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When can efforts to control nuisance and invasive species backfire?

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Abstract. Population control through harvest has the potential to reduce the abundance of nuisance and invasive species. However, demographic structure and density-dependent processes can confound removal efforts and lead to undesirable consequences, such as overcompensation (an increase in abundance in response to harvest) and instability (population cycling or chaos). Recent empirical studies have demonstrated the potential for increased mortality (such as that caused by harvest) to lead to overcompensation and instability in plant, insect, and fish populations. We developed a general population model with juvenile and adult stages to help determine the conditions under which control harvest efforts can produce unintended outcomes. Analytical and simulation analyses of the model demonstrated that the potential for overcompensation as a result of harvest was significant for species with high fecundity, even when annual stage-specific survivorship values were fairly low. Population instability as a result of harvest occurred less frequently and was only possible with harvest strategies that targeted adults when both fecundity and adult survivorship were high. We considered these results in conjunction with current literature on nuisance and invasive species to propose general guidelines for assessing the risks associated with control harvest based on life history characteristics of target populations. Our results suggest that species with high per capita fecundity (over discrete breeding periods), short juvenile stages, and fairly constant survivorship rates are most likely to respond undesirably to harvest. It is difficult to determine the extent to which overcompensation and instability could occur during real-world removal efforts, and more empirical removal studies should be undertaken to evaluate population-level responses to control harvests. Nevertheless, our results identify key issues that have been seldom acknowledged and are potentially generic across taxa.

Key words: density dependence; fecundity; instability; invasive species control; harvest; nuisance species; overcompensation; population model; removal study; stage-structured model; survivorship.

Introduction

The control of nuisance and invasive species is an important concern for preserving the integrity of ecosystems. One common control method is harvest, or the permanent removal of individuals from a population, which can be implemented through a variety of techniques including (but not limited to) hunting/fishing, trapping, poisoning, or biocontrol. Control through harvest has been attempted for a wide variety of taxa including aquatic invertebrates (Hein et al. 2006), fish (Weidel et al. 2007), birds (Brooks and Lebreton 2001, Frederiksen et al. 2001), mammals (Campbell and Donlan 2005, Howald et al. 2007), weedy plants (Buckley et al. 2001, Pardini et al. 2009), and pest insects (Faccoli and Stergulc 2008). Typically, the desired result of control efforts is to either eradicate the target population or to decrease abundance to levels that minimize adverse impacts.

However, increased mortality as caused by harvest can potentially lead to unintended and undesirable outcomes. Several theoretical and empirical studies have demonstrated that increased mortality can not only lead to greater variability in abundance and population instability, such as periodic cycling and even chaos (Costantino et al. 1995, 1997, Dennis et al. 1997, Cushing et al. 1998, Abrams and Quince 2005), but can also lead to an increase in total population abundance, which we refer to as overcompensation. Overcompensation has been observed in plants (Buckley et al. 2001, Pardini et al. 2009), insects (Nicholson 1957, Moe et al. 2002), and fish (Zipkin et al. 2008). In each of these empirical examples, increased mortality of individuals in the target population resulted in greater overall abundances, suggesting that overcompensation may have resulted from intra-demographic (such as population-level fecundity and survivorship) processes rather than external abiotic effects or as a result of niche opening due to decreased abundance of other species. For example, an intensive seven-year removal effort of a closed population of smallmouth bass (more than 53 000 individuals were removed and no other species was targeted) in a north temperate lake led to higher estimated abundances of bass, primarily as a result of an increase in juveniles. Analysis of the system suggested that high fecundity of adults and high juvenile survivorship together with reasonably high maturation rates of young juveniles

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may have been responsible for this undesirable response of the bass population to harvest (Zipkin et al. 2008).

The theoretical notion of increased mortality leading to greater population abundance was first addressed by Ricker (1954) but did not receive much subsequent attention for nearly a half century (see review by Abrams [2009]). Recent theoretical studies have explored this phenomenon and coined the terms "hydra effect" (Abrams and Matsuda 2005), "paradoxical increase" (Seno 2008), and "overcompensation" (De Roos et al. 2007) to describe this unexpected response to mortality. Although theoretical studies have examined the potential for overcompensation with respect to predator–prey dynamics (Abrams and Matsuda 2005, Abrams and Quince 2005, De Roos et al. 2008, Matsuoka and Seno 2008), environmental degradation (Abrams 2002), seasonality (Boyce et al. 1999, Jonzen and Lundberg 1999), and stage-specific mortality (Jonzen and Lundberg 1999, De Roos et al. 2007, 2008) less consideration has been given to the context of population control efforts (but see Seno 2008).

Predicting the response of a population to a control harvest can be challenging in part because of demographic structure (differences in vital rates based on age, size or stage) and density-dependent processes (Benton et al. 2004, Pardini et al. 2009). Under harvest, a population's growth rate may vary depending on the desired population size (i.e., how close or far a population is to carrying capacity) and upon which individuals are removed (Benton et al. 2006). While it is often possible to broadly characterize the demographic structure of a target population through an assessment of stage specific differences in survival and recruitment, it is frequently difficult to determine which demographic processes are density dependent. It is even more difficult to determine the functional form and strength of each density-dependent process because long-term data must be available for the target species of interest, and a variety of hypothesized relationships often provide suitable fits to available data (Pascual et al. 1997, Runge and Johnson 2002). Even when these relationships can be precisely specified, slight changes in vital rates can lead to very different population dynamics in response to harvest. In such cases, minor amounts of uncertainty in parameter estimates can result in erroneous or misleading predications (Zipkin et al. 2008).

Given the potential for unexpected and undesirable consequences as a result of mischaracterizing the population dynamics of nuisance species when implementing a control harvest, it is important to identify a framework and guidelines for such efforts. In this paper we develop a general model to explore the conditions under which control harvests can produce unintended results, such as overcompensation and instability in a targeted population. We propose a framework based on fecundity and annual survivorship for identifying groups of taxa that may respond to harvest in an undesirable manner. In situations where control through harvest is possible, we further assess the likely amount of effort required to achieve specified control objectives.

Methods

Model development

We developed a simple density-dependent, stage-structured model and used it to examine the equilibrium dynamics assuming sustained harvesting of a population with juveniles (J) and adults (A). De Roos et al. (2007) showed that a model with discrete juvenile and adult stages provided a good approximation to the dynamics of more complex models with both discrete and continuous size distributions. In developing our model, we chose to consider a parsimonious form that was qualitatively generic across taxa but still capable of producing a broad range of population-level dynamics in response to harvest. In cases where this simplification is not adequate, the model can be readily extended to accommodate more life stages as needed.

We modeled the population with first-order difference equations assuming an annual time step, during which individuals are harvested, adults breed, and then both stages experience natural mortality. Harvest was assumed to occur prior to breeding, which is a common strategy used in control efforts designed to minimize the number of individuals removed (Brooks and Lebreton 2001). We assumed that surviving juveniles become adults after one time step and that adults are capable of surviving for several time steps. The model counts individuals before harvest (i.e., a pre-breeding census); implying that juveniles at time t are one year old and adults are age two and older. We allowed juveniles and adults to be harvested in different proportions, h_j and h_a, to examine how various harvest strategies (that selectively target one stage or another) affect the population. The form of the general model is written as follows:

$$\begin{aligned} J_{t+1} &= A_t(1-h_a)\gamma \\ A_{t+1} &= J_t(1-h_j)s_j + A_t(1-h_a)s_a \end{aligned} \quad (1)$$

where s_j (annual juvenile survivorship), s_a (annual adult survivorship), and γ (fecundity) are the parameters describing the vital rates of the population.

Runge and Johnson (2002) argued that nondepensatory recruitment functions can be fundamentally described (to first order) by one of three relationships: linear (constant), hyperbolic (which we refer to as compensatory), and exponential (which we refer to as overcompensatory; Fig. 1). It is not necessary to consider depensatory recruitment (where reproduction decreases at low density, i.e., an Allee effect) in this context because an intensive harvest of such a population would likely drive it to extinction (Dennis 1989). A linear recruitment function is one in which γ is constant and was analyzed in this context by Hauser et al. (2006). Compensatory recruitment can potentially arise in populations that are governed by contest competition (i.e., where individuals have differential abilities to meet their needs). In the context of compensatory reproduction, competitively superior individuals are able to reproduce even as density increases because they do not lose access to resources (Brännström and Sumpter 2005). The simplest compensatory recruitment function was described by Beverton and Holt (1957) and is written in our model as follows:

$$\gamma_{\mathrm{BH}} = \frac{\alpha}{1 + \beta A_t(1 - h_{\mathrm{a}})} \tag{2}$$

where α is the maximum number of offspring produced by an adult in the absence of density dependence and β represents the strength of the density-dependent effects (and thereby determines the carrying capacity of the population for given values of α). The third type of recruitment function is overcompensatory, which can be generated through scramble competition (i.e., where individuals have equal access to resources). With overcompensatory recruitment, resources are depleted evenly as density increases which results in a more uniform decline in recruitment for all individuals (Brännström and Sumpter 2005). The simplest overcompensatory recruitment model was defined by Ricker (1954):

$$\gamma_{\mathrm{R}} = \alpha \exp(-\beta A_t[1 - h_{\mathrm{a}}]) \tag{3}$$

where α, $\beta > 0$ are again parameters that regulate the maximum level of per capita recruitment and the strength of the density dependence. Of these three recruitment relationships, the overcompensatory function (Eq. 3) is the only one capable of leading to instability and overcompensation as a result of harvest (see the Appendix for proof and more details). Unlike linear or compensatory recruitment where total recruitment must increase or saturate as the population increases, the overcompensatory function (Eq. 3) can maximize total recruitment at intermediate population abundances (for high values of α; Fig. 1). It is well established that the compensatory model produces stable equilibrium dynamics; by comparison, the overcompensatory model can produce stable, cyclic or chaotic dynamics (Wikan 2004).

