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SIMPLE MODELING SOLUTIONS FOR COMPLEX CONSERVATION PROBLEMS

By

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ABSTRACT OF THE DISSERTATION

Simple modeling solutions for complex conservation problems.

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Species are going extinct at a rate far higher than pre-human levels. For many species that are endangered, basic biological information may not be available to conservation managers. In these situations, mathematical models can be useful in providing insight into the biological requirements of species and to make credible predictions about how management actions may. Here, I present three modeling techniques that help to show the efficacy of management actions (Chapters 1&2) and the effects of exploitation on species with unique life histories (Chapter 3). I show that combining two foundational elements of ecological theory (matrix population models and functional responses) into one coupled model provides a flexible approach to determining the best conservation strategy to recover prey under threat from an invasive predator. I suggest a simple addition to existing population viability models that allows managers to calculate the probability that management action will improve the status of a declining population and the probability that enacting management will be no more effective than doing nothing. I illustrate the method by using previously published population viability analyses. For some management situations, doing nothing may be just as effective as enacting an expensive

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management strategy. Calculating these probabilities can provide tangible ways to balance risk and reward when making management decisions. Last, I present a game theoretic approach to model the behavior of sex changing fish. I produced estimates of maximum sustainable yield (MSY), biomass at maximum sustainable yield (B_{MSY}), and sex ratio for sex changing and non-sex changing stocks at different levels of fishing pressure and varying fertilization rates. The results suggest that sex changing stocks may be as robust to fishing as non-sex changing stocks. This game theoretic approach to evaluating hermaphroditic stocks can accommodate a wide variety of sex changing cues and allows a flexible model for understanding the effects of exploitation on hermaphroditic stocks. Models have proven useful in many conservation situations and will continue to aid managers. I have shown that simple additions to traditional models can provide more insight on the efficacy of management and how unique breeding behavior may be incorporated into conservation decision-making.

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INTRODUCTION

Species are going extinct at a rate 100 to 1000 times higher than pre-human extinction levels (Pimm, 1995). Conserving biodiversity necessarily involves spending considerable money and political capital on pulling species back from the brink of extinction. There is no all-purpose way to achieve this goal, and the tact taken must closely adhere to the biological requirements of the species of conservation concern. However, even very basic biological information on endangered species is often lacking, and parts of their life history are inaccessible for empirical study (Morris and Doak, 2002; Breckling et al., 2011). In such a situation, mathematical models are useful in order to gain insight into the biological requirements of the species, identify further knowledge gaps, and make plausible predictions about how management actions will fare once executed. Here, I provide simple modifications to existing models that are widely used in conservation, ecology, and evolutionary biology, in order to answer complex questions of conservation concern.

One such question is how best to manage invasive or problem predators. Invasive predators have pernicious effects on their prey often driving native species to extinction, especially on oceanic islands and island continents (Blackburn et al. 2004; Salo et al. 2007; Kovacs et al. 2012). For example, Savidge (1987) documented the swift extinction of native birds and reptiles caused by the brown tree snake (*Boiga irregularis*) after its introduction to Guam in the 1940s. The loss of these native prey species has led to fundamental shifts in ecological processes (Mortensen et al. 2008). The resultant efforts to control brown tree snakes have been epic but successful only to the extent that the

snake has not yet invaded other susceptible islands (Rödder and Lötters, 2010). Experiences such as this one argue strongly for a rapid management response to the incursion of an invasive predator (Kaiser and Burnett, 2010). However, quick action can lead to employment of improper strategies and the waste of resources if done without pausing long enough to gain some fundamental insights into the predator- prey dynamics that prevail in each situation (Keedwell et al., 2002; Whitehead et al. 2008, Chadès et al., 2012).

Conservation actions on behalf of the native prey often involve the employment of predator management measures such as lethal removal or birth control (Whitehead et al. 2008). Such measures can be controversial for ethical or legal reasons, and are nearly always expensive to mount (Boertje et al. 2010). For example, Busch and Cullen (2009) showed that the average cost of producing one additional yellow-eyed penguin (*Megadyptes antipodes*) nest through intensive predator management was \$68,600 NZD (\$56,214 USD). Given these constraints, ideally managers would possess a level of certainty on the efficacy of their management actions. In order to assess the efficacy of these management actions, a mathematical modeling approach is valuable.

Population viability analysis (PVA) is the most common modeling approach to guide management decisions. PVA has been extensively used to predict probabilities of extinction, compare and rank management strategies for at-risk species, and has been shown to do so accurately (Crouse et al. 1987; Doak 1995; Bustamante 1998; Brook et al. 2000; McCarthy et al. 2003). A typical PVA uses a population projection matrix consisting of vital rates (fecundity and survival) collected in the field to detail the life history of the target species. An age or stage-based matrix is then constructed using the

mean values for the vital rates or, more recently, the distribution of the vital rates. A subsequent elasticity analysis of the matrix elements compares the response of the finite rate of population increase (λ) to a proportional change in each element of the vital rate matrix (deKroon et al. 1986). The vital rate with the highest elasticity value is then targeted for management with the goal to increase (Crouse et al., 1987) or decrease (Gauthier and Brault, 1998; Harding et al., 2001) λ of the target species. Elasticity values may also be ranked to produce a suite of effective management options recognizing that the most effective option may not be the most feasible for legal, ethical, logistical, or financial reasons, and that the rankings should reflect this (Citta and Mills, 1999; Harding et al., 2001; Baxter et al. 2006; Verboom et al., 2007, Reed et al., 2009). Management based on these rankings is then assumed to affect the population by moving λ from some mean value before management to a mean value after management. More recent PVA techniques include perturbing vital rates in order to simulate management, and choosing the vital rate that can affect λ the most, regardless of the elasticity rankings (Wisdom et al. 2000). These techniques allow the manager to visualize the effect of management actions by considering the shift in the distribution of λ resulting from different management strategies rather than considering only the shift simulated management created in the mean value of λ .

The first chapter in this dissertation "How to effectively manage invasive predators to protect their native prey" considers a simple addition to current PVA models in order to answer the question "what is the best way to manage a predator in order to increase its prey?" In this chapter, I built stage-based, stochastic matrix models for a generalist predator and its rare prey. Three life histories of predator and prey were considered, short, moderate, and long lived. The populations were coupled by a type III functional response for each age class of the prey; i.e. each age class of the prey had a different functional response to reflect the difference in the difficulty of capturing older age classes. Each prey life history and predator life history was run in 9 possible combinations (i.e. short-lived predator vs. long-lived prey, moderate-lived predator vs. long-lived prey, etc.). We then generated recommendations for managing the predator based on our recommendations centered on how best to recover the prey population. Our recommendations were then compared to those made by a traditional PVA centered on how best to reduce the predator population.

The second chapter in this dissertation, "Extending population viability analysis to calculate how often conservation action is needed and is likely successful," considers the question "what is the probability of a management action achieving its goal?" In this this chapter, we added a final step to standard PVA models that calculates the probability that management will improve the status of a declining population, and the probability that implementing management will be no more effective than doing nothing at all. We suggest making the conservation goal explicit by setting a target value for λ then calculating the probability that proposed management will achieve that goal for a single realization of the model.

Another complex conservation question I aimed to answer in this dissertation is "what is the effect of harvest on sex-changing fish?" The ability to change sex has been documented in 48 families of teleost fish, including many commercially and recreationally important species (Sadovy de Mitcheson and Liu 2008; Erisman and Hastings 2011). While this is well known, most fisheries managers do not collect data on how fishing affects these species, specifically. They rather assume that hermaphroditic species can be managed as non-sex changing stocks (Alonzo et al 2008). Standard stock assessment models produce estimates of the amount of fish in the stock (total numbers and/or biomass) and do so with regard to a stock's biological points of reference. These points of reference are typically estimated using a model of population dynamics, in which fecundity, natural mortality, fishing mortality, age and sex distribution is used to project a population forward in time. It has been shown that failing to tailor assessments to the biology of hermaphroditic stocks may lead to poor estimates of biological points of reference (e.g. spawning biomass), or of the effects of exploitation on the stock, perhaps leading to collapse (e.g. Armsworth 2001; Alonzo and Mangel 2004; Heppell et al. 2006; Alonzo et al 2008, Brooks et al. 2008). Even so, standard stock assessments ignore the effects of fishing on this this life history trait.

