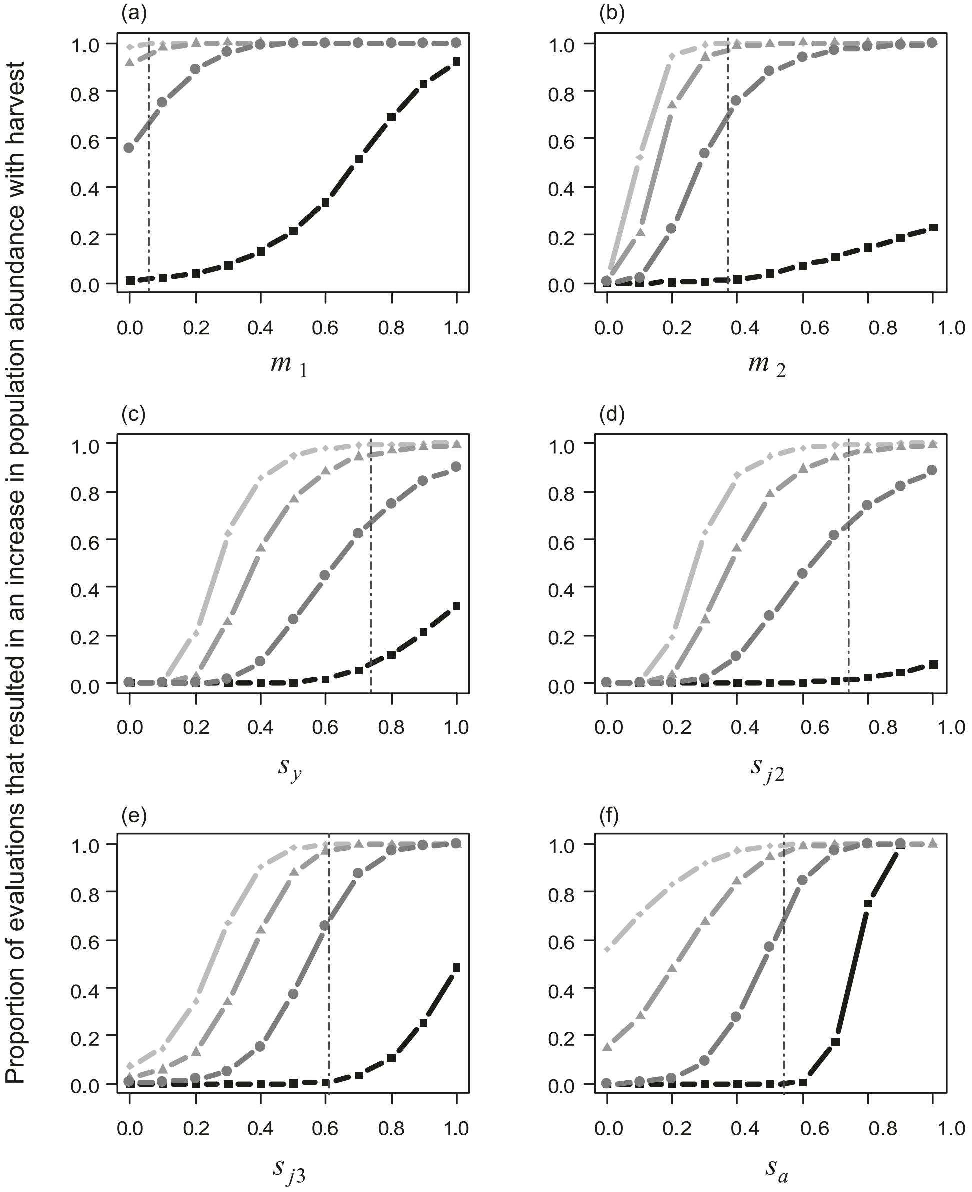
Fig. 4. Results of the analytical sensitivity analysis for the parameter α. The black line (with squares) shows the proportion of trials out of 10 000 evaluations that the derivative of the equilibrium population with respect to harvest was positive for each value of α (i.e., the population increased in response to harvest), assuming that the other parameters follow a beta distribution with mean values as in Table 1. The shaded line (with circles) shows the result under the naïve scenario that all other parameters are uniformly distributed across their potential ranges. The vertical line and shaded area show the estimated value for α (Table 1) with a 95% confidence interval.