For a population to increase in abundance in response to harvest, at least one vital rate must be overcompensatory (i.e., peak at some intermediate level). Numerous studies have documented overcompensatory relationships in the recruitment process (Ricker 1954, DeAngelis et al. 1991, Constantino et al. 1996, Dennis et al. 1997, Buckley et al. 2001, Pardini et al. 2009). Although nonlinear population responses to perturbation can occur during any stage of an organism's life cycle, we chose to examine the case where density dependence occurs during recruitment because density dependence has been well established in the reproductive process for many taxa including plants (Thrall et al. 1989, Buckley et al. 2001, Pardini et al. 2009), insects (Constantino et al. 1995, Dennis et al. 1997), fish (Cushing 1973, DeAngelis et al. 1991), birds (Both et al. 2000, Frederiksen et al. 2001), and small mammals (Klinger 2007). For simplicity, we assumed that juvenile and adult survivorship

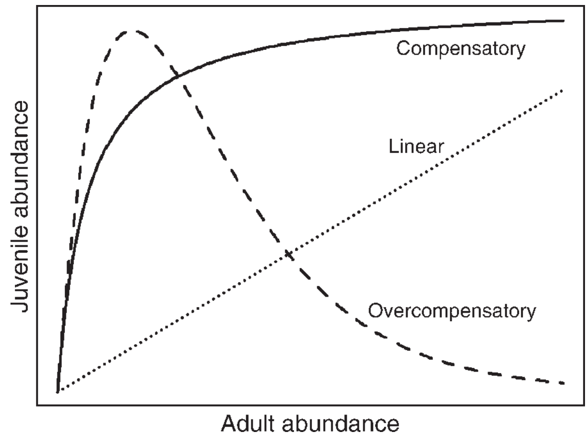

FIG. 1. Linear, compensatory, and overcompensatory recruitment functions.

parameters were constant. However, the model can still provide basic inferences on population-level responses to harvest regardless of that assumption (Zipkin et al. 2008).

Model analysis

A stable population (i.e., one that stays constant or stationary) that is subjected to harvest can either remain stable or become unstable. In cases where the population continues to be stable the equilibrium abundance can remain unchanged, decline or increase (i.e., overcompensation). When harvest destabilizes a population by causing periodic cycling or chaotic behavior, the average population size can either be smaller or larger than the equilibrium abundance in the absence of harvest. However, annual or periodic variations may be of greater interest in such cases. For the overcompensatory recruitment model, we determined analytically the conditions under which a population could become unstable or increase in abundance in response to harvest. We defined the carrying capacity of the population as the equilibrium abundance in the absence of harvest and solved each of the models for h_{j} and h_{a} to determine the harvest strategies (i.e., the proportion of juveniles [h_{j}] and the proportion of adults [h_{a}] harvested) that would hold the population at specified objectives (i.e., total population size or specific demographic structure). We examined the conditions that would result in an increase in equilibrium abundance for three types of harvest: a juvenile-only harvest ($h_{\mathrm{j}} > 0$ while $h_{\mathrm{a}} = 0$), an adult-only harvest ($h_{\mathrm{a}} > 0$ while $h_{\mathrm{j}} = 0$), and a harvest where both stages are targeted in equal proportion ($h_{\mathrm{j}} = h_{\mathrm{a}} > 0$) by examining the derivative of the equilibrium solution with respect to harvest to determine the response of the population to the onset of harvest (Zipkin et al. 2008) (see Appendix). These three harvest strategies were chosen because they represent endpoints on a continuum of harvest levels and, more importantly, can be applied in practice. Although a field study could be designed to

TABLE 1. Minimum values for the maximum per capita recruitment parameter, α, that can cause the following population responses in models with overcompensatory recruitment: (1) instability in the absence of harvest and (2) either overcompensation or instability. Values are presented for three different harvest strategies: juvenile-only harvest, adult-only harvest, and a harvest that targets both juvenile and adult life stages in equal proportions.

Response	$s_j = s_a = 0.2$	$s_j = 0.2$, $s_a = 0.8$	$s_j = 0.8$, $s_a = 0.2$	$s_j = s_a = 0.2$
Instability in the absence of harvest	38.0	403.4	9.5	100.9
Juvenile-only harvest				
Instability	NA	NA	NA	NA
Overcompensation in juvenile stage	10.9	2.7	2.7	0.7
Overcompensation in total population	14.0	7.4	7.4	8.9
Adult-only harvest				
Instability	NA	81	NA	21
Overcompensation in juvenile stage	10.9	2.7	2.7	0.7
Overcompensation in total population	11.3	5.3	3.0	4.0
Equal proportions harvest				
Instability	NA	118	NA	30
Overcompensation in juvenile stage	10.9	2.7	2.7	0.7
Overcompensation in total population	12.3	5.6	4.0	5.0

Note: Definitions of variables: s_j, annual juvenile survivorship; s_a, annual adult survivorship; NA, no values for the specified parameters were capable of causing instability (or overcompensation).

selectively target individuals of either one stage or another, it would typically be difficult to implement a removal of a specified proportion of each stage, particularly if the total population abundance was not known with precision. Similarly, a harvest strategy that targets both stages in equal proportion is analogous to removing individuals encountered, regardless of the stage, if it can be assumed that the contact process is proportional to population abundance.

We examined models with both compensatory and overcompensatory recruitment to compare the amount of effort required for population control. We used analytical results as well as additional simulation experiments to evaluate the potential for harvest as a control method under the full range of parameter values. We present the results from four stage-specific survivorship scenarios, which are representative of the spectrum of possible responses to harvest: (1) low juvenile and adult survivorship ($s_j = s_a = 0.2$), (2) low juvenile and high adult survivorship ($s_j = 0.2$, $s_a = 0.8$), (3) high juvenile and low adult survivorship ($s_j = 0.8$, $s_a = 0.2$), and (4) high juvenile and adult survivorship ($s_j = s_a = 0.8$). (See the Appendix for results under more parameter combinations including analytical solutions that determine the response of a population to harvest under any, and all, combination of parameter values.) For each of these scenarios, we considered only recruitment parameters that resulted in a stable population in the absence of harvest.

RESULTS

Instability (i.e., population cycling) as a result of harvest was relatively infrequent and only occurred when both maximum per capita recruitment was large and adult survivorship was high ($\alpha \geq 81$ when $s_j = 0.2$, $s_a = 0.8$ or when $\alpha \geq 21$ for $s_j = s_a = 0.8$) for populations with overcompensatory recruitment (Table 1). In cases where adult survivorship was high ($s_a = 0.8$), the adult-only harvest and the equal proportions harvest strategies, but not the juvenile-only harvest, could generate instability. When adult survivorship was low ($s_a = 0.2$), no harvest strategy could cause instability in a population that was stable in the absence of harvest (even though the model became unstable for comparatively lower values of α). The parameter β did not influence stability (see Appendix).

An increase in population-level abundance in response to harvest was possible under all harvest strategies for all combinations of survivorship parameter values with the overcompensatory recruitment model (Table 1). The determining factor as to whether or not the population increased in response to harvest was the value of the maximum per capita recruitment parameter, α. The parameter β again did not influence the dynamical response of the model with regards to overcompensation (see Appendix). Harvest strategies that targeted adults produced overcompensation for lower levels of recruitment (α) compared to strategies that focused on juveniles (Table 1). Overcompensation generally resulted from an increase in the abundance of juveniles; however, the adult-only harvest strategy was capable of causing increases in adult as well as juvenile abundance (Fig. 2). In cases where either juvenile or adult survivorship was high (80%), overcompensation in response to harvest was possible at low values of α for all harvest strategies that we explored (minimum values causing overcompensation ranged from 3 to 9). When both survivorship parameters were low ($s_j = s_a = 0.2$), overcompensation was observed with all harvest strategies for $\alpha \geq 14$. Even in the case of semelparous species (i.e., an organism that produces only once before death, corresponding to $s_a = 0$ in our model) with very low survivorship from birth to reproduction ($s_j = 0.01$), overcompensation occurred with harvest when maximum per capita fecundity (α) was greater than 100.5 individuals.