In the third chapter of this dissertation, "Evaluating the vulnerability of sexchanging fish to harvest: A game-theoretic approach," I used a game theoretic approach to model the sex changing behavior of a hermaphroditic stock. I then included this model in a standard population projection model, similar to those used in fisheries assessments. I evaluated the model across varying levels of exploitation and fertilization rate. I then compared the effects of exploitation and varying fertilization rates on the hermaphroditic stock to a non-sex changing stock that was otherwise identical.

Each of the main chapters of my dissertation was written as a stand-alone manuscript, formatted according to a target journal. Chapter 1 was written with Dr. Julie Lockwood and Dr. Nina Fefferman and is formatted for *Biological Conservation*. Chapter 2 was written with Dr. Julie Lockwood, Oliver Stringham and Dr. Nina

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How to effectively manage invasive predators to protect their native prey

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Abstract:

Invasive predators can have substantial effects on their native prey and often there is a need for rapid action to quell this impact. Conservation action is often employed on behalf of the native prey by means of predator removal or birth control, however, the decision to employ such actions are often the outcome of a population viability analysis (PVA) or similar method aimed at reducing the predator population. These models typically focus on one species and ignore the effects of that species' interaction with others. Thus, there is inherently a disconnect between what is being managed (the predator population) and the desired outcome of the management (the persistence of a prey population). We built stage-based, stochastic matrix models of an invasive generalist predator and its native prey and coupled these using a functional response. We generated management recommendations based on the number of times the prev population persisted, and considered a range of life history types for predators and prey. We compared the results of our model to those generated by a traditional elasticity analysis commonly used in PVA. Recommendations from our model disagreed with those made by traditional elasticity most often when considering management of shortlived predators, and showed complete agreement between methods when considering long-lived predators. We illustrate that traditional PVA approaches to managing predators for the benefit of prev can provide inefficient control recommendations. Our coupled predator-prey model provides a flexible yet comprehensive approach to exploring management actions designed to benefit native prey species, including the option of 'do nothing'.

Keywords: Population viability analysis, Invasive, Predation, Management, Elasticity, Functional response

1. Introduction

Invasive predators have pernicious effects on their prey often driving native species to extinction, especially on oceanic islands and island continents (Blackburn et al. 2004; Salo et al. 2007; Kovacs et al. 2012). Conservation actions on behalf of the native prey often involve the employment of predator management measures such as lethal removal or birth control (Whitehead et al. 2008). Such measures can be controversial for ethical or legal reasons, and are nearly always expensive to mount (Boertje et al. 2010). For example, Busch and Cullen (2009) showed that the average cost of producing one additional yellow-eyed penguin (Megadyptes antipodes) nest through intensive predator management was \$68,600 NZD (\$56,214 USD). Given these constraints, ideally managers would possess a level of certainty on the efficacy of their management actions. A standard tool in this context is a population viability analysis (PVA) centered on the invasive predator, where the goal is to identify how to efficiently drive their total numbers down through time (Harding et al., 2001). However, a central limitation to such PVAs is the failure to explicitly model the response of the native prey population to the control of the predator (Sabo 2008). Here we extend standard PVA models to include the response of a native prey population to invasive predator control. In so doing, we highlight when standard single-population PVAs fail to identify the most effective and efficient tactic for increasing the probability of native prey persistence.

Invasive predators can have rapid and lasting effects on their prey and, through this interaction, alter the ecosystem that they invade. For example, Savidge (1987) documented the swift extinction of native birds and reptiles caused by the brown tree snake (*Boiga irregularis*) after its introduction to Guam in the 1940s. The loss of these

native prey species has led to fundamental shifts in ecological processes (Mortensen et al. 2008). The resultant efforts to control brown tree snakes have been epic but successful only to the extent that the snake has not yet invaded other susceptible islands (Rödder and Lötters, 2010). Experiences such as this one argue strongly for a rapid management response to the incursion of an invasive predator (Kaiser and Burnett, 2010). However, quick action can lead to employment of improper strategies and the waste of resources if done without pausing long enough to gain some fundamental insights into the predator-prey dynamics that prevail in each situation (Keedwell et al., 2002; Whitehead et al. 2008, Chadès et al., 2012).

An established and quick approach to evaluating predator management options is to use mathematical models such a PVA (e.g., Harding et al. 2001). PVA has been extensively used to predict probabilities of extinction, compare and rank management strategies for at-risk species, and has been shown to do so accurately (Crouse et al. 1987; Doak 1995; Bustamante 1998; Brook et al. 2000; McCarthy et al. 2003). PVA uses a population projection matrix consisting of vital rates to detail the life history of the target species. A subsequent elasticity analysis of the matrix elements compares the response of the finite rate of population increase (λ) to a proportional change in each element of the vital rate matrix (deKroon et al. 1986). The vital rate with the highest elasticity value is then targeted for management with the goal to increase (Crouse et al., 1987) or decrease (Gauthier and Brault, 1998; Harding et al., 2001) λ of the target species. Elasticity values may also be ranked to produce a suite of effective management options recognizing that the most effective option may not be the most feasible for legal, ethical, logistical, or financial reasons, and that the rankings should reflect this (Citta and Mills, 1999; Harding et al., 2001; Baxter et al. 2006; Verboom et al., 2007, Reed et al., 2009).

Most often PVA is restricted to considering a single species, ignoring the effects of the interactions this species may have with others (Glen and Dickman, 2005). Many factors will contribute to the dynamics of a population under management consideration, creating a situation where it is desirable to directly manage the interactions themselves rather than one species in this interaction (Vucetich and Creel 1999). Despite this intuitive insight, Sabo (2008) found that such an approach to PVA was very rare only occurring in 19 of 378 published PVAs he reviewed. Only three of those 19 PVAs modeled the interaction explicitly. Sabo (2008) also showed that the predictive value of a single-species PVA was poor for a prey population when the interaction with its predator is not explicitly considered. Sabo (2008) argued that the performance of such models could be markedly improved by explicitly modeling both the predator and prey populations, linked by their interaction.

Following this advice, we built a stage-based, stochastic matrix model for an invasive generalist predator and its rare native prey, and coupled these matrices using a type III predator-prey functional response. We chose a type III functional response because we model a generalist predator and its effects on rare prey. This functional response allows the predator to switch to another prey as the prey becomes difficult to find, or to accelerate its feeding on the rare prey as the population of the prey increases. This relationship is in contrast to a type II functional response where at low prey densities the number of prey consumed has a linear relationship with the abundance of prey (Holling 1959). Such functional responses may be quite suitable for other predator-prey dynamics, which is a topic we come back to below. We generated recommendations for controlling the invasive predator using an elasticity analysis on just the predator matrix, thus mimicking standard previously published PVA approaches to predator management problems. We also generated management recommendations from our coupled predator-prey matrix model, where the interaction is explicitly considered. We note when the recommendations from the coupled model disagreed with those produced using only predator elasticities (Fig. 1). We also noted how often a predator control measure allowed the prey population to persist through the time frame of our model. We considered this number an index of the effectiveness of an adopted predator management strategy, and it gave us another metric to use in evaluating the usefulness of our coupled predator-prey matrix model.

