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ARTICLE

Stage-Structured Simulations Suggest That Removing Young of the Year Is an Effective Method for Controlling Invasive Smallmouth Bass

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Abstract
Smallmouth Bass *Micropterus dolomieu* is an invasive fish for which few control methods have been developed or tested. Adult removal is most common, but this strategy is labor-intensive and can result in an increase in population abundance (i.e., overcompensation). Using a stage-structured matrix model, we tested removal of young of the year as a control method, both alone and in combination with three supplemental removal strategies. Our results suggest that young of the year removal alone does not lead to overcompensation and can be expected to control some populations of Smallmouth Bass in a reasonable timeframe (e.g., 75% reduction in abundance after 10 years at 68% removal). Lower rates of removal of young of the year are required if this method is combined with supplemental removal strategies (especially those that also target immature bass). Where feasible, we recommend that managers include young of the year removal as part of their control plans. Future research should focus on incorporating more biological realism into simulation models and testing this method in the field.

Smallmouth Bass *Micropterus dolomieu* (henceforth, SMB) is considered an invasive species in 11 countries on four continents (Loppnow et al. 2013). Impacts of SMB predation on small prey such as dace and minnows include reductions in abundance, changes in habitat use, and even extirpation (Schlosser 1987; MacRae and Jackson 2001; Trumpickas et al. 2011). Smallmouth Bass also prey on juvenile sport fish such as endangered Pacific salmon *Oncorhynchus* spp. and Walleye *Sander vitreus*, sometimes negatively affecting their populations (Johnson and Hale 1977; Rieman et al. 1991; Fayram et al. 2005; Carey et al. 2011). Competition with invasive SMB for prey often forces Lake Trout *Salvelinus namaycush* to consume suboptimal prey, which can lead to inhibited growth or Lake Trout extirpation (Yule and Luecke 1993; Vander Zanden et al. 1999; Morbey et al. 2007). Predation and competition by SMB can also affect populations of amphibians, crustaceans, and waterfowl (Hunter 1988; Kiesecker and Blaustein 2008; Sanderson et al. 2009).

Managers in areas such as Maine, New York, Colorado, British Columbia, Washington, and northern Minnesota have attempted to control invasive SMB, but few proven control options are available and attempts to reduce abundance are usually unsuccessful (Loppnow et al. 2013). To our knowledge, as of 2014, methods that have not been used for SMB control include biological control, sterilization, induced winterkill, and explosives. Removal via angling (D. P. Boucher, Maine Department of Inland Fisheries and Wildlife, unpublished report) and netting (Gomez and Wilkinson 2008; Boucher, unpublished report) have proven ineffective. Although susceptible to removal by electrofishing (especially adult SMB), but this method generally fails to reduce their abundance in the long-term (Boucher 2005; Weidel et al. 2007; Burdick 2008; Hawkins et al. 2008). Waterlevel manipulation has been attempted once with unknown results (Kleinschmidt Energy and Water Resource Consultants 2008). The piscicides rotenone and Supaverm have been effective at

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controlling invasive SMB (Smith 1941; Ward 2005), but only at high cost and with substantial nontarget effects.

Attempts at controlling invasive species occasionally result in greater total population abundance of that species, a phenomenon known as overcompensation, or the hydra effect (Zipkin et al. 2008; Abrams 2009; Strevens and Bonsall 2011). The concept of compensation is most commonly applied to invasive plants, which may increase their growth rate or seed production after control attempts (e.g., Pratt et al. 2005; Garren and Strauss 2009). A compensatory response is sometimes observed in SMB as well. For example, researchers observed an increase in SMB abundance (particularly juveniles) after the mass removal of adults from an Adirondack lake (Weidel et al. 2007). Overcompensation probably resulted from higher recruitment of juveniles to the spawning population in the absence of adults (Ridgway et al. 2002) along with improved offspring survival (Zipkin et al. 2009).

Control methods that target early life stages of SMB instead of adults could avoid overcompensation by maintaining intraspecific competition and other mechanisms that limit recruitment. Elasticity analysis indicates that survival in the first 4 years of life has the greatest effect on the SMB population growth rate (Loppnow et al. 2013). Managers could capitalize on this leverage point by targeting young of the year for control of invasive SMB. Removing young on the nest could be done several ways, including removing nest-guarding males, destroying nests mechanically or chemically, dewatering shallows during spawning, or improving conditions for nest predators. Dispersed young could be targeted by trapping, netting, or predator enhancement. Many of these methods are inexpensive, are safe for humans and the environment, and could be implemented by affected stakeholders. In addition, young of the year removal may be less likely to cause overcompensation because it could be done in such a way that the adult population remains intact.