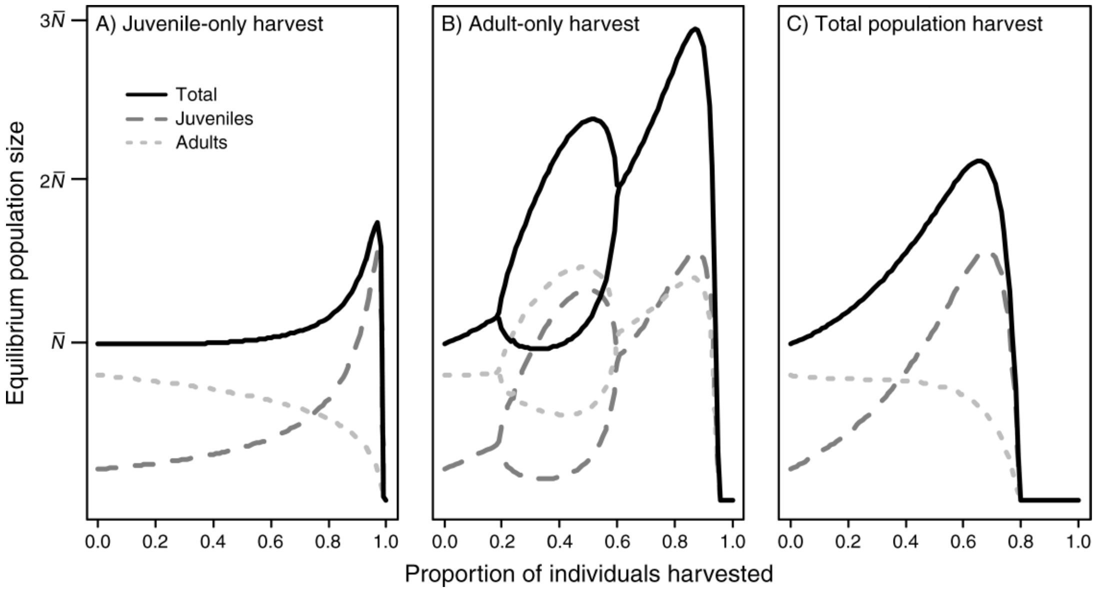

FIG. 2. Equilibrium abundances for a population with overcompensatory recruitment under three harvest strategies: (A) juvenile-only harvest, (B) adult-only harvest, and (C) both stages harvested in equal proportions. Each panel shows the equilibrium (and stage-specific) abundance for the population as harvest is varied from a proportion of 0.0 to 1.0 individuals. The *y*-axis marks the equilibrium population abundance in the absence of harvest, $\overline{N}$, and the levels where equilibrium abundance is doubled and tripled. In the parameter space in panel B where the equilibrium abundance at a specified harvest level varies the circles indicate the range of periodic cycling in the population. Demographic parameter values were $s_j = s_a = 0.8$ (juvenile and adult survivorship) and $\alpha = 25$ (maximum per capita recruitment). The exact value of $\overline{N}$ is dependent on the value of the parameter β.

While the degree of overcompensation varied widely and in some cases abundance declined quickly as additional harvest was implemented, Fig. 2 demonstrates that overcompensation can occur with even strong harvest pressures. For a population with high annual survivorship ($s_j = s_a = 0.8$) and reproductive potential ($\alpha = 25$), total population abundance did not decline until more than 70% of all individuals or nearly 100% of either juveniles or adults were removed from the population (Fig. 2). Additionally, the population experienced periodic cycling in abundance when adults only were harvested at annual levels between 20% and 60% (Fig. 2B). Table 2 summarizes the risk factors for populations with various combinations of fecundity and survivorship values and provides examples of such populations drawn from the invasive species literature.

In general, a population with overcompensatory recruitment required a greater harvest to achieve the same target abundance compared to a population with compensatory recruitment (Fig. 3) but this response was dependent upon the value of maximum per capita recruitment, α. As the value of α increased, the disparity between the two models increased for given levels of survivorship. The amount of additional harvest effort required to reduce population abundance was dependent on juvenile and adult survivorship. When annual survivorship was low for both stages ($s_j = s_a = 0.2$), similar harvests could achieve near equal reductions in abundance, especially when $\alpha \leq 10$. Regardless of the recruitment process, high juvenile and low adult survivorship ($s_j = 0.8$, $s_a = 0.2$) required a larger harvest, compared with the opposite scenario in which juvenile survivorship was low but adult survivorship was high ($s_j = 0.2$, $s_a = 0.8$). In the case of high survivorship of both stages ($s_j = s_a = 0.8$), the required harvest to reduce population abundance was largely dependent on the functional form of the recruitment process. For instance, a population with the same maximum per capita recruitment ($\alpha = 7$) required 60% harvest of both stages to reduce the population to 50% of the carrying capacity when the recruitment process was overcompensatory by comparison with a 22% harvest achieving the same target population abundance when recruitment was compensatory (Fig. 3). However, the minimum total harvest required to collapse a population was the same with both compensatory and overcompensatory recruitment (for equivalent parameter values) because as the population approached smaller and smaller sizes, per capita recruitment approached α (see Appendix).

Modifications to the model

Our model is parsimonious, yet overly simplified. To test the validity of our results, we modified the assumptions of the model. Here we present three additional forms of the model: (1) density dependence in juvenile survivorship only, (2) density dependence in adult survivorship only, and (3) increased length of the juvenile stage. While there are many potential model variations to explore (see Abrams 2009), analysis of these three forms (in conjunction with the original

TABLE 2. Summary of risks associated with harvest for populations with various recruitment and survivorship characteristics including possible examples of such populations drawn from the nuisance and invasive species literature.

Maximum annual recruitment per adult	Survivorship		Potential associated with harvest		Populations drawn from the nuisance and invasive species literature
	Juvenile	Adult	Instability	Overcompensation	
Small (<3)	all values	all values	none	none	Double-crested Cormorant (Bedard et al. 1995); northern pike (Myers et al. 1999); Yellow-legged Herring Gull (Brooks and Lebreton et al. 2001); Indian House Crow (Brook et al. 2003); feral goats (Campbell and Dolan 2005); rusty crayfish (Hein et al. 2006)
Medium (3–10)	low low/high high	low high low	none none none	none moderate high	alewife (Myers et al. 1999); invasive rodents (Howard et al. 2007); invasive bullfrogs (Kaefer et al. 2007)
High (10–20)	low low high	low high low/high	none none none	moderate high high	pea clams (Keller et al. 2007); smallmouth bass (Zipkin et al. 2008)
Very high (>20)	all values	all values	moderate–high	very high	rapeseed pollen beetles (Hokkanen 2000); scentless chamomile (Buckley et al. 2001); Asian clam, zebra mussels, river snails (Keller et al. 2007); garlic mustard (Pardini et al. 2009); Prussian carp (Leonardos et al. 2008)

Note: To thoroughly assess the potential for overcompensation and instability for the species presented in this table (and others), the basic model (Eq. 1) should be modified to incorporate the important demographic processes that are specific to the target population.

version) assists in determining more precisely the demographic characteristics that have likely caused instability and overcompensation as a result of harvest in empirically observed populations. For each scenario we briefly discuss the range of population-level responses to harvest.

In our original model, density dependence was assumed to occur in only reproduction yet survivorship rates can also be influenced by population density. We modified the model (Eq. 1) to include density dependence in each of the survivorship terms separately. In the first modification, juvenile survivorship at time t ($s_{j,t}$) was assumed to be an overcompensatory process whose value was reliant upon the size of the population:

$$s_{j,t+1} = s_j \exp\Big(-\beta[J_t(1-h_j) + A_t(1-h_a)]\Big). \quad (4)$$

Here we assumed that the recruitment term γ (Eq. 1) was constant ($\gamma = \alpha$, as is in the linear recruitment model). We found that harvest was capable of causing instability in a stable population with adult-only and equal proportion harvest strategies, but only when both per capita recruitment (a constant value in this case) and adult survivorship were very high. However, overcompensation was only possible with a juvenile-only harvest strategy (Table 3). In another variation, we similarly modified adult survivorship in the model. When adult survivorship, $s_{a,t}$, was the only density-dependent vital rate, harvest consistently led to a decline in abundance for all values of parameter combinations in the model that we explored (Table 3).