2. Methods

2.1. Coupled Predator-Prey Model

In order to evaluate a range of possible predator-prey scenarios, we generated data to simulate vital rates for three different predator populations reflecting three different life histories: a long-lived predator, moderate-lived predator (average life span between that of a short-lived and a long-lived species), and a short-lived predator. We matched these predators with a range of prey life histories; a long-lived prey, moderate-lived prey, and short-lived prey. Each species (predator or prey) consisted of three life stages: newborn (from birth to the juvenile stage), juveniles (from the end of the newborn stage until sexual maturity) and adults (post-sexual maturity). We used stage-based rather than age-based models to accommodate species with life stages lasting longer than one time-step. Thus, each species was represented by a 3X3 matrix of vital rates where the rates in each

cell were chosen from a range of values that reflect each life history type (Table 1).). *A* is the vital rate matrix for the prey (N) and predator (C) populations so that

$$A_{N} = \begin{array}{cccc} 0 & 0 & F_{N} \\ S_{N_{NB}} & 0 & 0 \\ 0 & S_{N_{J}} & S_{N_{A}} \end{array}$$
$$A_{c} = \begin{array}{cccc} 0 & 0 & F_{c} \\ S_{c_{NB}} & 0 & 0 \\ 0 & S_{c_{J}} & S_{c_{A}} \end{array}$$

(1)

where $F_{i \in \{N,C\}}$ is fecundity, and $S_{i \in \{N_{NB}, N_{J}, N_{A}, C_{NB}, C_{J}, C_{A}\}}$ is survival of the relevant stage class.

The vital rates for each life history type fall within reported ranges from empirical studies of birds, mammals, and reptiles (Heppel 1998; Simons et al., 2000; Jouventin and Dobson, 2002; Gardali et al., 2003; Gaillard and Yoccoz, 2003). The choice of these ranges ensured that expected life-history tradeoffs among vital rates were maintained for each predator and prey type. Thus, for example, a long–lived predator cannot simultaneously have relatively high fecundity since these vital rates are negatively correlated in such life histories (Stearns 1989).

Each matrix was allowed to project forward one time-step so that

$$\overline{N}_{(t+1)} = A_N \times \overline{N}_t$$
$$\overline{C}_{(t+1)} = A_C \times \overline{C}_t$$
(2)

where \overline{N} and \overline{C} are population vectors representing the numbers of prey (N) and predators (C) in each stage at time *t*. N, the total prey population size is calculated by adding the

number prey in each stage class that remain after interacting with the predator and C, the total predator population size, is the total number of predators at a given timestep. We allowed our model to continue for t = 10 time steps, which for most vertebrate predator-prey systems would equal 10 years. We chose this time frame to reflect the likely time window for managing the invasive predator as, once detected, quick action to manage the invader is crucial to minimizing the damage it may cause (Lockwood et al., 2013). Thus, our model reflects this time horizon and the associated population dynamics.

We chose to illustrate the use of our model using the effects of a newly established terrestrial vertebrate predator population on its prey, and as such we set the initial total population size of the predator at a low value (50) and at an age distribution that is adult-heavy and not stable in all realizations. Terrestrial vertebrates are most often introduced as non-natives either as purposeful releases (e.g., biocontrol releases on mongooses) or as accidental escapees from ships or airplanes (e.g., rats on islands). All available evidence suggests that such introductions involve few individuals (<100), and that these individuals tend to be adults (Long 1982, 2003; Kraus 2009). Our model parameters are easily modified for systems where this assumption is not realistic (e.g., release of fish via stocking efforts; Fuller et al. 1999), although almost certainly non-native populations are released away from their stable age distribution no matter the transportation mechanism (Järemo and Bengtsson, 2011).

Although the values of the predator vital rate matrix were allowed to vary (above, Table 1), all combinations of vital rates ensured that the predator population would increase through time no matter the abundance of the modeled prey. That is, we assumed a one-way dependence of the prey on the predator. This reflected our assumption that the invasive predator had a generalist diet, and the modeled prey was only one of the many species it could consume in its non-native habitat. This assumption generally holds true for invasive predators (Rödder and Lötters, 2010; Glen et al., 2011; Layman and Allgeier, 2012). The realized rate of increase for the predator across all realizations averaged 1.13 (variance = 0.047). We set a ceiling for the predator population so as not to exceed 1500 individuals, thus ensuring growth to the ceiling absent the implementation of management measures.

In order to mimic a rare prey species, the initial population size for the prey population was set to 1000 and the ceiling was set at 1500. All prey populations were initially set at a stable age distribution, and in all realizations the prey increased in abundance in the absence of the invasive predator (average $\lambda = 1.17$, variance = 0.032).

The predator and prey populations interacted via a type-III functional response of a predator to its prey (Holling 1959) according to the following equations:

$$N_{NB_{t+1}} - \left(C_A + C_J + P_{eat}(C_{NB})\right) \left(\frac{k_1 N_{NB_t}^2}{D_1^2 + N_{NB_t}^2}\right) = N_{NB_{remain}}$$
$$N_{J_{t+1}} - \left(C_A + C_J + P_{eat}(C_{NB})\right) \left(\frac{k_2 N_{J_t}^2}{D_2^2 + N_{J_t}^2}\right) = N_{J_{remain}}$$
$$N_{A_{t+1}} - \left(C_A + C_J + P_{eat}(C_{NB})\right) \left(\frac{k_3 N_{A_t}^2}{D_3^2 + N_{A_t}^2}\right) = N_{A_{remain}}$$

Our model is robust to the type of functional response chosen, as we had qualitatively similar results with both type II and type III functional responses (results not shown).

We set N_{NB} as the number of newborn prey, N_J as the number of juvenile prey, and N_A as the number of adult prey in the initial population vector. We set C_{NB} as the number of newborn predators, C_J as the number of juvenile predators, and C_A as the number of adult predators that make-up the population vector \vec{C} . We defined P_{eat} as the percentage of prey eaten compared to an adult, *k* as the maximum feeding rate of a predator (1/*h* where *h* is handling time), and *D* is the half saturation constant (e.g. the point where feeding rate is half-maximal given by $1/\alpha h$ where α is the capture efficiency). We multiplied the functional response by the total number of predators feeding on prey to determine the number of prey in each age class that was consumed. This number was subtracted from N_{NB} , N_J , and N_A . The values $N_{NBremain}$, $N_{Jremain}$, and $N_{Aremain}$ are the number of newborn, juvenile and adult prey remaining after their interaction with predators.

The way we formulated the predator-prey interaction dictates that each stage of the prey matrix (newborn, juvenile, and adult) interacted independently with the predator population. Thus, the functional response of the predator is not the same for different stages of the prey life cycle. The newborn age class was the easiest to capture and the shortest to handle. This element of our model ensures that predation pressure on the prey reflects the empirical observation that handling time and capture efficiency are different for predators feeding on different sized prey (Aljetlawi et al. 2004). This formulation also allows adult and juvenile predators to consume the same amount of prey, while also ensuring that newborns did not. We set newborn prey consumption to be a percentage

 (P_{eat}) of the prey consumed by an average adult. This age structure within the functional response of predators to their prey means that predation pressure is not a 1:1 function with the number of predator individuals in the model. Parameters *h* and α were chosen from uniform distributions and used to calculate *k* and *D* in the functional response. The distributions were adjusted so that adult prey was the most difficult to catch and newborn prey was the easiest, however, the uniform distribution for each parameter was rather wide capturing a very large range of values for *h* (8 seconds -1 day) and α (0-1). This serves to test the robustness of our model to varying predation parameters. After the populations interacted via predation, the remaining number of individuals in each age class of the prey population (N_{NBremain}, N_{Jremain}, N_{Aremain}) was used to create a population vector (\overline{N}) for use in projecting to the next time-step (Eq.1).

2.2. Comparisons Between Coupled– and Single–Population Models

We allowed each predator type to interact with each prey type (Fig 1), thus producing nine possible coupled predator-prey models. We ran 10,000 realizations of each of these nine models, where in each realization the matrix elements for the predator and prey were drawn from a pre-set distribution described in Table 1. This model structure allowed us to incorporate uncertainty in the matrix elements (vital rates) of the predator and prey (within the bounds set in Table 1), and thus judge the sensitivity of our results to such variation.

In our initial runs of our coupled predator-prey model, we enacted no predator control measures thus allowing each of the nine models to run for 10 years in each of the 10,000 realizations. We tallied the number of times out of 10,000 that the prey population went

extinct. This value indicated the probability of each predator type driving each prey type to extinction absent any effort at predator management (do-nothing option), and thus serves as a benchmark for evaluating the effects of predator management on the prey population.