An important first step in evaluating young of the year removal as a management tool for invasive SMB is to examine the feasibility and efficacy of this approach, both alone and in combination with other control methods. To this end, we incorporated young of the year removal into an existing stage-structured population model (Zipkin et al. 2008) and then simulated a range of control scenarios that involved young of the year removal. Our analysis addressed three primary research questions: (1) can young of the year removal lead to overcompensation, (2) how much young of the year removal is needed to control SMB, and (3) how might young of the year removal be combined with supplemental removal methods to enhance control? This information is important because it allows managers to identify the extent to which young of the year removal is appropriate for their system.

METHODS

Model structure.—To explore young of the year removal as a control option for invasive SMB, we modified the annual, stage-structured, matrix population model in Zipkin et al. (2008; Figure 1). The parameters for this model were estimated by Zipkin et al. (2008), using a long-term data set on introduced SMB in Lake Opeongo, Ontario, Canada (Shuter et al. 1987). Shuter and Ridgway (2002) found that relationships estimated from this data set are reasonably representative of relationships for other SMB populations in the region, where invasive SMB are increasingly an issue. The model is a prebreeding census model with four life stages: yearlings (Y), age-2 juveniles (J2), age-3+ juveniles (J3), and adults (A). We assumed a 1:1 sex ratio and considered that all SMB in the model were males. At the start of each time step, some individuals in each stage experience natural mortality. The proportion of yearlings that survive then become age-2 juveniles, and the surviving juveniles either move to the next life stage or remain as juveniles as determined by maturation parameters. Model parameters for survival, maturity, and reproduction are given in Table 1. The population is allowed to equilibrate before removal mortality is applied. Supplemental removal (not specifically targeted at young of the year) occurs postcensus and prebreeding, as in a spring electrofishing scenario.

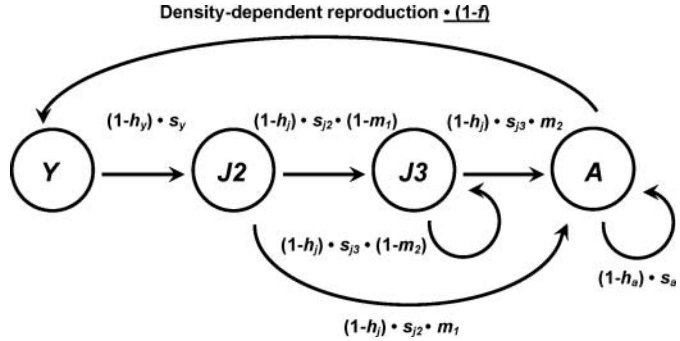

FIGURE 1. A schematic of the stage-structured population model from Zipkin et al. (2008) with underlined alterations. *Y* represents yearlings, *J2* represents age-2 juveniles, *J3* represents age-3+ juveniles, and *A* represents adults. *s* is the proportion surviving, *m* is the proportion maturing, *h* is the proportion removed by supplemental removal, and *f* is the proportion of young of the year removed. Density-dependent reproduction occurs via a Ricker stock–recruitment relationship.

Density-dependent reproduction occurs via a Ricker stock–recruitment relationship in which adult abundance determines the number of yearlings in the next time step. The Ricker relationship assumes that recruitment peaks at some abundance of stock and subsequently declines at higher abundances due to limitation by intraspecific pressures (Ricker 1954). This relationship is essential to modeling overcompensation. Overcompensatory recruitment of SMB to the yearling stage is supported by field data suggesting that juvenile growth is limited by abundance and that fewer bass spawn at high population abundance (Ridgway et al. 2002; Shuter and Ridgway 2002). Individual-based model simulations also support the use of a Ricker stock–recruitment relationship (DeAngelis et al. 1991; Dong and DeAngelis 1998).

TABLE 1. Population parameters used in the Smallmouth Bass matrix model (adapted from Zipkin et al. 2008). Normal values are taken from the Lake Opeongo population; variations are alternative parameter values that can lead to an overcompensatory response to removal.