Since maturation rates vary among juveniles in many species, we examined the consequences of harvest in a population where juveniles could remain as such for more than one time step:

$$J_{t+1} = A_t(1-h_a)\gamma + J_t(1-h_j)s_j(1-m)$$

$$A_{t+1} = J_t(1-h_j)s_j m + A_t(1-h_a)s_a. \quad (5)$$

In this variation, m is the annual maturation rate for juveniles, and γ is again defined as in our original model using the overcompensatory recruitment function from Eq. 3. Overcompensation and instability were possible under all harvest strategies, even when both stage-specific survivorship and maturation rates were low, again dependent on the value of α. When both juvenile and adult survivorship were fairly low ($s_j = s_a = 0.2$) and we assumed that the annual maturation rate was 50%, overcompensation still occurred in all harvest strategies for $\alpha \geq 30$. A delay to the onset of reproduction for a subset of juveniles (i.e., $m < 1$) dampened the maximum magnitude of overcompensation and required less total harvest to collapse the population compared to the case when all surviving juveniles matured. However for intermediate harvest levels, overcompensation (when it occurred) could be larger in situations where $m < 1$ (than for $m = 1$; Fig. 4).

DISCUSSION

Our analytical and simulation results demonstrate that while harvest can be an effective method for reducing the abundance of nuisance and invasive species, overcompensation and cycling in abundance are also possible

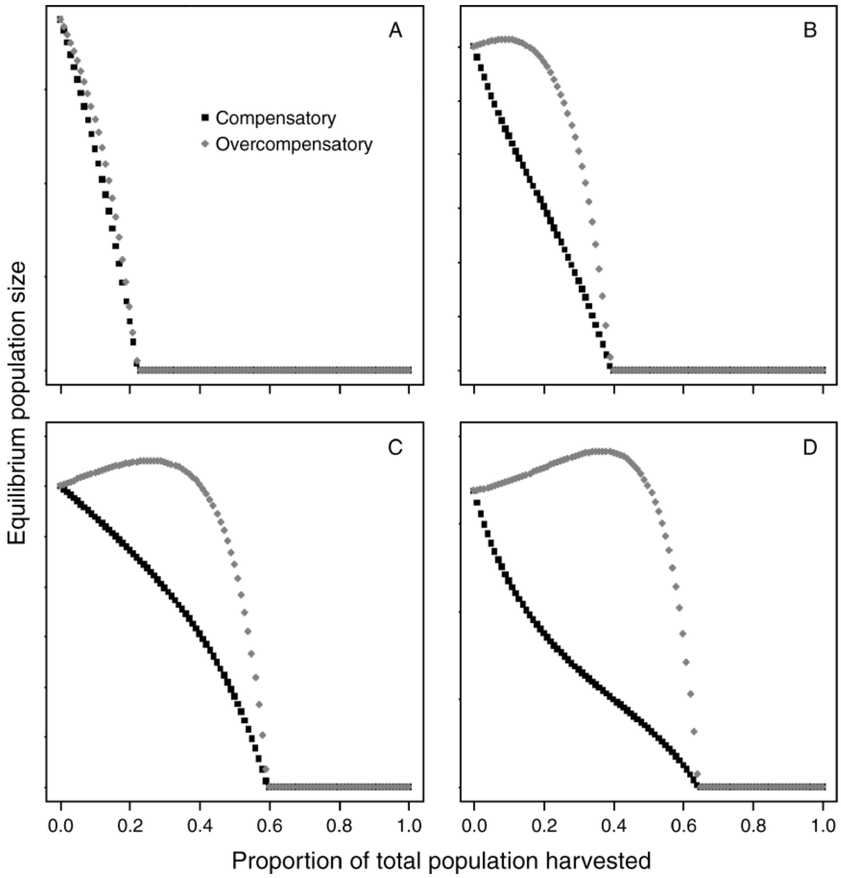

FIG. 3. Comparison of equilibrium abundances for populations with compensatory vs. overcompensatory recruitment under a harvest strategy that targets both stages in equal proportions. Maximum per capita recruitment was fixed at $\alpha = 7$, and survivorship values were (A) $s_j = s_a = 0.2$ (low juvenile and adult survivorship), (B) $s_j = 0.2$, $s_a = 0.8$ (low juvenile and high adult survivorship), (C) $s_j = 0.8$, $s_a = 0.2$ (high juvenile and low adult survivorship), and (D) $s_j = s_a = 0.8$ (high juvenile and adult survivorship).

(and in some cases likely) population-level responses. The key parameter determining the trajectory of the response to harvest was the fecundity term, α. Our results reveal that the parameter β (which determines the equilibrium population size for given values of α) does not affect the dynamics of the model, suggesting that absolute abundance should not influence a population's response to harvest. Populations with similar recruitment relationships should behave similarly regardless of the carrying capacity.

We modeled a hypothetical population with density-dependence in only the fecundity term, but the response

TABLE 3. Summary of the effects of harvest on populations with (1) density dependence in juvenile survivorship only and (2) density dependence in adult survivorship only.

Model variations	$s_j = s_a = 0.2$	$s_j = 0.2$, $s_a = 0.8$	$s_j = 0.8$, $s_a = 0.2$	$s_j = s_a = 0.2$
Density dependence in juvenile survivorship only:				
Instability	NA	adult-only and total harvest ($\alpha \geq 83$)	NA	adult-only and total harvest ($\alpha \geq 23$)
Overcompensation in total population	juvenile-only harvest ($\alpha \geq 14$)	juvenile-only harvest ($\alpha \geq 5$)	juvenile-only harvest ($\alpha \geq 4$)	juvenile-only harvest ($\alpha \geq 2$)
Density dependence in adult survivorship only:				
Instability	NA	NA	NA	NA
Overcompensation in total population	NA	NA	NA	NA

Notes: In both of these models, per capita recruitment (specified as α) is a fixed value. For the model in which density dependence occurs in the juvenile stage, the values presented for s_j are the maximum juvenile survivorship; actual annual survivorship varies according to Eq. 4. This is similarly true for adult survivorship s_a in the model with density dependence in the adult stage. "NA" indicates that no values for the specified parameters were capable of causing instability (or overcompensation).

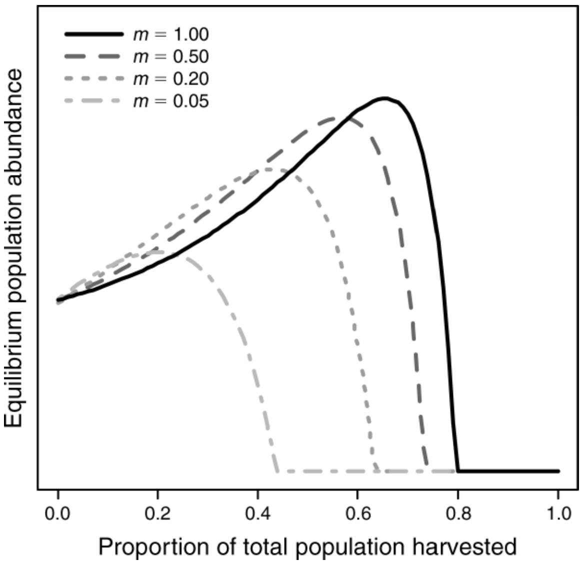

FIG. 4. Comparison of equilibrium abundances for populations with various juvenile maturation rates, $m \leq 1$, undergoing a total population harvest. Demographic parameter values were $s_j = s_a = 0.8$ (juvenile and adult survivorship) and $\alpha = 25$ (maximum per capita recruitment).

to harvest would have been qualitatively equivalent if survivorship (or any other stage-transition parameter, such as maturation) had also been density dependent (Buckley et al. 2001, Zipkin et al. 2008, Pardini et al. 2009). This is further supported by the observation that, in our study, fecundity consistently determined the response of the population to harvest, even at high values of stage-specific survivorship. We confirmed our results by modifying our base model to assess how harvest would affect a population with density-dependence in only survivorship. The population-level responses in the modified models (Table 3) were inconsistent with observations of overcompensation in response to harvest, suggesting that empirical examples of overcompensation are not well characterized by models with density dependence in only survivorship. Our original model, in which density dependence occurred during recruitment, is supported by empirical studies where harvest of either adults-only or juveniles and adults led to overcompensation and/or instability (Nicholson 1957, Costantino et al. 1995, 1997, Buckley et al. 2001, Moe et al. 2002, Cameron and Benton 2004, Zipkin et al. 2008).