To evaluate the effect of management options in our coupled predator-prey models we utilized perturbation analysis. For each of the nine predator-prey models described above, we sequentially reduced each vital rate in each matrix by 50% each year and recorded the effect this reduction had on the persistence of the prey population after 10 years. For each realization where the prey population persisted to year 10, we recorded the vital rate that was perturbed. We then tallied the number of times that each perturbed vital rate allowed prey persistence, and divided this by 10,000. This effort resulted in a ranking of vital rate matrix elements from those that were more to less likely to ensure prey persistence. In terms of management options, the life stages represented by these vital rates should be the target of either lethal removal or fecundity reduction in order to ensure prey persistence. We produced this ranking for each of the nine coupled predatorprey matrix models (Fig. 2). We also tallied the number of times the outcome was uniform across all management actions, including 'do-nothing.' In this case, we can conclude that the persistence of the prey was not necessarily attributable to the management action employed. Conversely, the number of times the outcomes were not uniform across management actions shows how frequently a management action was the causal agent in persistence of the prey (Table 2).

To mimic single-species PVA results, we calculated the elasticity of the predator matrix generated within each realization described above per Caswell (1989). Under standard PVA protocols, the vital rate that has the highest elasticity and has the greatest potential to be changed by management is targeted for action. For each realization, we ranked the predator vital rate elasticity scores (Fig. 2). We then calculated the number of times a vital rate was selected for management (i.e. had the highest elasticity) and divided this by the number of realizations (10,000). When a vital rate had a percentage of 100, that life stage was always selected for management regardless of any underlying variation in matrix values. As this percentage decreased from 100, the variation in matrix values increasingly influenced the ranking of life stages for management; thus making the resultant management recommendations less certain.

Finally, we correlated the absolute change in the growth rate (λ) for each vital rate given by eigenvalue elasticity analysis with the number of times the prey population did not persist when perturbing each vital rate (Fig. 3). Here one would expect a negative correlation when the two models agree because, as the change in λ of the predator increases, the number of realizations where the prey population does not persist is expected to decrease. And one would expect the reverse (positive relationship) when the two models disagree using the same logic.

3. Results

The agreement between a traditional elasticity analysis on each predator matrix and our coupled predator-prey model ranged from almost complete disagreement to almost complete agreement (Table 2, Fig. 3a-c), depending on the scenario.

Disagreement between models was most often seen when considering management options for a short-lived invasive predator (Fig 2a-c, Fig. 3a). In such situations, the elasticity analysis more often chose newborn survival as the most important life stage for lethal removal followed by a reduction in fecundity, juvenile and adult survival. However, there was little separation between these options with each vital rate ranking highly in about a quarter of the realizations (Fig. 2a-c). No matter the life history of the prey, our coupled model most often suggested a reduction in the fecundity of short-lived predators as the most effective at ensuring prey persistence (Fig. 2a-c). The management aimed at the remaining vital rates also showed some effectiveness in conserving the prey population, with little evidence to suggest one of these second-tier options was particularly more desirable than another (Fig. 2a-c). The correlation coefficients between models were positive and ranged from 0.79 - 0.81, and the R² values were fairly high (0.629 to 0.6542). For the management option of doing nothing, 80 - 83% of the realizations resulted in the prey going extinct. In our coupled predator-prey model, management actions aimed at the predator resulted in net benefits for prey persistence in 21 - 22% of the realizations (Table 2, Fig. 3a).

For a moderate-lived predator, elasticity analysis overwhelmingly chose reduction in adult survival as the most efficient management option (Fig. 2d-f). Elasticity values differed by no more than 2% for the remaining predator vital rate matrix elements, indicating that as a group these second-tier options were not often ranked highly for management (Fig. 2d-f). Our coupled predator-prey model produced different recommendations depending on the life history of the prey and thus produced discordant recommendations as compared to elasticity (Fig. 2d-f). In the coupled model, a reduction in predator fecundity most often resulted in persistence of the prey, with a reduction in predator adult survival also often ranking highly. A reduction in newborn or juvenile predator survival was occasionally ranked as the best management option (Fig. 2d-f). The correlation coefficient between models was positive but low ranging from 0.44 - 0.64, with the R² values consistently showing low values (0.195 - 0.405). For the 'do nothing' management option, 88 - 91% of realizations resulted in the prey going extinct. Difference in prey persistence was attributable to one of the management strategies in our coupled model in 27 - 30% of the realizations (Table 2, Figure 3b).

For a long-lived predator, the elasticity analysis suggested a reduction in adult survival as the appropriate management action in nearly 100% of the realizations (Fig. 2g-i). Occasionally a reduction in the other vital rates was identified as useful for reducing the population growth of the predator, however these instances were very rare (<1%). The results from our coupled predator-prey model strongly agreed with elasticity consistently ranking a reduction in adult survival as the most efficient predator management action (Fig. 2g-i). The correlation coefficients between models were negative and high (-0.985 – -0.992) and the R² values ranged from 0.970 – 0.983. For the management option of 'doing nothing', 91 – 93% of the realizations resulted in the prey going extinct. From 25 – 27% of the coupled model realizations resulted in any management action ensuring persistence of the prey population (Table 2, Fig. 3c).

4. Discussion

All options for management of invasive predators, including doing nothing, carry high moral, legal and economic costs. Given this, there is a premium on clearly and quickly demonstrating a conservation benefit for the native species this predator consumes (Côté and Sutherland 1997). Our results show that in some circumstances the most effective

option for reducing predator numbers will not result in the persistence of the prey. This mismatch is caused by two factors, neither of which are novel in regards to their mathematical influence on PVA recommendations (Sabo 2009, Fefferman and Reed 2006) but both of which are ignored in standard one-species population viability analyses that aim to manage predators for the benefit of prey. We show that these two factors show composite effects on the efficiency of chosen predator management efforts and we review the influence of each below.

First, not all predator individuals consume prey at the same rate, and not all prey are equally susceptible to predators. In the context of predator management, the use of single-species PVAs assumes that a reduction of predator individuals will result in more prey individuals. Thus, the faster management actions can remove predators, the faster the prey population should recover. Predator-prey interactions are far more complex than this assumption allows (e.g., Aljetlawi et al. 2004). A predator-prey functional response is at least dependent on the rate at which predators encounter prey, and the handling time and capture efficiency of the predator (Holling 1959). Our model allows for sizedependent predation by allowing each age class of predator to interact independently with each age class of prey. This formulation allowed for the possibility that the life stage with highest impacts on predator population growth (elasticity) was not the life stage that had the highest predation rate on prey. Thus, managing for this life stage would not be the most effective approach for increasing prev persistence. We show this effect most clearly for newborn predators. By definition in our model, newborn predators consume a fraction of the prey that the older age classes consume. In realizations where newborn survival has the highest elasticity, a reduction in newborn survival occasionally does not

result in the highest probability of prey persistence (e.g., moderate-lived predators). Based on our results, we suggest that adding this level of realism into conservation focused predator-prey models is logistically easy (as we show here) and well warranted. We chose a generalist predator and a rare prey so that the predator will not satiate on any single age class, thus the functional responses are independent of each other. However, there are situations where the predator may satiate on a more abundant prey stage, which would affect the feeding rate of the predator on the other stages of the prey. The effect of this on our model is unknown.

Second, elasticities associated with PVAs typically assume a stable age distribution in the predator population (Citta and Mills, 1999; Heppell et al., 2000; Fefferman and Reed, 2006), which is unlikely to be the case for invasive populations or populations where one life stage is being actively managed (Koons et al., 2005; Järemo and Bengtsson, 2011). Our results show that this assumption can lead to inefficient management decisions when controlling predators for the conservation benefit of their prey. There are two mechanisms that can drive this inefficiency. If the predator population is newly introduced, there is a high probability that it will not have reached a stable age distribution by the time management is enacted (Järemo and Bengtsson, 2011). Also, the management enacted for predator control involves lethal removal of individuals or sharp reductions in fecundity. These actions will, by themselves, throw a population out of a stable age distribution to produce management recommendations, and thus our results often disagreed with elasticity recommendations. This disagreement was
especially pronounced when considering short-lived predators since the age distribution of such species can be rather elastic (Koons et al., 2005).