Parameter	Description	Normal value	Variations
α	Ricker parameter—maximum per capita recruitment	5.503055	10.0, 15.0, 20.0, 25.0
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	0.8, 0.9
s_a	Proportion of A that survive annually	0.54	0.7, 0.8, 0.9
m_1	Proportion of J2 that mature into A	0.0560	0.2, 0.3, 0.4, 0.5, 0.6, 0.7, 0.8, 0.9, 1.0
m_2	Proportion of J3 that mature into A	0.3725	0.7, 0.8, 0.9, 1.0

We modified the Zipkin et al. (2008) model by incorporating young of the year removal. We modeled this method by removing a proportion (*f*) of the offspring that were produced each year. The remaining offspring entered the population as yearlings:

$$Y_{t+1} = A_t(1-h_a)ae^{-A_t(1-h_a)}(1-f), \quad (1)$$

where h_a is the proportion of adults removed, and α and β are parameters governing the Ricker stock–recruitment relationship. Because the model has a coarse time step of 1 year, young of the year removal represents any additional mortality on age-0 SMB, both on the nest or dispersed.

Young of the year removal and overcompensation.—We first used our model to determine whether young of the year removal can lead to overcompensation in a population of SMB. For these simulations we used normal population parameters and then, in turn, used each of the parameter variations known to encourage overcompensation (Zipkin et al. 2008; Table 1). Once population abundance reached equilibrium, we modeled young of the year removal as a fixed percentage (1–100%) in all subsequent years and allowed the population to reequilibrate. If equilibrium abundance increased in any of these scenarios, we concluded that young of the year removal caused overcompensation.

Young of the year removal as a control option.—To test the efficacy of young of the year removal as an option for controlling invasive SMB, we determined the proportion of young of the year that must be removed each year to reduce total population abundance by 75% in 10 years. This management goal is arbitrary but realistic. So that simulations were relevant to populations that might be difficult to control (because of the potential for overcompensation), we evaluated young of the year removal as a control option for the "normal" parameter set and for each individual parameter variation in Table 1.

Young of the year removal combined with supplemental removal.—To determine which combinations of young of the year removal and supplemental removal would provide the best control, we simulated several integrated management strategies. We developed different integrated management strategies by pairing young of the year removal with one of the following supplemental removal strategies: removing equal proportions of all life stages, removing adults only, and electrofishing (for each 1% of A removed, 0.4% of J2 and J3 and 0.2% of Y are removed; Zipkin et al. 2008). We were interested in these alternative control strategies because they simulate relatively common SMB control methods such as netting and electrofishing (Loppnow et al. 2013) and can lead to overcompensation under certain conditions (Zipkin et al. 2008).

We subjected two simulated SMB populations to each management strategy: one population with normal parameters and one with $\alpha = 25$. We chose the latter because it is the parameter variation in Table 1 that promotes the highest degree of overcompensation (Zipkin et al. 2008). Therefore, our results span the likely range of possibilities. In each simulation, we independently varied the annual amount of young of the year removal and supplemental removal from 0 to 100% in 1% increments. For the electrofishing scenario, 100% removal refers to 100% removal of adults along with removal of other age-classes scaled relative to the percentage of adults removed. Under each of these combinations, we determined the number of years it would take for that management strategy to reduce total population abundance by 75%.

RESULTS

Young of the Year Removal and Overcompensation

Removing young of the year in the range 1–100% did not lead to overcompensation in simulations with normal population parameters or simulations that involved parameters that promote overcompensation (see Table 1 for parameter variations). In all simulations, young of the year removal reduced the equilibrium abundance.

Young of the Year Removal as a Control Option

Young of the year removal was sufficient to meet the management goal of a 75% reduction in total population abundance in 10 years for all parameter variations. The percentage of young of the year that had to be removed annually to reach this goal was ~68% for a population with normal parameters (Figure 2).

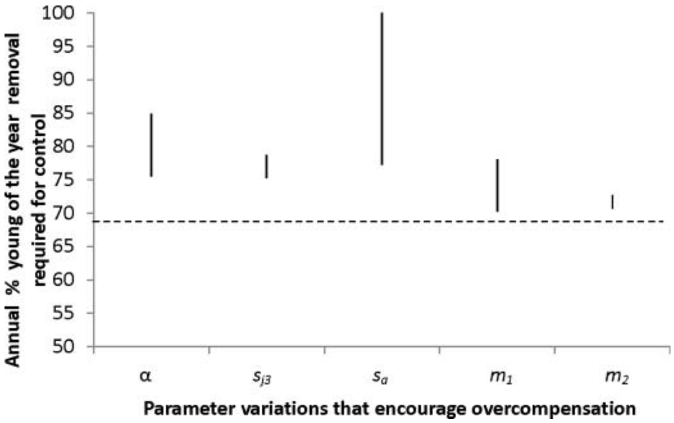

FIGURE 2. Percentage of young of the year removal required annually to reduce simulated Smallmouth Bass population abundance by at least 75% in 10 years. The dashed line represents the amount of young of the year removal that was required for control, given the normal parameter set. Each solid line represents the range of young of the year removal that was required for control for each parameter in the range of parameter values that could promote overcompensation (see Table 1 for parameter values).