Sensitivity analysis — simulation-based approach

All survivorship and maturation parameters produced stable equilibriums throughout their ranges when each of the other parameters was held constant at its estimated value (in both the presence and absence of harvest). The stock–recruitment slope parameter, with values of $\alpha \geq 30$, produced cyclic levels of population abundance in the absence of harvest, although abundance stabilized when even small levels of harvest were applied. To avoid this cyclic behavior in our results, we limited the numerical sensitivity analysis to the range in which α produced stable equilibriums in the absence of harvest (i.e., $1 \leq \alpha \leq 25$). Running the model with the parameter values estimated from the Lake Opeongo data set did not result in an increase in population abundance with harvest. We used the results of the numerical sensitivity analysis to (*i*) demonstrate the extent to which each parameter would need to change (if all others were held constant) to produce an increase in population abundance with harvest and (*ii*) determine the magnitude of such increases when they occurred. The minimum value for each parameter (when all other parameters

Fig. 5. Results of the analytical sensitivity analysis for (*a–b*) the maturation parameters (m_1, m_2) and (*c–f*) the survivorship parameters (s_y, s_{j2}, s_{j3}, s_a). The sign for eq. 6 is evaluated in 10 000 trials where each parameter is varied over its possible range (from 0 to 1 by increments of 0.1), and all other survivorship and maturation parameters are drawn from their unique distributions. Each panel shows the proportion of these trials that resulted in an increase in population abundance under harvest for α values of 5 (solid line with squares), 10 (dark shaded line with circles), 15 (light shaded line with triangles), and 20 (lightest shaded line with diamonds). The vertical broken lines show the estimated parameter value, using the smallmouth bass data from Lake Opeongo (Table 1).



were held at their estimated value) that would result in an increase in abundance under all four harvest strategies is presented in Table 2.

Increasing the value of the α parameter resulted in increases in the equilibrium population abundance $\widehat{N}$ of smallmouth bass under all harvest strategies except the yearling-only strategy. For $\alpha \geq 10$, the equilibrium population abundance was larger when all stages were harvested equally, when only age-2 and older juveniles were harvested, and when only adults were harvested. In those cases, the equilibrium abundances of both the yearling and juvenile stages also increased with harvest. Under the adults-only harvest strategy, $\alpha \geq 20$ also produced an increase in the equilibrium abundance of the adult stage. This was the only scenario in the sensitivity analyses in which an increase in the equilibrium abundance of the adult stage was observed with any type of harvest. When only the age-1 bass were targeted, $\alpha \geq 10$ led to an increase in the equilibrium of yearlings but not an increase in the total population $\widehat{N}$ (i.e., the increase in yearlings was less than the observed decreases in age-2 and older juveniles and adults, therefore total population size declined with harvest).

Increasing the maturation rate of *J*2 individuals (m_1) or adult survivorship (s_a) also produced increases in the equili-

Table 2. Results of the simulation-based sensitivity analysis.

	Total population harvest				Age-1 only harvest				Age-2+ juvenile only harvest				Adult only harvest			
Parameter	N	Y	$J2 + J3$	A	N	Y	$J2 + J3$	A	N	Y	$J2 + J3$	A	N	Y	$J2 + J3$	A
α	10	10	10	×	×	10	×	×	10	10	10	×	10	10	10	20
s_y	×	0.8	×	×	×	0.8	×	×	×	0.8	×	×	0.9	0.8	0.8	×
s_{j2}	×	0.8	×	×	×	0.8	×	×	×	0.8	×	×	0.9	0.8	0.8	×
s_{j3}	1.0	0.7	1.0	×	×	0.7	×	×	×	0.7	×	×	0.7	0.7	0.7	×
s_a	0.8	0.6	0.8	×	×	0.6	×	×	0.9	0.6	0.8	×	0.7	0.6	0.6	×
m_1	0.6	0.1	0.6	×	×	0.1	×	×	0.9	0.1	0.7	×	0.2	0.1	0.1	×
m_2	×	0.5	×	×	×	0.4	×	×	×	0.5	0.9	×	0.5	0.5	0.5	×