Our primary goal was to illustrate that traditional PVA models can provide suboptimal management recommendations for invasive predator control. However, our coupled predator-prey model is highly flexible in that the vital rate matrices can be modified to match the life histories of any type of predator, or prey. Our model can also be modified to capture the particulars of any predator-prey interaction by shifting the values in the functional response equations, or by combining or elaborating the equations for each age class. It can thus be used in a variety of circumstances where the conservation dilemma is how best to reduce the impacts of a predator on its prey (e.g., stoats, *Mustela ermine*, and brown kiwi, *Apteryx mantelli*; Robertson et al., 2011); the management of invasive predators is but one example of such a dilemma. In addition, the two components to our model (matrix models and functional responses of predators to their prey) are foundational elements in ecological theory. This theory provides a rich source of information for constructing each component appropriately for a given conservation situation. We suggest that the model we describe here can be used as a highly useful prototype in a variety of situations where the interaction between species is of paramount conservation concern. We also suggest that acknowledging age-structured predator-prey functional responses in particular places a high premium on empirical data that can be used to parameterize these equations; especially in situations where predators are driving prey towards extinction.

Beyond the flexibility of our model, we suggest that when predator-prey interactions are the subject of conservation actions the output of our model is far more intuitive and

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relevant in terms of the recommendations it offers than standard PVA. For example, using elasticity to rank management actions does not provide information on the magnitude of a vital rate's effect on the growth rate of the prey population (Wisdom and Mills, 1997). Our approach shows a quantifiable effect on the prey population (the number of times its population goes extinct) and thus provides a far more natural way to interpret results. Similarly, due to the stochastic nature of our coupled predator-prey model, there are realizations in which the prey persists under all conservation scenarios, meaning that doing anything (or nothing) would result in the persistence of the prey. Thus, our model tells a manager how often a conservation action will make any difference to the survival of the prey species, however, the implications of such action may change if many prey species of concern are affected by the generalist predator (e.g. brown tree snake). This information allows a manager to consider the cost of conservation actions against the probability that any such actions are at all effective. For example, in our scenarios the 'do-nothing' option resulted in prey extinction in over 80% of all realizations. However, enacting resulted in prey persistence in only around 20% of realizations (Table 2). Whether these actions would be warranted given this level of potential conservation success depends heavily on the magnitude and range of associated costs, but by providing this information our model allows managers to explicitly consider this trade-off.

Species invasions can lead to native species extinctions, with the ill-effects of invasive predators on their native prey being particularly noteworthy. The continued rise in the number of non-native species worldwide suggests that the need to control invasive predators will itself grow. However, there are many situations in which predator

management may be well-warranted, including cases where the predator is native to the ecosystem in which it is causing conservation concern (e.g. range shift due to climate climate change; Nori et al., 2011). Our coupled predator-prey model provides a flexible yet comprehensive approach to exploring a range of management actions designed to benefit native prey species. Our results show that the need for such a model is real, and can potentially save managers (and stakeholders) considerable monetary and social capital by more effectively identifying the most efficient management options given the situation.

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Table 1. Values (mean and standard deviation) for vital rates used to create short-, medium-, and long-lived predators, and prey. In each realization of our model, the values used for fecundity matrix elements were chosen from a normal distribution and the values for survival probability were drawn from a beta distribution. Values for survival probabilities are converted from the alpha and beta parameters used in the beta distribution.

Trophic Level	Life History	Fecundity	Newborn Survival	Juvenile Survival	Adult Survival
Predator	Short-lived	6 (3.5)	0.4 (0.10)	0.35 (0.15)	0.4 (0.15)
	Moderate-lived	2.3 (0.750)	0.49 (0.110)	0.56 (0.170)	0.614 (0.13)
	Long-lived	1.2 (0.95)	0.680 (0.12)	0.797 (0.07)	0.89 (0.02)
Prey	Short-lived	6.5 (3.5)	0.42 (0.10)	0.38 (0.15)	0.45 (0.18)
	Moderate-lived	2.0 (0.60)	0.534 (0.165)	0.675 (0.10)	0.744 (0.08)
	Long-lived	0.89 (0.115)	0.592 (0.105)	0.775 (0.06)	0.944 (0.05)

Table 2. Correlation coefficient and adjusted R^2 for correlations in Figure 2, and the percentage of realizations in which the prey persistence was directly attributable to the prescribed conservation action of perturbing a vital rate. SL= Short-Lived, ML= Moderate-Lived, and LL = Long-Lived. Life history listed first is the predator (i.e. SL vs. LL represents a short-lived predator and long-lived prey).

Model	Correlation Coefficient	R^2	% Runs where prey persistence was attributable to prescribed management
SL vs. SL	0.793	0.6290	22.32%
SL vs. ML	0.809	0.6542	20.65%
SL vs. LL	0.804	0.6457	22.40%
ML vs. SL	0.637	0.4053	28.57%
ML vs. ML	0.442	0.1953	26.71%
ML vs. LL	0.625	0.3905	30.38%
LL vs. SL	-0.985	0.9696	25.70%
LL vs. ML	-0.992	0.9831	25.20%
LL vs. LL	-0.986	0.9716	26.08%

Figure 1. A schematic diagram of how management recommendations from our coupled predator-prey model are generated and compared to the corresponding recommendations provided by PVA elasticity analysis.

Figure 2a-i. Conservation management recommendations made by traditional PVA elasticity analysis compared to recommendations made by our coupled predator-prey model. Vital rates are listed on each x-axis in the order of their ranking by elasticity analysis, highest to lowest. The percentage of model realizations (out of 10,000) in which that vital rate had the highest ranking is in parentheses. Bar height represents the frequency (out of 10,000 realizations) in which our coupled model showed that perturbation to the corresponding vital rate resulted in prey persistence. F = fecundity, NBS= newborn survival, JS = juvenile survival, AS = adult survival. 2a-c is a short-lived predator and a) short-lived, b) moderate-lived, and c) long-lived prey. 2d-f is for a moderate-lived predator and a) short-lived, b) moderate-lived, and c) long-lived prey. 2g-i is for a long-lived predator and a) short-lived, b) moderate-lived, and c) long-lived prey.

Figure 3a-c. The correlation between conservation management recommendations made by our coupled predator-prey model and those made by traditional PVA elasticity analysis. The x-axis represents the amount of change in λ of the predator population at each vital rate given by a traditional elasticity analysis. The y-axis is the number of times the prey population did not persist under recommendations produced by our coupled model. 3a shows a short-lived predator and all three life histories of prey, 3b shows a moderate-lived predator and all three life histories of prey, and 3c shows a long-lived predator and all three life histories of prey.



Figure 1.



Figure 2.



Figure 3.

Extending population viability analysis to calculate how often conservation action is needed and is likely successful

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Abstract

Population viability analysis (PVA) has become a mainstay in efforts to manage species threatened with extinction. The mechanics of a PVA model produce distributions of population growth rates, where the shape of that distribution is dictated by various uncertainties. PVA models are used to guide management decisions by evaluating how proposed actions would shift a distribution of growth rates, with the starting distribution reflecting the absence of management and the ending distribution the implementation of management. These two distributions may overlap, and the degree to which they overlap has heretofore been unexplored in terms of how this informs conservation actions. Here we provide a simple method for using these two distributions to calculate the probability of management improving the status of a declining population, and the probability that implementing management will be no more effective than doing nothing at all. We illustrate this method using 14 previously published PVA models. For these PVA models, our analysis shows that the probability of the recommended management action achieving a target growth rate ranged from 0.14 to 0.98. Calculating and reporting these probabilities provide managers and policy-makers with tangible ways of balancing risks and rewards to their actions.