Previous theoretical work has demonstrated how additive mortality can lead to an increase in total population (or stage-specific) abundance and/or biomass using both continuous (De Roos et al. 2007, Abrams 2009) and discrete (Matsuoka and Seno 2008, Seno 2008) single species models. We focused on the dynamics of a single targeted population, but the potential for overcompensation and instability as a result of increased mortality has also been demonstrated theoretically with interacting species (De Roos et al. 2008). For example, predators (with specified saturating functional responses to prey consumption) can increase in response to higher levels of mortality (Abrams and Matsuda 2005, Abrams and Quince 2005). Instability has similarly been demonstrated in consumer resource models (Schreiber and Rudolf 2008) as a result of increased levels of mortality. These results suggest that it may be important to consider interactions among species when devising control harvest strategies for nuisance species. While several studies have focused on theoretical models, few have attempted to relate theoretical results to empirical observations, especially with regards to overcompensation. Our study attempts to link ecological theory to empirical examples and highlight the specific vital rate (maximum per capita fecundity) and density-dependent process (recruitment) that is likely responsible for unintended population responses to targeted control efforts.

It is difficult to assess the extent to which overcompensation and instability may occur during efforts to control nuisance and invasive species. Since we modeled the population in discrete time intervals, our results may be most relevant to species with distinct breeding periods. Some empirical examples of overcompensation (i.e., Buckley et al. 2001, Moe et al. 2002) were observed in experimental populations where synchronous reproduction can exacerbate scramble competition and heighten overcompensation (but see Zipkin et al. 2008 for an exception). More research is needed to empirically evaluate population-level responses of invasive species to control harvests. Studies that harvest a target species at various population densities and then monitor abundance are needed to determine the potential frequency of overcompensation and instability in response to control efforts. Nevertheless, our results suggest the following cautionary guidelines when considering harvest as a method of population control. First, it is essential to determine if population density affects the recruitment processes. Second, if density-dependent recruitment is evident, it is important to identify the maximum per capita fecundity for the target organism to assess whether harvest is likely to cause overcompensation or instability in the population (Table 2). In situations where maximum annual fecundity is relatively small (i.e., three or less surviving offspring per adult annually), all levels of harvest are likely to lead to a stable population with reduced abundance, regardless of the recruitment relationship (and even if the population does not strictly adhere to all of our model assumptions such as when a population has more stages or longer time to maturity—because these factors increase the time to an individual's first reproductive event). But when maximum per capita fecundity is large, harvest can cause the equilibrium population abundance to increase substantially and become more variable, even at high levels of harvest effort (Fig. 2). In cases where fecundity is large, it is crucial to more accurately determine the functional form of the relationship between population density and recruitment. Third, it is necessary to estimate annual stage-specific survivorship (and its potential variability) in order to assess the amount of effort required to achieve the targeted abundance. When adult survivorship is high, harvest strategies that target adults will be more effective at reducing population abundance compared to situations in which adult survivorship is low; in such cases, strategies that target both juveniles and adults will be more effective.

Our original model assumed that juveniles mature and reproduce after age 1, but if time to first reproduction was increased, our modified model (Eq. 5) suggests that harvest might successfully be implemented in populations with even greater potential fecundity. This result allows us to rule out the possibility for control measures to "backfire" in many taxa, for example, most bird and mammal populations (Table 2). Indeed, overcompensation and population cycling as a result of harvest have only been empirically documented in populations that have large reproductive potential at small abundances, as in certain plant (Thrall et al. 1989, Buckley et al. 2001, Pardini et al. 2009), invertebrate (Nicholson 1957, Costantino et al. 1995, Costantino et al. 1997, Moe et al. 2002, Cameron and Benton 2004), and fish (Zipkin et al. 2008) species. By contrast, harvest control efforts have been successfully and broadly applied to nuisance mammals (Campbell and Donlan 2005, Howald et al. 2007), though efforts to control nuisance bird populations remain poorly documented and have been considered unsuccessful (Bedard et al. 1995, Brook et al. 2003).

Fecundity has been recognized as an important characteristic of successful invasive populations (see Kolar and Lodge 2001) in plants (Burns 2008), freshwater molluscs (Keller et al. 2007), and fish (Vila-Gispert et al. 2005). We believe that this same trait that can enhance the ability of a species to become a successful invader may also be responsible for the challenges associated with eradicating or maintaining these populations at reduced abundances.

The amount of effort required to maintain a population at a specified abundance is highly dependent upon density-dependent processes, the desired population size and the harvest strategy (i.e., which stages are targeted). If maximum fecundity is low, harvest strategies will be similar across different forms of recruitment, in which case it may be less important to identify the exact recruitment relationship. When fecundity is large, it will be necessary to more clearly understand the recruit relationship to determine the required amount of effort to control a population. Additionally, there may be a trade-off associated with some harvest strategies in populations with overcompensatory recruitment; a harvest strategy that can reduce the abundance of adults could also lead to an increase in juveniles (Fig. 2A, C). Depending on the harvest objectives, this may or may not be desirable. For instance, the intensive harvest of an invasive population of smallmouth bass resulted in decreased abundance of adults (which are largely responsible for negative impacts on the fish community) and a simultaneous increase in juveniles (Zipkin et al. 2008). Because juveniles can provide forage for other native fish predators, this result may not be entirely negative (Weidel et al. 2007). However, this tradeoff may not be acceptable for other target organisms where the distinction between the negative impacts of juveniles and adults is negligible.

Under some circumstances, it may be possible to implement a harvest without complete knowledge of the recruitment process if the control objective is eradication. This is because the minimum total harvest required to collapse a population is identical (or less for depensatory recruitment) for all populations, with known parameter values, if density dependence only occurs in recruitment (Fig. 3). (Analysis of a model with constant recruitment produces the same results because population dynamics are assessed through linear stability analysis, which assumes a linear approximation near the origin; see Appendix.) However, we caution against this approach because inevitable uncertainty around demographic parameter estimates or total population abundance could lead to widely inaccurate estimates of the minimum harvest necessary to collapse a population. In addition, density-dependent processes may occur during other life stages which would increase the harvest level required to collapse a target population of invasive or nuisance species.

Although deterministic population dynamics alone can lead to unintended results in a control harvest, stochastic elements (or random variation) can also affect harvest. Vital rates are likely to vary depending on environmental variations and abiotic processes, which can alter the optimal harvest strategy (Lande et al. 1995, Engen et al. 1996, Hunter and Runge 2004). We focused our analyses on the equilibrium response of a population to harvest but an investigation of the transient dynamics may be necessary, especially if stochastic factors have a substantial impact on reproduction or mortality. Our results assume a closed population, but the presence of substantial immigration into a target population will require a larger control effort and complete eradication may not be possible (Brook et al. 2003, Howald et al. 2007). Similarly, we assumed that harvest occurred prior to breeding (to minimize the number of individuals for removal); however, harvest efforts can occur during any time of the year and the timing of removal can be important to the response of a population to harvest (Boyce et al. 1999, Jonzen and Lundberg 1999).

Models can be useful in assessing the feasibility of population control through harvest, but it will always be necessary to incorporate the specific processes that determine the trajectory of a target population and have substantial empirical data available to parameterize such models. It is important to understand density-dependent processes and demographic structure as well as the specific vital rates of a population, to the extent possible, prior to implementing control efforts. In some situations, harvest may not be effective until removal rates are very high. Pardini et al. (2009) estimated that control of garlic mustard would not be successful until greater than 85% of adults or 95% of rosettes were removed annually. The message here is clear: control efforts of high-risk species (as defined in Table 2) require careful consideration and should only be undertaken if there is strong commitment and ability to remove nearly every individual. Our results demonstrate the complex dynamics that can arise in response to harvest and how inherent aspects of population characteristics can influence the success or failure of efforts to remove nuisance and invasive species.

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Literature Cited

Abrams, P. A. 2002. Will small population sizes warn us of impending extinctions? American Naturalist 160:293–305.

Abrams, P. A. 2009. When does greater mortality increase population size? The long history and diverse mechanisms underlying the hydra effect. Ecology Letters 12:462–474.

Abrams, P. A., and H. Matsuda. 2005. The effect of adaptive change in the prey on the dynamics of an exploited predator population. Canadian Journal of Fisheries and Aquatic Science 62:758–766.

Abrams, P. A., and C. Quince. 2005. The impact of mortality on predator population size and stability in systems with stage-structured prey. Theoretical Population Biology 68: 253–266.

Bedard, J., A. Nadeau, and M. Lepage. 1995. Double-crested Cormorant culling in the St. Lawrence River Estuary. Colonial Waterbirds 18:78–85.

Benton, T. G., T. C. Cameron, and A. Grant. 2004. Population responses to perturbations: predictions and responses from laboratory mite populations. Journal of Animal Ecology 73: 983–995.

Benton, T. G., S. J. Plaistow, and T. N. Coulson. 2006. Complex population dynamics and complex causation: devils, details and demography. Proceedings of the Royal Society B 273:1173–1181.

Beverton, R. J. H., and S. J. Holt. 1957. On the dynamics of exploited fish populations. Chapman and Hall, London, UK.