Note: Shown is the minimum value for each parameter that led to an increase in the equilibrium population abundance (and each of the stages) with all other parameters held constant at their estimated values under four harvest strategies: harvest of the total population, harvest of age-1 yearlings only, harvest of age-2 and older juveniles, and harvest of adults. An × indicates that the population (or stage) did not increase with any values of the parameter.

brium population abundance $\widehat{N}$ (specifically in the yearling and age-2 and older juvenile stages), when only age-2 and older juveniles were harvested, adults alone were harvested, or each stage was harvested in equal proportions, but not when only age-1 individuals were harvested. The maturation rate of $J3$ individuals (m_2) and the survivorship parameters s_y (from age-1 to age-2), s_{j2} (from age-2 to age-3), and s_{j3} (survivorship of immature age-3 and older bass) were less influential. Increasing the value for each of these parameters led to an increase in $\widehat{N}$ only with the adult-only harvest strategy.

In cases when harvest resulted in increased values of $\widehat{N}$, the magnitude of the increases was highly variable (Table 3). Increasing the parameter α produced the largest increases in abundance for given harvest levels. At $\alpha = 25$, the population increased by as much as 25% (over the equilibrium abundance in the absence of harvest) when only age-2 and older juveniles were harvested and when equal proportions of each stage were harvested and 66% when only adults were harvested. Additionally, the adult-only harvest produced the largest increases in the total population abundance compared with the other harvest strategies.

Simulation results with Lake Opeongo parameter values

In the absence of harvest, the estimated equilibrium population size was stable at approximately 27 600 smallmouth bass ($Y = 9000$, $J1 = 6700$, $J2 = 7600$, and $A = 4300$) using the parameter values generated by the Lake Opeongo data set. The cohort analysis estimated that the Little Moose Lake bass abundance in the spring of 2000 (prior to the initiation of the removal) was approximately 7000 individuals, excluding age-0 fish. The Lake Opeongo bass population estimate was almost four times greater than the estimated population size in Little Moose Lake, which is not unexpected given that Lake Opeongo is much larger (5860 ha) than Little Moose Lake (271 ha). The carrying capacity for the model is determined by the parameter β (for given values of α). The nondimensional version of the model (where we set $\beta = 1$) demonstrated that β does not have an effect on the population dynamics, so this discrepancy in equilibrium population size did not influence our results.

Using the parameter values generated with the Lake Opeongo data set, the smallmouth bass population did not increase in abundance with harvest. Under all harvesting scenarios, the equilibrium population (and each of the stages) was reduced in the presence of harvest. The model population declined to zero with a total annual harvest of as little as 18% (where each stage is harvested in equal proportion). Alternatively, harvesting either 37% of age-2 and older juveniles ($h_j = 0.37$, $h_y = h_a = 0$) or 44% of the adults ($h_a = 0.44$, $h_y = h_j = 0$) also resulted in a population collapse.

The short-term population responses to harvest (Fig. 6) were similar to the long-term dynamics in that we never observed the population increasing in response to harvest with the Lake Opeongo parameters when simulations were initiated using the equilibrium population size and structure. This suggests that the observed increase in smallmouth bass abundance in Little Moose Lake may not simply reflect transient dynamics on a path to a consistently reduced population resulting from continual harvest. Furthermore, altering the annual harvest in the model (so that each harvest value is time-variant) to reflect the changing effort in Little Moose Lake also did not produce increases in population abundance (Fig. 6).