Simulations with parameters that promoted overcompensation required 2–32% more removal of young of the year.

Young of the Year Removal Combined with Supplemental Removal

Strategies that included both young of the year removal and another control option varied in the number of years that it took to achieve control (defined as a 75% reduction in total abundance; Figure 3). For all simulations, the time to control transitioned rapidly from 50+ years to less than 20 years with increasing effort. In other words, there appeared to be a minimum threshold of effort beyond which control was likely to be effective. The population with a tendency to overcompensate ($\alpha = 25$) consistently required more young of the year removal or supplemental removal to achieve control than did the normal population.

The time required to achieve control was generally shortest when young of the year removal was combined with the removal of an equal proportion of all life stages (Figure 3A, B), intermediate when supplemental removal was via electrofishing (Figure 3, E and F) and longest when supplemental removal focused exclusively on adults (Figure 3C, D). Regardless of which supplemental removal method was used, a low supplemental removal rate meant that an annual young of the year removal rate of roughly 45% (normal scenario) to 80% (scenario highly prone to overcompensation) was necessary to achieve control within 20 years. On the other hand, the effects of young of the year removal were negligible if supplemental removal rates were higher than 20–40% for equal proportion removal, 45–75% for electrofishing, and 60–90% for adult-only removal.

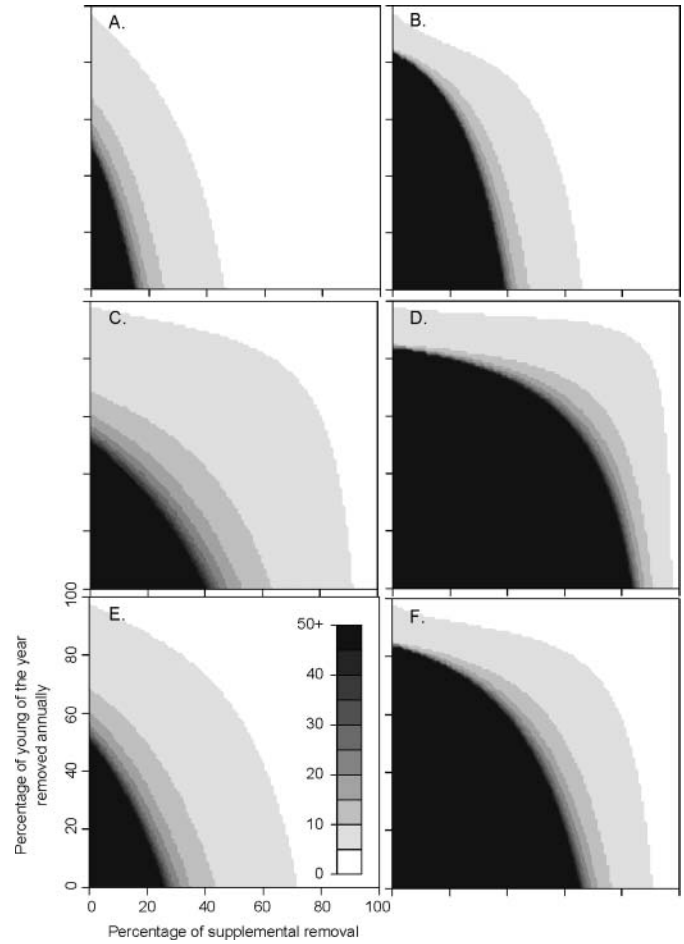

FIGURE 3. Years of management required to decrease the abundance of simulated Smallmouth Bass populations by 75% under all possible combinations of young of the year removal and supplemental removal for three supplemental removal strategies and two parameter sets. **(A, B)**, Equal proportions of each life stage are removed; **(C, D)**, only adults are removed; **(E, F)** electrofishing-type removal is used. Normal population parameters were used for the simulations in **A**, **C**, and **E**; α was increased to 25 for **B**, **D**, and **F** to promote overcompensation.

DISCUSSION

Our simulations suggest that young of the year removal can be an effective SMB control method, especially when combined with supplemental removal methods. If young of the year removal is used alone, then at least 65–70% of this age group must be removed annually to achieve a 75% reduction in total SMB abundance in 10 years. Although this amount of young of the year removal might be feasible in small systems, it may be difficult to achieve in large or deep systems. If young of the year removal is used in combination with supplemental removal methods, then our simulations suggest that the required rate of young of the year removal can be much lower. Of course, effective supplemental removal rates may be difficult to achieve and higher rates of both young of the year removal and of supplemental removal are necessary for populations that are prone to overcompensation.