Both, C., J. M. Tinbergen, and M. E. Visser. 2000. Adaptive density dependence of avian clutch size. Ecology 8:3391–3403.

Boyce, M. S., A. R. E. Sinclair, and G. C. White. 1999. Seasonal compensation of predation and harvesting. Oikos 87:419–426.

Brännström, A., and D. J. T. Sumpter. 2005. The role of competition and clustering in population dynamics. Proceedings of the Royal Society B 272:2065–2072.

Brook, B. W., N. S. Sodhi, M. C. K. Soh, and H. C. Lim. 2003. Abundance and projected control of invasive house crows in Singapore. Journal of Wildlife Management 67:808–817.

Brooks, E. N., and J. D. Lebreton. 2001. Optimizing removals to control a metapopulation: application to the Yellow-legged Herring Gull (*Larus cachinnans*). Ecological Modeling 136:269–284.

Buckley, Y. M., H. L. Hinz, D. Matthies, and M. Rees. 2001. Interactions between density-dependent processes population dynamics and control of an invasive plant species, *Tripleurospermum perforatum* (scentless chamomile). Ecology Letters 4:551–558.

Burns, J. H. 2008. Demographic performance predicts invasiveness of species in the *Commelinaceae* under high-nutrient conditions. Ecological Applications 18:335–346.

Cameron, T. C., and T. G. Benton. 2004. Stage-structured harvesting and its effects: an empirical investigation using soil mites. Journal of Animal Ecology 73:996–1006.

Campbell, K., and C. J. Donlan. 2005. Feral goat eradications on islands. Conservation Biology 19:1362–1374.

Costantino, R. F., J. M. Cushing, B. Dennis, and R. A. Desharnais. 1995. Experimentally-induced transitions in the dynamic behavior of insect populations. Nature 375:227–230.

Costantino, R. F., R. A. Desharnais, J. M. Cushing, and B. Dennis. 1997. Chaotic dynamics in an insect population. Science 275:389–391.

Cushing, D. H. 1973. Dependence of recruitment on parent stock. Journal of Fisheries Research Board of Canada 30: 1965–1976.

Cushing, J. M., R. F. Costantino, B. Dennis, R. A. Desharnais, and S. M. Henson. 1998. Nonlinear population dynamics: models, experiments and data. Journal of Theoretical Biology 194:1–9.

DeAngelis, D. L., L. Godbout, and B. J. Shuter. 1991. An individual-based approach to predicting density-dependent dynamics in smallmouth bass populations. Ecological Modeling 57:91–115.

Dennis, B. 1989. Allee effects: population growth, critical density, and the chance of extinction. Natural Resources Modeling 3:481–538.

Dennis, B., R. A. Desharnais, J. M. Cushing, and R. F. Costantino. 1997. Transitions in population dynamics: equilibria to periodic cycles to aperiodic cycles. Journal of Animal Ecology 66:704–729.

De Roos, A. M., T. Schellekens, K. T. Van Kooten, and L. Persson. 2008. Stage-specific predator species help each other to persist while competing for a single prey. Proceedings of the National Academy of Sciences (USA) 105:13930–13935.

De Roos, A. M., T. Schellekens, T. Van Kooten, K. Van De Wolfshaar, D. Claeseen, and L. Persson. 2007. Food-dependent growth leads to overcompensation in stage-specific biomass when mortality increases: the influence of maturation versus reproduction regulation. American Naturalist 170:E59–E76.

Engen, S., R. Lande, and B. E. Sæther. 1996. Harvesting strategies for fluctuating populations based on uncertain population estimates. Journal of Theoretical Population Biology 186:201–212.

Faccoli, M., and F. Stergulc. 2008. Damage reduction and performance of mass trapping devices for forest protection against the spruce bark beetle, *Ips typographus* (Coleoptera Curculionidae Scolytinae). Annals of Forest Science 65:309.

Frederiksen, M., J. D. Lebreton, and T. Bregnballe. 2001. The interplay between culling and density-dependence in the great cormorant: a modelling approach. Journal of Applied Ecology 38:617–627.

Hauser, C. E., E. G. Cooch, and J. D. Lebreton. 2006. Control of structured populations by harvest. Ecological Modeling 196:462–470.

Hein, C. L., B. M. Roth, A. R. Ives, and M. J. Vander Zanden. 2006. Fish predation and trapping for rusty crayfish (*Orconectes rusticus*) control: a whole-lake experiment. Canadian Journal of Fisheries and Aquatic Science 63:383–393.

Hokkanen, H. M. T. 2000. The making of a pest: recruitment of *Meligethes aeneus* onto oilseed Brassicas. Entomology Experiments Applied 95:141–149.

Howald, G., D. J. Donlan, J. P. Galvan, J. C. Russell, J. Parkes, A. Samaniego, Y. Wang, D. Veitch, P. Genovesi, M. Pascal, A. Saunders, and B. Tershy. 2007. Invasive rodent eradication on islands. Conservation Biology 21:1258–1268.

Hunter, C. M., and M. C. Runge. 2004. The importance of environmental variability and management control error to optimal harvest policies. Journal of Wildlife Management 68: 585–594.

Jonzen, N., and P. Lundberg. 1999. Temporally structured density-dependence and population management. Annales Zoologici Fennici 36:39–44.

Kaefer, I. L., R. A. Boelter, and S. Z. Cechin. 2007. Reproductive biology of the invasive bullfrog *Lithobates catesbeianus* in southern Brazil. Annales Zoologici Fennici 44:435–444.

Keller, R. P., J. M. Drake, and D. M. Lodge. 2007. Fecundity as a basis for risk assessment of nonindigenous freshwater molluscs. Conservation Biology 21:191–200.

Klinger, R. 2007. Catastrophes, disturbances and density-dependence: population dynamics of the spiny pocket mouse (*Heteromys desmarestianus*) in a neotropical lowland forest. Journal of Tropical Ecology 23:507–518.

Kolar, C. S., and D. M. Lodge. 2001. Progress in invasion biology: predicting invaders. Trends in Ecology and Evolution 16:199–204.

Lande, R., S. Engen, and B. E. Sæther. 1995. Optimal harvesting of fluctuating populations with a risk of extinction. American Naturalist 145:728–745.

Leonardos, I. D., A. C. Tsikliras, V. Eleftheriou1, Y. Cladas, I. Kagaloul, R. Chortatou, and O. Papigioti. 2008. Life history characteristics of an invasive cyprinid fish (*Carassius gibelio*) in Chimaditis Lake (northern Greece). Journal of Applied Ichthyology 24:213–217.

Matsuoka, T., and H. Seno. 2008. Ecological balance in the native population dynamics may cause the paradox of pest control with harvesting. Journal of Theoretical Biology 252: 87–97.

Moe, S. J., N. C. Stenseth, and R. H. Smith. 2002. Density-dependent compensation in blowfly populations give indirectly positive effects of a toxicant. Ecology 83:1597–1603.

Myers, R. A., K. G. Bowen, and N. J. Barrowman. 1999. Maximum reproductive rate of fish at low population sizes. Canadian Journal of Fisheries and Aquatic Science 56:2404–2419.

Nicholson, A. J. 1957. The self-adjustment of populations to change. Cold Spring Harbor Symposium 22:153–173.

Pardini, E. A., J. M. Drake, J. M. Chase, and T. M. Knight. 2009. Complex population dynamics and control of the invasive biennial *Alliaria petiolata* (garlic mustard). Ecological Applications 19:387–397.

Pascual, M. A., P. Kareiva, and R. Hilborn. 1997. The influence of model structure on conclusions about the viability and harvesting of Serengeti wildebeest. Conservation Biology 11: 966–976.

Ricker, W. E. 1954. Stock and recruitment. Journal of Fish Research Board of Canada 11:559–623.

Runge, M. C., and F. A. Johnson. 2002. The importance of functional form in optimal control solutions of problems in population dynamics. Ecology 83:1357–1371.

Schreiber, S., and V. H. W. Rudolf. 2008. Crossing habitat boundaries: coupling dynamics of ecosystems through complex life cycles. Ecology Letters 11:576–587.

Seno, H. 2008. A paradox in discrete single species population dynamics with harvesting/thinning. Mathematical Biosciences 214:63–69.

Thrall, P. H., S. W. Pacala, and J. A. Silander. 1989. Oscillatory dynamics in populations of an annual weed species *Abutilon theophrasti*. Journal of Ecology 77:1135–1149.

Vila-Gispert, A., C. Alcaraz, and E. Garcia-Berthou. 2005. Life-history traits of invasive fish in small Mediterranean streams. Biological Invasions 7:107–116.

Weidel, B. C., D. C. Josephson, and C. E. Kraft. 2007. Littoral fish community response to smallmouth bass removal from an Adirondack lake. Transactions of American Fisheries Society 136:778–789.