Discussion

The population model that we developed is capable of producing the dynamic observed in response to the intensive removal of smallmouth bass from Little Moose Lake: an increase in the yearling and juvenile stages that leads to an increase in the total population abundance. The sensitivity analyses revealed that the value of α, the maximum per capita recruitment in the absence of density dependence, was a key factor in determining the response of the population to harvest. Changes in α produced the greatest changes in the population response to harvest, both in terms of whether or not an increase in population abundance was observed and also with regard to the magnitude of the increase. Although the model did not predict an increase in abundance using the parameters generated from the Lake Opeongo smallmouth bass population, small changes in maturation ($m_1 > 0.2$) or adult survivorship ($s_a \geq 0.7$) along with moderate increases in the maximum reproductive rate ($\alpha \geq 10$) would have resulted in increased equilibrium abundance with harvest. Although when parameter values were changed only slightly, the magnitude of the overcompensatory response (as predicted by the model) would be much smaller than what was observed in Little Moose Lake CPUE data.

The model demonstrated that commonly observed values of α reported in the fisheries literature (Myers 2001) could produce an increase in population abundance with harvest.

Table 3. Maximum percent increase (as measured from the equilibrium population abundance in the absence of harvest) of total population size under harvest and the harvest level that produced the maximum for three harvest strategies: harvest of the total population, harvest of age-2 and older juveniles, and harvest of adults.

	Equal proportion harvest	Harvest of only age-2+ juveniles	Adult-only harvest
α			
10	0.5% at $h = 3\%$	×	8.6% at $h_a = 24\%$
15	7.3% at $h = 11\%$	6.5% at $h_j = 25\%$	27.2% at $h_a = 42\%$
20	16.3% at $h = 17\%$	16.5% at $h_j = 37\%$	46.8% at $h_a = 53\%$
25	25.7% at $h = 21\%$	27.3% at $h_j = 45\%$	66.1% at $h_a = 60\%$
s_{j3}			
0.8	×	×	3.0% at $h_a = 14\%$
0.9	×	×	8.7% at $h_a = 25\%$
s_a			
0.7	×	×	1.8% at $h_a = 8\%$
0.8	1.5% at $h = 4\%$	×	8.5% at $h_a = 15\%$
0.9	9.8% at $h = 9\%$	1.9% at $h_j = 31\%$	22.8% at $h_a = 21\%$
m_1			
0.2	×	×	0.2% at $h_a = 3\%$
0.3	×	×	1.1% at $h_a = 8\%$
0.4	×	×	2.5% at $h_a = 13\%$
0.5	×	×	4.1% at $h_a = 18\%$
0.6	×	×	5.8% at $h_a = 22\%$
0.7	0.3% at $h = 3\%$	×	7.6% at $h_a = 25\%$
0.8	0.8% at $h = 5\%$	×	9.3% at $h_a = 28\%$
0.9	1.4% at $h = 7\%$	0.4% at $h_j = 22\%$	11.0% at $h_a = 31\%$
1.0	2.2% at $h = 9\%$	1.7% at $h_j = 35\%$	12.5% at $h_a = 34\%$
m_2			
0.6	×	×	0.3% at $h_a = 5\%$
0.7	×	×	0.9% at $h_a = 8\%$
0.8	×	×	1.5% at $h_a = 10\%$
0.9	×	×	2.2% at $h_a = 12\%$
1	×	×	2.8% at $h_a = 14\%$

Note: Example: when the parameter α was increased to 15 (while all other parameters were held constant at their estimated values), under the adult-only harvest strategy, the total population size was maximized at a 42% harvest of adults and the equilibrium population was 27.2% larger than in the absence of harvest. An × indicates that the population did not increase with harvest or that the percent increase was less that 0.1%.