It is encouraging and not altogether surprising that young of the year removal on its own does not cause overcompensation. Simulations by Zipkin et al. (2008) showed a similar result, predicting overcompensation only for removal of older life stages. This result is also consistent with the hypothesis that adult removal leads to overcompensation by increasing recruitment of juveniles to the spawning population and therefore producing more offspring (Ridgway et al. 2002).

To control SMB in a way that is both efficient and avoids triggering overcompensation, we recommend removal strategies that target young SMB. When used in combination with young of the year removal, we found the removal of all age classes in equal proportions is most effective. However, targeting and removing SMB in these proportions is perhaps not realistic. Electrofishing appears to be a viable alternative, provided it removes both some yearlings and juveniles. Adult removal was least effective, particularly when applied to a population prone to overcompensation (Figure 3D). This result is consistent with an elasticity analysis of several SMB matrix models, in which population growth rate is shown to be most sensitive to the survival of young fish (Loppnow et al. 2013). The relatively stronger influence of equal proportion removal than young of the year removal is also consistent with this logic because this supplemental removal scenario included the largest proportion of yearlings.

When considering how best to integrate young of the year removal into a control plan for invasive SMB, managers should bear in mind that complete eradication is unlikely and that high rates of young of the year removal are generally required for control. Whether or not these rates can be achieved depends on the system and how removal is implemented. We recommend targeting young SMB while on the nest if possible, given the challenges of locating and capturing dispersed young of the year. If spawning areas are known, physical or chemical destruction of nests could be a straightforward and effective method. Because SMB generally spawn at depths of 2 m or less (Brown et al. 2009), a drawdown during the spawning season to expose the eggs could be an option for destroying nests in reservoirs or flowing water. Removing nesting bass via electrofishing to expose eggs and fry to predation is another relatively efficient approach. Dispersed young of the year bass can be captured using minnow traps (Dunlop et al. 2005), seining, and electrofishing (Miller and Storck 1984). Whether any of these methods is effective for control is unknown, however, and using them to remove sufficient numbers of dispersed young of the year would likely require more effort than removing young on the nest.

Although our results suggest that young of the year removal is an effective strategy for SMB control, this conclusion is based on a relatively simple stage-structured matrix model. For example, due to the nature of the stage-structured model and the Ricker stock–recruitment relationship, all adults are assumed to be reproducing. So when we remove adult SMB we likely overestimate the effect on the spawning population by culling a relatively large proportion. Then again, the Ricker model we adopted might have underestimated the effect of adult removal on the abundance of spawning adults by not adequately accounting for a density-dependent increase in the recruitment of juveniles to the spawning population. Given that Zipkin et al. (2008) had to assume extreme parameter values to cause overcompensation, a Ricker model may be too simple an approach for adequately capturing the complex and fine-scale biological processes and interactions that can lead to competitive release. For example, the availability of food, mates, and spawning sites can all change with removal. Much remains to be learned about SMB population dynamics, and debate as to how best to model the stock–recruitment relationship (Shuter and Ridgway 2002; Allen et al. 2011) could also account for the sometimes unrealistic parameter values. We also assumed that the rate of young of the year removal was consistent from year to year, which may not be possible if the ability to locate young of the year declines with population abundance. Additionally, due to the coarse time step of the model, we were unable to simulate specific methods of young of the year removal, information that could prove useful for managers. Given these limitations and potential biases in our model, it may be prudent to consider evaluating young of the year removal within an individual-based modeling framework that is transparent and can accommodate fine-scale and complex biological processes. Ultimately, we recommend field trials to compare the real-world practicality, feasibility, and effectiveness of young of the year removal with our predictions.

In conclusion, we recommend combining young of the year removal with a supplemental removal strategy to control invasive SMB and avoid overcompensation by this species. Our simulations suggest there are many feasible combinations of young of the year removal and supplemental removal that can result in control in less than 10 years. Real-world successes of targeting young invasive fish, such as with the Sea Lamprey *Petromyzon marinus* (Lavis et al. 2003), lend further credence to targeted removal of young of the year. This control method is also likely to be applicable to fish with similar life histories, such as Largemouth Bass *M. salmoides*. Young of the year removal has the potential to reduce population abundance in a diversity of situations.

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