Keywords

Population viability analysis, management, policy, conservation, stochasticity

Introduction

Population viability analysis (PVA) is commonly used to evaluate extinction risk and identify ways to reduce this risk (Boyce 1992; Mills et al. 1999). Its prominence as a tool to guide conservation action is reflected in its use by the IUCN to rank species' likelihood of extinction, and its use in legislation to halt commercial activity in favor of protecting endangered species (Crouse et al. 1987; Lande 1988; Crowder et al. 1994; IUCN 1994). By perturbing one or more vital rates in a matrix projection model, PVA users can mimic possible management actions. The change in vital rate(s) that results in the largest increase in population growth rate is then targeted by practitioners for action (Possingham et al. 1993; Wisdom et al. 2000). Because of the inclusion of uncertainty in PVAs, a perturbation of one (or more) vital rate(s) results in a distribution of population growth rates that reflect a given management action. When conservation management is applied in real life, however, there is only one realized outcome: the one we observe. By only considering the shift we create in the distribution of a growth rate via management, or the shift in the mean of these distributions, we are ignoring the amount of overlap the final (after management) and initial (absent management) distributions have with one another. We show that this overlap has substantial implications for how PVA may be interpreted in conservation management and policy. We illustrate a simple extension to PVAs that allows one to calculate the probability that management will improve the status of a declining population, and the probability that implementing management will be no more effective than doing nothing at all.

The most common form of PVA uses a population projection matrix consisting of vital rates to detail the life history of the target species (e.g., age-specific growth, survival

and fecundity rates). The growth rate of the population (λ) is calculated from this matrix, and the elements of this matrix can be perturbed (independently or in concert) to explore their influence on how rapidly the population will grow in response (deKroon et al 1986, Crouse et al. 1987; Lindenmayer and Possingham 1996). There are a variety of sources of uncertainty in models, and the need to incorporate these into matrix-based PVA models has long been recognized (Boyce 1992). There are methods by which parametric uncertainty can be incorporated into PVA models (e.g., McGowan et al. 2011) and methods to separate process variance (natural variation in the data) from sample variance (collection error) in order to use only the natural variance to parameterize a model (Kendall 1998; White et al. 2002). No matter the mechanism, the inclusion of stochastic elements in PVAs has the effect of producing a distribution of population growth rates that are possible given known forms of uncertainty.

The often unstated assumption in making recommendations from PVAs is that implementing an intervention that mathematically shifts the mean (traditional PVA [e.g. Johnson and Braun 1999]) or the entire distribution (more recent techniques [e.g. Wisdom et al 2000; Johnson et al 2010]) upward, will necessarily achieve an observed increase in the success/survival of a probability. However, in most cases there will be a portion of the initial distribution of growth rates (unmanaged) that overlaps with the final distribution of growth rates (managed). The degree to which these two distributions overlap defines two distinct probabilities. The first is the probability that doing nothing will result in the same outcome as enacting management (e.g., Robinson et al. 2013). The second, and perhaps the more troubling possibility, is that implementing management actions will increase population growth, but will not push λ to the target value; in which case management simply did not achieve the desired goal. Explicitly defining and reporting these probabilities enhances the usefulness of PVA models by providing ways to calculate the various risks associated with conservation actions (including no action). If these risks are made transparent to conservation practioners and policy-makers, they have a more complete tool-kit at their disposal for making difficult judgments on how to balance the risks versus rewards of their actions.

To achieve this goal, we suggest a two-step approach where the initial step is to make the conservation goal explicit by setting a target λ value (which is surprisingly rare; see below), and then the second step is calculating the probability that proposed management actions will in fact achieve this value in any one realization of the model. Thus, instead of asking "how much can we change the distribution or average λ over many stochastic realizations"; we can ask "what is the probability of using a management action to reach a target growth rate?" Thus our approach is not intended to replace currently practiced PVAs but enhances them to better serve conservation decisionmaking by making it clear how often proposed management actions are likely to lead to achieving population persistence, and how often enacting management will be expected to be no more viable than doing nothing.

Methods

We searched Web of Science® for published PVAs using the search term "population viability analysis" over the years 1995 – 2013. Searches were limited to journals containing "Conservation" and/or "Management" in their title. We retained the first 50 publications that reported a PVA for one or more species. These 50 publications ranged

in publication date from 1999 – 2011. Of those 50, only 11 reported survival and fecundity estimates for each age/stage class, made a statement of population status or reported λ prior to management (i.e. was the population declining, stable, or increasing before management), reported a clear management goal, and made an unambiguous management recommendation based on the PVA performed.

We replicated PVA models for the 14 populations described within these 11 publications, recording the distribution of population growth rates (λ) before and after the interventions recommended for management in each paper. We used correlation analysis to compare the mean λ of our distributions to the mean λ reported in each publication to ensure that the models we developed gave the same results as the models presented in each publication (see Results).

We recorded from each publication the original author's stated conservation goal in terms of the value of λ they desired based on the model they presented; i.e. if the model claimed a λ value of 0.95 was achievable by management, we used $\lambda=0.95$ as the target. When a target greater than one was given we used $\lambda \ge 1$ as the target. When no target λ value was given, for example when a paper suggested that management would stem the decline of a population, improve λ , or achieve a stable population; we assumed the target to be $\lambda \ge 1$. We recognize that often the goal of specific management actions is not always $\lambda \ge 1$ as in the case of Perlut et al. (2008). If the target was not $\lambda \ge 1$, we realize that using the target of $\lambda \ge 1$ will inflate the number of times that management does not achieve its goal when analyzed by our method. The goal of this decision, however, was not to determine whether a specific recommendation was 'right' or 'wrong', but simply to present how our method would be applied to PVA results. When authors suggested multiple management options could achieve a conservation goal, we chose the most optimistic for use in our evaluation. This choice produces conservatively optimistic probabilities of attaining success (see below). When authors suggested that multiple management strategies should be changed simultaneously to achieve a stated goal, or when one management strategy was able to affect multiple vital rates in concert, we allowed those vital rates to be affected together. For example, Coluccy et al. (2008) suggested that adaptive harvest management to improve adult survival, and habitat management to improve duckling survival, would together increase λ for mallards (*Anas platyrhynchos*) in the Great Lakes region to a target level. In this case, we allowed both management strategies to occur simultaneously in our analysis.

We utilized our model to produce two distributions of λ for each of the 14 populations gleaned from the above publications; one distribution in the absence of any management action, and one distribution incorporating the effects of the suggested management in effect (Figure 1). These distributions were the result of paired stochastic draws from the vital rates. That is, for a given model iteration, the same random matrix was used to determine λ for a non-managed and for a managed population. We then affixed the author-stated target value of λ (if less than 1) to each distribution (see above, Figure 1). This allowed us to quantify a number of meaningful metrics: (1) A = the number of times out of 10,000 realizations that intervention pushed an initial λ from below the target value to a managed value equal to, or over, the stated target (2) B = the number of times out of 10,000 realizations that the original, un-managed population yielded a value of λ equal to or greater than the stated target value (gray shading within Figure 1). (3) C = the number of times λ remained below the target value even after

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including the positive effects of a recommended management action (black shading within Figure 1). The frequency of each of these three outcomes is dictated by how far below the target growth rate the population sits pre-management, and the extent to which suggested management actions can move growth rates up to and past the stated target value (Figure 1).

We represent the frequency of each of these three outcomes within pie charts, where the shading matches the corresponding outcome (Figure 2). Thus, the white segment in any given pie chart indicates the probability that a recommended management action achieved its stated goal (outcome A above). The extent of gray in the chart indicates the frequency with which a population growth rate was already equal to, or exceeded, the target growth rate before the effects of management were included (outcome B), and the extent of black in the chart indicates the frequency of cases in which enacting management failed to move growth rates at least to the target value (outcome C). By combining the number of realizations that ended in outcomes A and C above, we determined the number of realizations in which management was needed (i.e. λ was below the target value before management was applied). We then computed $\frac{A}{A+C}$ to determine how often management is expected to achieve stated goals, given that it is needed. We also computed A+B to capture the number of realizations that ended in the achievement of the target growth value, no matter how that value was attained (with or without management action).