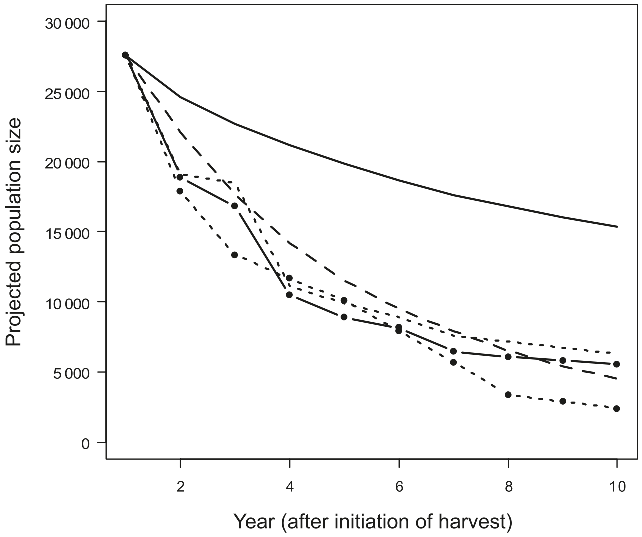
In addition, Gross and Kapuscinski (1997) showed that greater than half of fall smallmouth bass recruits were produced by 5.4% of spawning males in a Lake Opeongo embayment, suggesting that very few individuals are capable of producing a large number of offspring. Yet, although α is an essential factor, this parameter alone cannot produce the dynamic of increased population abundance with harvest. The model demonstrated that the overcompensation in yearling and juvenile bass abundance was only observed when either high juvenile survivorship ($s_y, s_{j2}, s_{j3} > 0.5$) or high maturation ($m_1 > 0.6$) and adult survivorship ($s_a > 0.7$) rates occurred in conjunction with large per capita recruitment. Because high reproduction rates are generally associated with high mortality, this may, in part, be the reason why the overcompensatory response is not more widely observed in fish populations. Furthermore, the magnitude of the increase in population abundance with harvest was large (greater than 25% of the equilibrium abundance in the absence of harvest) only in cases where α was high ($\alpha \geq 15$ for the adult-only harvest strategy and $\alpha \geq 25$ for the equal proportion and age-2+ juvenile harvest strategies). It is possible that increases in population abundance with harvest may be more prevalent than previously expected but undetectable because the magnitude of the increases are very small or preharvest population information is unavailable.

When is a fish population likely to respond to harvest by increasing in abundance?

A population can only respond to harvest with an increase in abundance if at least one density-dependent relationship (i.e., in recruitment, survivorship, maturation, etc.) is overcompensatory. For example, if we had modeled our population with a typical Beverton–Holt recruitment function (Beverton and Holt 1957) in which recruitment saturates with increasing spawner abundance, projections would have shown that harvest caused a decline in abundance over the entire parameter space. An overcompensatory recruitment function with a steep slope near the origin (i.e., high value for α) is the most plausible hypothesis for an increase in population abundance in response to the intense harvest in Little Moose Lake.

Our model identified two scenarios under which an in-

Fig. 6. Short-term dynamics for the population model under harvest using the Lake Opeongo parameter estimates. This graph shows the projected population size for 10 years under several harvest strategies: solid line, 15% harvest of all stages; long-dashed line, 10% harvest of age-1 individuals, 20% harvest of age-2 and older juveniles, and 50% harvest of adults; short-dashed line, equal harvest among all stages with proportion varying to reflect changing effort in the harvest intensity; solid line with points, varying harvest among the stages (to incorporate differences in potential catchability of individuals) and time varying to reflect changing effort; short-dashed line with points, randomly selected harvest for each stage (10%–40% for age-1 individuals, 10%–50% for age-2 and older juveniles, and 30%–70% for adults) in each year.



crease in population abundance could occur with harvest. The first (case 1) is characterized by midrange per capita recruitment in the absence of density dependence (approximately $5 \leq \alpha \leq 10$), high maturation rate for young juveniles, $J2$ individuals ($m_1 > 0.6$), and high adult survivorship ($s_a > 0.7$). The second (case 2) is a population with high per capita recruitment in the absence of density dependence (approximately for $\alpha > 10$), high survivorship of immature fish ($s_y, s_{j2}, s_{j3} > 0.5$), and reasonably high annual maturation rates for older juveniles, $J3$ individuals ($m_2 > 0.2$).

We speculate that the first and second cases above are similar to the two population categories — maturation regulated and reproduction regulated — described by De Roos et al. (2007) in an analysis of overcompensation in a stage-structured biomass model. In their study, De Roos et al. (2007) suggested that when a population is maturation regulated, strong competition occurs among juveniles and therefore maturation is more resource-limited than reproduction. Within a reproduction-regulated population, competition is stronger among adults, and as a result, reproduction is more limited. Overcompensation in stage-specific biomass in response to harvest is possible in both scenarios (De Roos et al. 2007). We suggest that in our case 1 modeling scenario in which overcompensation occurs as a result of harvest, adult survivorship must be high, implying that competition may be more intense among juveniles than adults. The opposite is true in the case 2 scenario where juvenile survivorship must be high, suggesting that adult competition may be regulating the population at equilibrium.