Wikan, A. 2004. Dynamical consequences of harvest in discrete age-structured population models. Journal of Mathematical Biology 49:35–55.

Zipkin, E. F., P. J. Sullivan, E. G. Cooch, C. E. Kraft, B. J. Shuter, and B. C. Weidel. 2008. Overcompensatory response of a smallmouth bass population to harvest: release from competition? Canadian Journal of Fisheries and Aquatic Science 65:2279–2292.

APPENDIX

Analysis of population models with compensatory and overcompensatory recruitment (*Ecological Archives* A019-063-A1).

Ecological Archives **A019-063-A1**

Elise F. Zipkin, Clifford E. Kraft, Evan G. Cooch, and Patrick J. Sullivan. 2009.

When can efforts to control nuisance and invasive species backfire?

***Ecological Applications* 19:1585–1595.**

Appendix A. Analysis of population models with compensatory and overcompensatory recruitment.

For the models containing both compensatory and overcompensatory recruitment, the maximum per capita rate of increase for a population (i.e., the per capita rate of growth at low population density) was:

$$R_0 = \frac{\alpha s_j (1-h_j)(1-h_a)}{1-s_a(1-h_a)} \tag{A.1}$$

where s_j (annual juvenile survivorship), s_a (annual adult survivorship) and α (maximum per capita recruitment) are the vital rates of the target population, and h_j and h_a are the annual harvests (proportions removed) of juveniles and adults, respectively. If $R_0 < 1$ then populations declined to extinction, regardless of the functional form of recruitment. Note that the maximum rate of increase (R_0) did not rely on the parameter β, the magnitude of density dependence in the recruitment term. Equation A.1 demonstrates that if the combined harvest of juveniles and adults reduces the maximum rate of juveniles that mature to adults to a level below the total mortality of adults (natural and harvest), then the population collapses.

The compensatory recruitment model

Instability and overcompensation were not possible with the compensatory recruitment model: harvest always produced a decline (or no change) in the equilibrium population abundance – as determined through linear stability analysis. We used the equilibrium solutions and solved for h_j and h_a to determine the harvest strategies that would hold the population at a specified constant abundance:

$$\begin{aligned} h_j &= 1 - \frac{A(\alpha - J\beta) - Js_a}{Js_j(\alpha - J\beta)} \\ h_a &= 1 - \frac{J}{A(\alpha - J\beta)} \end{aligned} . \tag{A.2}$$

The parameters J and A refer to the desired long-term abundances of juveniles and adults, respectively. Any given values of h_j and h_a between 0 and 1 (0–100% harvest) resulted in a unique equilibrium abundance for both juveniles and adults.

When survivorship of juveniles was low ($s_j = 0.2$), changes in the maximum per capita recruitment parameter α had a large impact on the harvest strategy that was required to hold a population at a reduced abundance. As α increased, larger proportions of the population needed to be harvested to maintain the same percent reduction in equilibrium abundance (Fig. A1a,c). The relative value of juveniles and adults (with respect to proportional contributions to future growth of the population) was near equal when survivorship for both stages was low, which was evident by the observation that harvesting similar proportions of either juveniles or adults could achieve the same total population size. In the scenario where juvenile survivorship was high but adult survivorship was low ($s_j = 0.8$, $s_a = 0.2$), the relative value of juveniles and adults was again near equal when the targeted population size was 50% or less of the carrying capacity – the equilibrium population abundance in the absence of harvest. However, the relative value of juveniles was larger than adults when the targeted population size was closer to the carrying capacity, in that it was necessary to harvest more adults than juveniles to achieve the same total population abundance (Figs. A1c and A2c). When survivorship of adults was high ($s_a = 0.8$), the relative value of adults was greater than the relative value of juveniles (Fig. A1b,d and A2b,d).

In cases where survivorship of both stages was high ($s_j = s_a = 0.8$), changes in the maximum per capita recruitment parameter α did not affect the harvest strategy when the targeted population abundance is $\geq 50\%$ of the carrying capacity (Fig. A1d). As the desired population size decreased below 50% of the carrying capacity, increased values of α required greater adult harvests for a given juvenile harvest to achieve the same total population abundance. For example, an approximate harvest of 90% of juveniles held a population at 25% of the carrying capacity when either $\alpha = 5$ or $\alpha = 25$. However, the same percent reduction required an adult harvest of approximately 90% when $\alpha = 25$ compared to 65% adult harvest when $\alpha = 5$ (not shown).

The overcompensatory recruitment model

Provided that $R_0 > 1$, the equilibrium population was stable if:

$$\ln\left(R_0\right) < \frac{2 - s_a(1-h_a)}{1 - s_a(1-h_a)} \tag{A.3}$$

as determined through linear stability analysis. Otherwise, the population cycled in abundance around the fixed point (and could experience chaotic behavior when α was raised to very high values; other parameters are 0–1 bounded). Note that the condition for stability was independent of the parameter β. Equations A.3 demonstrates the potential for harvest to cause instability in a population that is stable in the absence of harvest (and stabilize a population that was unstable).

We evaluated the sign of the derivative of the equilibrium population abundance with respect to harvest when harvest equals zero to determine the analytical condition under which an overcompensation in abundance could occur with harvest. A positive derivative indicated that implementation of harvest would result in an increase in equilibrium abundance; a negative derivative indicated that the population would decline with the onset of harvest (Zipkin et al. 2008). We further examined the response of the population to increased levels of harvest through simulations to ensure that our analytical results accurately characterized the response of the population to all levels of harvest. An increase in overall population abundance was possible with the overcompensatory recruitment model with all three harvest strategies that we examined: juvenile-only harvest, adult-only harvest, and a harvest where both stages were targeted in equal proportion. When the stages were harvested in equal proportions, overcompensation in the total population occurred when:

$$\ln\left(R_0\big|_{h_j=h_a=0} \right) > 1 + \frac{s_j}{(1-s_a)(1+s_j)+(1-s_a)^2} \tag{A.4}$$

where $R_0\big|_{h_j=h_a=0}$ is the maximum per capita rate of increase for a population in the absence of harvest (i.e., $h_j = h_a = 0$). Overcompensation in the total population occurred with an adult-only harvest when:

$$\ln\left(R_0\big|_{h_j=h_a=0} \right) > \frac{1+s_j-s_a}{\left(1-s_a\right)\left(1+s_j\right)}. \tag{A.5}$$

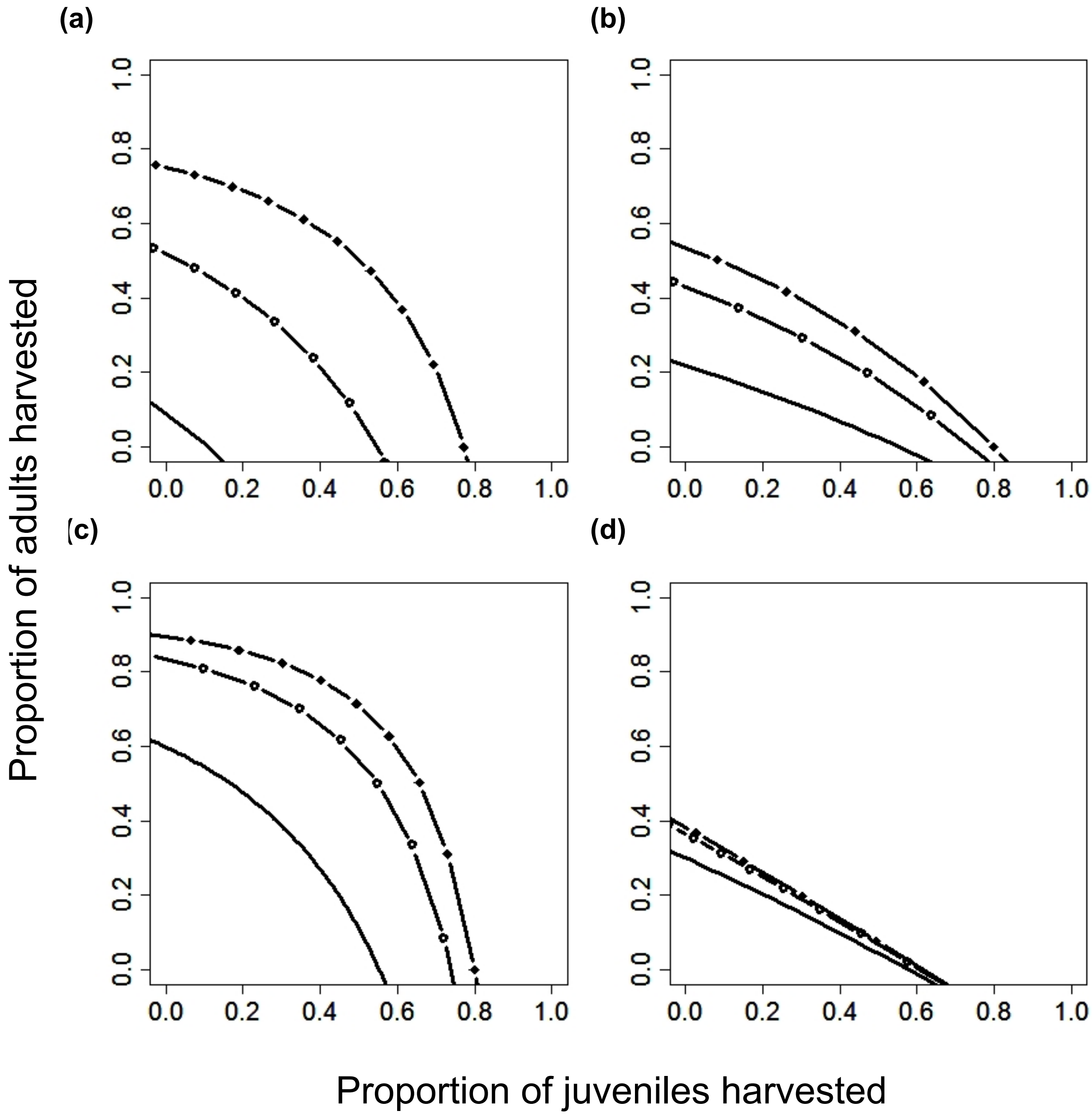
Note that overcompensation was also independent of the parameter β and that the condition for overcompensation was more stringent for a harvest where stages were targeted equally compared to an adult-only harvest strategy (i.e., for a given set of demographic parameter values, an adult-only harvest always lead to overcompensation when a harvest of equal proportions lead to overcompensation). It was necessary to rely on simulations to determine the conditions for overcompensation with a juvenile-only harvest because when both juvenile and adult survivorship were high (>80%) the overall population size initially decreased with a small juvenile harvest but could increase as h_j increased for $\alpha \geq 9$.