Results

The correlation between mean λ from our model and the mean λ reported within each publication was very high (correlation coefficient = 0.975 and R² = 0.95 for models using information without management actions included; correlation coefficient = 0.999 and R² = 0.99 for models created where management actions were included) (Figure 3). The discrepancies between our λ -value and those reported in the original publication were well within a range consistent with stochastic variation. This result indicates that our model formulation accurately mimics that of each individual PVA, and that further evaluation of the results from our models yields nearly identical results to models reported by the original authors.

Our results reveal widely differing relative frequencies for each of the three possible outcomes (Table 1; Fig. 2). The probability that any one realization resulted in λ reaching a pre-determined target value (outcome A white shading) ranged from 0.14 to 0.98. In only two of the 14 PVAs did at least a half of the realizations fall into this category (Fig. 2). The probability that any one realization resulted in a growth rate that was at or above the target value of λ , without accounting for the positive effects of management action (outcome B gray shading), ranged from 0.015 to 0.47 (Fig. 2). This is interpreted as the number of times the conservation goal was attained without any management action. Finally, the probability that any one realization resulted in λ failing to attain the target value even when the positive effects of management are included ranged from 0.054 to 0.60 (outcome C, black shading, Fig. 2). This number is interpreted as the number of times management was applied to a population but failed to achieve the conservation goal.

By combining the results above, we calculated that the probability that management

action was needed to achieve the target λ value ranged from 0.26 to 0.99. For all but one of the models, management was required in more than half of the realizations (Table 1). We also determined how often management can be expected to work when it is needed, which ranged from 0.25 to 0.99 (Table 1). Finally, we calculated that the probability that λ was equal to or exceeded the target value regardless of whether management was applied ranged from 0.40 to 0.99 (Table 1).

Discussion

The choice of management action, including no action, for a species in peril must be made carefully with full knowledge of the costs and benefits to each option (Baxter et al. 2006)). The use of population modeling techniques such as PVA can guide these decisions by recommending one management strategy over others based on the projected increase in population growth that will result from each proposed action (Possingham et al. 1993). Such relative predictions have been shown to be accurate and robust to uncertainty (McCarthy et al. 2003). However, PVA is used in many cases to make predictions about the effectiveness of a particular management strategy relying only on the average outcome over many stochastic realizations, or the shift in the distribution of λ , and not the probability that any one particular outcome will occur (McCarthy et al. 2001). We illustrate here how a simple change to how we evaluate the outcome of PVA results can better inform policy decisions. Our approach explicitly recognizes that reallife management is a one-shot occurrence, and thus it is more appropriate to visualize the outcome of management actions as probabilities and not as simple changes in mean values or shifts in distributions.

We highlight three probabilities that we think are especially useful to consider when developing conservation policy. First is the probability that a suggested management action will successfully move a population to at least some target growth rate, if not into active positive growth. This information is what one thinks of when considering the recommendations of PVAs. It answers the question of how likely it is that expending monetary and political effort to enact a management action will in fact result in the species of concern persisting into the near future. Of the 14 PVAs we explored, this outcome was surprisingly rare, typically occurring in fewer than 30% of the realizations, and dipping down as low as 15% in some cases. This result suggests that the management recommendations from PVAs do not often stem from model realizations where population growth rates are transformed from decreasing to (at least) persisting, but are instead driven by specific cases in which increases in the growth rate do not alter the fate of the population.

Second, and related to above outcome, we highlight the importance of calculating the probability that the target population already demonstrates a growth rate at or above the target. This probability seems counter-intuitive at first since this species should not be the center of conservation attention if it is not truly in decline. However, a population can show a mean negative growth rate and still have some realizations where growth rate is positive if either (a) the mean is not far below zero and/or (b) the variation around this mean growth rate is high. Our approach explicitly recognizes these two possibilities, and provides clear, actionable information about how this should influence management recommendations.

The mean population growth rate will increase if this, and the above outcomes, make

up the majority of the realizations in a PVA; these are all the realizations in which the growth rates meet or exceed the target. In nearly all of the 14 PVAs we evaluated, these two outcomes comprised more than 50% of the realizations, and thus together they pushed the mean growth rate high enough to suggest that management should be enacted. What we show is that the increase in mean growth rate was at least as influenced by outcome B as it was outcome A. Thus, in many cases using a standard PVA output to guide management decisions places undue optimism on the effects of the suggested action simply because there was no attempt to parcel out which realizations had growth rates above a target because of stochasticity versus management. Using methods to incorporate uncertainty into the models or to separate sample from process variance will improve the accuracy of PVA models in the face of stochasticity and may aid in decoupling the effects of stochasticity versus management (Fox and Kendall 2002; McGowan et al. 2011). Also, using more recent methods such as Life-stage Simulation Analysis (LSA) that explicitly report the distribution of λ before and after management can help visualize the range of values that λ may take under different management options (Wisdom et al. 2000). When our method is combined with these, it can provide a very accurate probability of a given management action being responsible for achieving a target goal.

Third, our approach allows the calculation of how often management actions may be enacted and the population will still attain a target growth rate. In some ways this probability is the most useful output of our approach since it informs policy-makers of the odds that they will expend limited political and monetary capital and yet have no evidence at the end that these actions resulted in persistence for the threatened species.

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The degree to which we see this across the 14 PVAs we evaluated varied quite a lot. As with outcome A, the prevalence of this outcome is determined in large part by how much the suggested management action could influence population growth in an absolute sense, and how much uncertainty there was in the system.

From a policy standpoint, our approach allows decision-makers to clearly quantify and understand the risks and rewards associated with any particular management action. As a concrete example, Perlut et al. (2008a) performed a PVA on savannah sparrows (Passerculus sandwichensis) in the Champlain Valley, Vermont (USA), and determined that the population was in decline (average $\lambda = 0.99$). They suggested that increasing adult survival by 5% via management would lead to a growing population (average $\lambda =$ 1.04). When we computed the probability of various outcomes in this model, we calculated that the probability of management moving the population from decreasing to increasing was just 17%. We also showed that there was a 48% probability that the growth rate was already above 1 before any management was applied. For some policymakers, success may not depend on *how* a growing population was achieved but rather that a growing population was achieved. For savannah sparrows, we calculated a 64% probability that the population would be persistent or increase, if the recommended management is included. In a situation such as this, where the population is expected to achieve persistence without management almost 50% of the time, a "do-nothing" approach may be a viable option, particularly when the management action recommended is very expensive (e.g. predator removal; Busch and Cullen 2009). On the other hand, if the recommended management action is inexpensive (e.g. conspecific attraction; Ward and Schlossberg 2004), a policy-maker may chose to enact the action to increase the

chance of persistence, even if it is only by a slight margin. Thus, for the savannah sparrow, the decision to enact management that will increase adult survival depends critically on the associated costs, and the willingness to bear those costs by effected parties, given the projected reward in achieving population persistence.

Our primary goal was to provide a framework by which PVA can be evaluated to determine how often a certain outcome is expected rather than how much we can change population growth rate over many stochastic realizations. Our approach does not supplant PVA models but instead enhances the information they provide so that the risks and rewards of recommended management actions are made clear (McCarthy et al. 2003). We suggest that our approach to evaluating the outcome of PVAs can improve the use of PVA models and provide greater insight into what is driving their results.

Acknowledgments

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Figure 1. Schematic diagram of the output generated from population viability analyses (PVAs), which is composed of a range of possible population growth rates (λ). The distribution of growth rates is a product of incorporating environmental and demographic stochasticity, and thus reflects the range of growth rates deemed reasonable given our understanding of natural variation in the system. We evaluated the output of 14 published PVAs using two distributions of λ -values: one calculated without management actions in effect (top panel), and another calculated with management actions in effect (top panel). We designated target growth rates (vertical lines) for each PVA based on information provided in each publication. Based on these factors, we calculated three outcomes: (1) the probability that growth rate was increased from a declining value to at least an increasing value (2) the probability that the growth rate was above the target value before management was enacted (gray areas), and (3) the probability that the growth rate remained below the target after management was incorporated (black areas).