In the case of Little Moose Lake, the smallmouth bass population may be regulated by competition among adults, based on slow growth rates and low levels of recruitment prior to the initiation of removal (Weidel et al. 2000). Analysis of diet data from the Little Moose Lake population showed that the ratio of adult to juvenile ingestion rates (defined as q by De Roos et al. (2007)) was less than one and has decreased since the onset of the removal (unpublished data), which further implies that adult competition may be an important factor driving the overcompensatory response of the yearling and juvenile stages. The model presented by De Roos et al. (2007) predicted that in a reproduction-regulated population, harvesting any or all stages of the population could result in an increase in juvenile biomass (as was observed empirically with respect to abundance). Additionally, the CPUE data from Little Moose Lake yields a much higher, if not unrealistic, value of α ($\alpha = 84.3$). Available data from Little Moose Lake cannot be used to accurately generate stock–recruitment parameter values because of the short length of the time series and also because the catchability of smallmouth bass is likely length-dependent, which would bias estimates of α. Still, the very large estimated value of α from available data provides anecdotal evidence that the recruitment of smallmouth bass in Little Moose Lake may be large. The magnitude of the population increase in overall abundance shown in the CPUE data also suggests that the value of α may be high, given that sensitivity analyses revealed that the greatest increases in abundance occurred with the largest values of α. If adult competition in the Little Moose Lake bass population was released through harvest, per capita recruitment could be large, indicating a situation that is similar to the case 2 scenario (i.e., high per capita recruitment in the absence of density dependence, $\alpha > 10$, and high survivorship of immature fish, $s_y, s_{j2}, s_{j3} > 0.5$).

Is there an optimal control harvest strategy?

The optimal harvest strategy is highly dependent on the control objective. If the goal of the harvest is to reduce the overall population abundance (regardless of demographic structure), then in situations in which the population's reproduction rate at low spawner abundance is large, harvest will not be effective until very high levels are achieved. In such cases, it may not be beneficial to remove any individuals unless it is possible to remove nearly all of the population. In other situations, the structure of the population may be of greater importance. For example, increased abundance of large smallmouth bass (>200 mm) in Little Moose Lake has altered food web linkages and has had a measured impact on the abundance of other littoral fish species (Lepak et al. 2006; Weidel et al. 2007). Therefore a key management goal is to minimize the impact of large bass (and reduce the total biomass of the bass) rather than simply reduce the overall population abundance. In such cases, a management tradeoff exists between a reduction in abundance of one life stage and a potential overcompensatory response in another. In this situation, continued regular harvesting may be necessary to maintain a reduction in adults.

If it remains impossible to eliminate all bass from the lake, the best Little Moose Lake smallmouth bass management strategy may be to reduce the proportion of adult fish (>200 mm) that are harvested. The sensitivity analyses showed that removal of adults caused the largest increase in yearling and juvenile abundances. Because we do not have annual population abundance estimates, it is difficult to determine exactly how many adults should be harvested to both achieve the management objectives described above and not produce an overcompensation of yearlings or juveniles. However, some reduction in the harvest of adults would likely mitigate the observed overcompensatory response without producing large increases in adult abundance, as well as reduce the effort necessary to maintain the positive effects of the removal.