We solved the model for h_j and h_a to determine the harvest strategies that would hold the population at specified abundances. The harvest strategies were dependent on one another so that:

$$h_j = 1 - \frac{\alpha A - e^{A\beta(1-h_a)} J s_a}{\alpha J s_j} \qquad \text{or alternatively} \qquad h_a = 1 - \frac{1}{A\beta} \ln\left(\frac{\alpha (A - J s_j + J s_j h_j)}{J s_a} \right) \text{(A.6)}$$

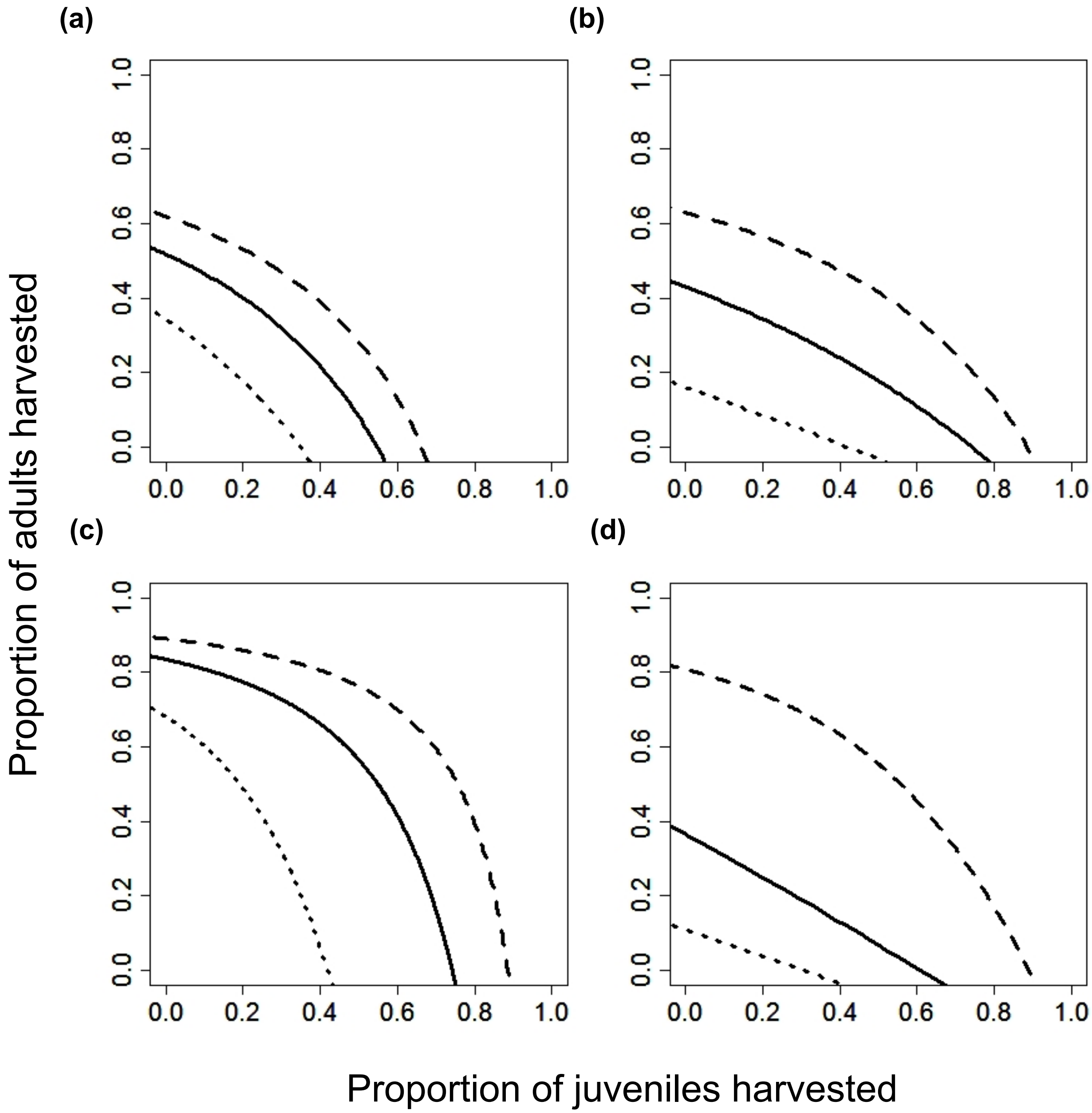
where J and A are again the desired long-term abundances of juveniles and adults. The harvest vectors in Eq. A.6 demonstrate that it is possible for more than one harvest strategy (i.e., proportion of juveniles and proportion of adults harvested) to produce the same population size and structure (unlike with the compensatory recruitment model, where a given harvest strategy produced a unique population structure).

FIG. A1. Harvest vectors to reduce a structured population with compensatory recruitment to 50% of the equilibrium abundance where $\alpha_1 = 5$ (solid line) $\alpha_1 = 15$ (open circles) and $\alpha_1 = 25$ (closed squares) for a population with (a) $s_j = s_a = 0.2$ (low juvenile and adult survivorship), (b) $s_j = 0.2$, $s_a = 0.8$, (low juvenile and high adult survivorship), (c) $s_j = 0.8$, $s_a = 0.2$ (high juvenile and low adult survivorship), and (d) $s_j = s_a = 0.8$ (high juvenile and adult survivorship). Each point on a harvest vector represents a proportion of juveniles and a proportion of adults to be harvested that will hold the population at 50% of the carry capacity (equilibrium abundance in the absence of harvest). The structure of the population (the total number of juveniles vs. adults) varies with each point on the vector.



(a)
(b)
(c)
(d)
Proportion of adults harvested
Proportion of juveniles harvested
0.0
0.2
0.4
0.6
0.8
1.0

FIG. A2. Harvest vectors to reduce a population with juveniles and adults and compensatory recruitment (where $\alpha = 15$) to 75% (short dash), 50% (solid line), and 25% (long dash) of the carry capacity (equilibrium abundance in the absence of harvest) for a population with (a) $s_j = s_a = 0.2$ (low juvenile and adult survivorship), (b) $s_j = 0.2$, $s_a = 0.8$, (low juvenile and high adult survivorship), (c) $s_j = 0.8$, $s_a = 0.2$ (high juvenile and low adult survivorship), and (d) $s_j = s_a = 0.8$ (high juvenile and adult survivorship). Each point on a harvest vector represents a proportion of juveniles and a proportion of adults to be harvested that will hold the population at the specified targeted abundance.



LITERATURE CITED

Zipkin, E. F., P. J. Sullivan, E. G. Cooch, C. E. Kraft, B. J. Shuter, and B. C. Weidel. 2008. Overcompensatory response of a smallmouth bass population to harvest: release from competition? Canadian Journal of Fisheries and Aquatic Science 65:2279–2292.