Observations with Lake Opeongo parameter values

Implementing the model with parameter values generated from the Lake Opeongo smallmouth bass population did not produce an increase in total population abundance (or in any of the stages) under the harvesting scenarios that we evaluated. However, our results indicated that slight changes in individual parameter values can produce an increase in population abundance under three (age-2 and older juvenile only, adult only, and all stages in equal proportion) of the four harvest strategies that we examined. Several potential reasons could account for this apparent discrepancy. First, the 54 years of data from Lake Opeongo encompass a period in which smallmouth bass invaded and began to colonize the lake following their introduction in the 1920s (Shuter and Ridgway 2002). When creel surveys were initiated in 1937, smallmouth bass were still becoming established in this large lake. The stock–recruitment relationship could have been fundamentally different during the colonization period compared with the subsequent time period in which the population had become well established. This is evidenced by the value for α being higher (α = 9.3) when we re-estimated the stock–recruit relationship excluding data from the first 20 years of data collection. Second, the parameter values are time-invariant in the model. We averaged annual survivorship and maturation to produce a constant value for each parameter, which is a very restrictive assumption. In natural systems, these rates vary annually and can be affected by a number of biotic and abiotic factors. For example, juvenile survivorship and growth of smallmouth bass is dependent on both population abundance and summer air temperatures (Shuter and Ridgway 2002); therefore the average values used in our model ignored interannual variation. In addition, the natural mortality parameter for adult survivorship included recreational fishing mortality. If the parameter s_a was re-estimated excluding the fishing mortality, adult survivorship would be higher. Increasing adult survivorship would result in an increase in abundance with harvest but that alone could not produce the magnitude of the increase that was observed in the smallmouth bass CPUE data from Little Moose Lake. Finally, it is possible that there are fundamental differences between the smallmouth bass populations in Lake Opeongo and Little Moose Lake. One indication that the stock–recruitment relationship may be different in the the two lakes is evident in the large difference in the values of α generated by the CPUE data from Little Moose Lake (α = 84.3) and the data from Lake Opeongo (α = 5.5). Although we cannot confidently assess the validity of the Little Moose Lake value (for reasons previously described), the very high value of α suggests that smallmouth bass recruitment in Little Moose Lake may be substantially different from that in Lake Opeongo.

It is possible that the CPUE data from Little Moose Lake do not accurately reflect the changes in bass abundance. Although we tried several methods to estimate yearly abundances, including depletion and cohort analyses, we were unable to develop robust population estimates because, in part, CPUE data and population abundances are not likely related by a simple factor (Schoenebeck and Hansen 2005). Although harvest effort has varied over the eight removal years, the methods for the removal have remained constant and the intensity of the removal has remained high. At the initiation of the harvest, 5014 smallmouth bass were removed in the spring of 2000. The cohort analysis estimated that there were approximately 7000 individuals present during the initial harvest. This suggests that nearly 72% of bass that were present were removed in the spring of 2000. As a result, we believe that the CPUE data can serve as a proxy for establishing that the population is responding to harvest by overcompensating.

Model extensions

The sensitivity analysis results in part reflect how density dependence was incorporated into the model. The decision to include density dependence in the stock–recruitment relationship (rather than in another stage or in multiple stages) was based on empirical studies of smallmouth bass life history and population dynamics that demonstrated the presence of density dependence in the recruitment process (DeAngelis et al. 1993; Dong and DeAngelis 1998; Shuter and Ridgway 2002). DeAngelis et al. (1991) used an individual-based model to show that the relationship between the number of smallmouth bass nests and the number of yearling recruits was overcompensatory, which they described as “not unlike a Ricker (1954) curve”. DeAngelis et al. (1993) found a similar Ricker-like relationship between the number of fertilized eggs and the number of age-0 smallmouth bass that survived through the early part of the growing season. Dong and DeAngelis (1998) further showed that cannibalism and intense intraclass and interclass competition within a smallmouth bass population can lead to overcompensation in the recruitment of age-0 fish.

In addition, studies on juvenile and adult smallmouth bass suggested that there may be a density-dependent relationship between the number of mature fish and the number of fish that actually spawn (Raffetto et al. 1990; Ridgway et al. 1991; Shuter and Ridgway 2002). Ridgway et al. (2002) developed the juvenile transition hypothesis to describe their observation that as the population of mature males increases, the proportion that spawn declines (Ridgway et al. 1991; Ridgway et al. 2002; Shuter and Ridgway 2002). To incorporate this observation, we modified the equation for the yearling stage (eq. 1) to include a saturation function for the number of adults that spawn:

$$(7)\qquad Y_{t+1} = \frac{A_t(1-h_\mathrm{a})}{1+\delta A_t(1-h_\mathrm{a})}\alpha \mathrm{e}^{-\beta\frac{A_t(1-h_\mathrm{a})}{1+\delta A_t(1-h_\mathrm{a})}}$$

The parameter δ controls the negative effects of increasing the number of adults on the proportion that spawn. During the parameterization process, the best fit to the Lake Opeongo stock–recruit data occurred when $\delta = 0$, in which case the model simplifies to a standard Ricker recruitment function. Therefore, we did not use this modified stock–recruitment relationship for further analyses.

Observations of the smallmouth bass population in Little Moose Lake suggested that size at maturity has remained fairly constant but length at age has increased since the onset of the removal (unpublished data). This suggests that maturation rates may have increased over the time period of the removal, which begs the question as to whether this change would be enough to drive an overcompensatory response in the bass population. We looked at this scenario by modifying the maturation rate of age-3 individuals, the parameter m_1. Because this parameter was sensitive at low values of α (and α was estimated at approximately 5.5 through the parameterization process), we speculated that if the maturation rate of $J2$ individuals was a density-dependent function of the number of adults in the population, then perhaps that parameter could be driving the observed increase in population abundance. The revised model included the time-variant maturation parameter:

$$m_{1,t+1} = m_{\min} + \frac{m_{\mathrm{add}}}{1 + \mu A_t} \tag{8}$$

where $m_{\min}$ is the maturation rate when the adult population is large (we set $m_{\min}$ to the estimated value for m_1 from the parameterization process), m_{add} is the maximum addition onto $m_{\min}$, and μ regulates the effects of adult population density on m_{add}. Though we did not have data to parameterize m_{add} and μ, we were able to determine that even under a “favorable” parameterization (i.e., one in which $m_{1,t+1}$ reached high values with even modest reductions to A), the addition of a density-dependent time-variant maturation rate (when the value of $m_{\min} = m_1$) was not enough by itself to lead to overcompensation with harvest. The major variation in the results with this revised model was that as harvest was increased, it became increasingly difficult to collapse the population.

We focused our analyses on equilibrium dynamics in response to harvest because we were interested in the long-term response of smallmouth bass to an intense harvest. However, further analyses could focus on the short-term dynamics of the Little Moose Lake study population and time-varying harvests to better understand the mechanisms responsible for population-level overcompensation in response to intense harvest. The presence of a “saw tooth” temporal pattern in young-of-the-year and yearling abundance is consistent with alternating strong year classes suppressing each subsequent year class. This could occur as a result of intense competition between the yearling and juvenile stages or through cannibalism, both of which have been previously used to justify use of the Ricker recruitment curve (Claessen et al. 2004). Our results support the use of the Ricker equation, but further analyses could explicitly incorporate these processes into the model.

Our model, together with empirical observations from the Little Moose Lake smallmouth bass population, demonstrates the potential for fish population abundance to increase in response to harvest. Although an increase in stage-specific or population-level abundance in response to harvest has been reported for a number of taxa (Slobodkin and Richman 1956; Buckley et al. 2001; Cameron and Benton 2004) and discussed theoretically (Dennis et al. 1997; Abrams and Matsuda 2005; De Roos et al. 2007), this type of response has not been previously documented empirically within a fisheries context. Studies of fish population responses to perturbations have shown that when overcompensation has occurred, it was in the form of individual growth or maturation rates (Weatherley and Gill 1981; Miglavs and Jobling 1989; DeAngelis et al. 1993). Our results show that one potential response of fish populations to harvest can be overcompensation in stage-specific abundances, which can subsequently lead to an overall increase in total population abundance. This is especially important to consider when the objective of harvest is control. In some instances, control through harvest may not be a feasible strategy. Alternatively, observed increases in population abundance may be a temporary result in situations in which complete mortality of all life stages cannot be quickly imposed; yet this response might ultimately disappear as control measures become more effective. Overall, our results show that the decision to reduce abundance through harvest must take into consideration the demographic characteristics and the density-dependent processes of the targeted population.

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