Figure 2. For the 14 population viability analyses (PVAs) we evaluated, we tallied the number of the following outcomes: (1) the probability that growth rate was increased from below the target value to at least the target value(white areas, Outcome A), (2) the probability that the growth rate was above the target value before management was enacted (gray areas, Outcome B), and (3) the probability that the growth rate remained below the target after management was incorporated (black areas, Outcome C).

Figure 3. Correlation analysis between the λ -value reported in each of 11 published population viability analyses (PVAs) and our λ -values derived from re-creating these models. The two lines represent the correlation between λ -values generated without management in effect (solid line), and λ -values generated with management in effect (dotted line). The strong correlation between values indicates that our models successfully replicated those within each published PVA.

Table 1. The number of PVA realizations out of 10,000 that resulted in one of three possible outcomes (see text, Figure 2). Also included are the number of realizations where $\lambda <$ target and thus management was needed, the number of times when λ rose above the target when starting < target, and the number of times $\lambda >$ target regardless of management.

Study	Outcome A	Outcome B	Outcome C	Management was needed [*]	Management was needed and it worked [£]	Persistent population [§]
Beaudry et al.	3277	4680	2043	5320	61.59%	7957
(2010)						
Coluccy et al.	1758	4129	4113	5871	29.94%	5887
(2008)						
Haines et al.	1423	7438	1139	2562	55.54%	8861
(2006)						
Hudgens et al.	2254	3646	4100	6354	35.47%	5900
(2011)						
Johnson and	1516	4034	4450	5966	25.41%	5550
Braun (1999)						
Lambert et al.	2124	1833	6043	8167	26.01%	3957
(2006)						
Lenarz et al.	4957	422	4621	9578	51.74%	5379
(2010)						
Perlut et al	1761	4677	3562	5323	33.08%	6438
(2008) a						
Perlut et al	2401	4718	2881	5282	45%	7119
(2008) b						
Perlut et al	1969	3611	4420	6389	30.82%	5580
(2008) c						
Perlut et al	2931	3335	3734	6665	43.98%	6266
(2008) d						

Ramp and Ben-	5332	3867	801	6133	83.93%	9199	•
Ami (2006)							
Zambrano et al.	1713	3152	5135	6848	25.01%	9525	
(2007)							
Zhang and Zheng (2007)	9796	150	54	9850	99.45%	9946	

*The number of times management was needed is calculated as the sum of Outcomes A and C. *The number of times when management increased population growth rates to at least equal the target rate was calculated as Outcome A/Outcome A + Outcome C. *The number times when the population growth rate allowed a persisting population was calculated as

Outcome A + Outcome B.







Figure 2.

Similarity of models



Figure 3.
Evaluating the vulnerability of sex-changing fish to harvest: A game-theoretic approach

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Abstract

Hermaphroditism has been widely documented in many commercially and recreationally important species, yet the effects of fishing on stocks with this life history trait are not considered in most stock assessments. This failure to do so can lead to poor estimates of data vital to understanding the health of hermaphroditic stocks. Here, we present a game theoretic approach to model the sex changing behavior of a hermaphroditic stock and produce estimates of MSY, B_{MSY} and sex ratio, then compare these to a non-sex changing stock. We tested each stock at varying levels of exploitation and fertilization rates. We show that a hermaphroditic stock with flexible timing of sex change produces similar MSY and slightly higher B_{MSY} than non-sex changing stocks. Sex changing stocks also had a higher proportion of males in the population than did non-sex changing stocks as exploitation increased. While sex changing stocks were able to maintain their sex ratio, the age at which fish changed sex decreased with increased exploitation, suggesting smaller overall body size for individuals in heavily exploited sex changing stocks. Our game theoretic approach to evaluating hermaphroditic stocks can accommodate a wide variety of sex changing cues and behaviors and allows a flexible model for understanding the effects of exploitation on hermaphroditic stocks.

Keywords: fisheries, exploitation, hermaphroditism, protogyny, game theory, black sea bass

1. Introduction

The ability to change sex (hermaphroditism) has been widely documented in teleost fish, having been confirmed in 48 families from thirteen orders including many recreationally and commercially important species (Sadovy de Mitcheson and Liu 2008; Erisman and Hastings 2011). While hermaphroditism is common knowledge among fisheries managers, and some managers collect data specific to such species (i.e. sex ratio), most assessments of hermaphroditic stocks are conducted using the same methods as non-sex changing fish (Alonzo et al. 2008). The failure to tailor assessments to the biology of hermaphroditic stocks may lead to poor estimates of biological points of reference (e.g. spawning biomass), or of the effects of exploitation on the stock, perhaps leading to collapse (e.g. Armsworth 2001; Alonzo and Mangel 2004; Heppell et al. 2006; Alonzo et al 2008, Brooks et al. 2008). A common theme amongst existing research is that the specifics of when and why an individual changes sex are critical to achieving sustainability in the fishery (Alonzo and Mangel 2005). Here we develop an evolutionary game theory model that depicts the sex-changing behavior of a protogynous hermaphrodite (changing from female to male), which we then we embed within a standard fisheries yield model. Game theory allows us to incorporate size relative to the population, sex ratio, and male/male competition into the decision of whether or not to change sex for black sea bass (Centropristis striata). We then evaluate how these factors influence estimates of fisheries yield, and compare these estimates to those of an otherwise identical gonochoristic population.

In many studies on the effects of fishing on protogynous populations, it is assumed that a female will change sex at a given age or size (Alonzo and Mangel 2004) or that a female will change sex at an age proportional to the average age/size of the population (Armsworth 2001). Given these assumptions, in a size-selective fishery the sex ratio becomes highly female biased and the population suffers from sperm limitation. These effects may lead to rapid population declines in the face of fishery-induced mortality, and eventual collapse (Armsworth 2001; Alonzo and Mangel 2004). However, species that show plasticity in the timing of their sex change are as resilient to fishing as non-sex changing stocks (Alonzo and Mangel 2005; Molloy et al 2007, Ben Miled et al 2010). This resiliency is driven by the ability of the stock to compensate for selective loss of one sex by the other sex transitioning at an earlier age or size than in the absence of fishing. Even when sex ratios become highly female biased due to size-selective harvest of males, the stock can still maintain resiliency if the fertilization rate remains high (Brooks et al. 2008). Together these results strongly suggest that managers cannot derive simple sustainable harvest rules for all hermaphroditic fish; in short, the details matter.

We gain some insight into these details from reviewing the evolutionary theory behind sex changing populations. A primary prediction is that a hermaphroditic species will change sex at a size where the reproductive rate of the first sex equals that of the second sex (Warner 1975). This, however, is not the case for many wild populations of hermaphrodites, as many will change sex earlier than predicted under the size-advantage theoretical model, suggesting factors other than size play a role in triggering sex change (Kazancioğlu and Alonzo 2010; Rogers and Koch 2011). From empirical tests of sexchange theory, we know that sex change in hermaphroditic fish will depend on a combination of social as well as endogenous cues (Werner and Swearer 1991; Alonzo and Mangel 2005; Benton and Berlinsky 2006). For example, Sakai et al. (2002) showed that large females of the protogynous wrasse, *Halichoeres melanuurs*, exhibited male sexual behavior immediately after male removal and became functionally male within 2-3 weeks of removal. However, when the largest female was relatively small, she was less likely to perform the male role. Reluctance to perform the male role at smaller body size is presumed to be due to strong female mate choice for larger males and male/male competition (Sakai 2002). The existing body of research on this topic thus suggests that sex change is driven by a combination of exogenous (e.g., social) and endogenous (e.g., body size) cues. In terms of what this means for harvesting such species, models that evaluate the sustainability of these fisheries must be flexible enough to capture the complexities of each species' sex change 'rules' (Alonzo and Mangel 2005).

Evolutionary game theory provides a modeling framework by which complex cues of sex change can be represented. Game theory has been used to study hermaphroditic life histories in fishes and many have shown the conditions under which sex change is expected to evolve, and the timing of sex change in such species (Charnov 1982; Kazancioğlu and Alonzo 2009, Ben Miled 2010). Game theory is a logical way to represent the life histories of hermaphroditic species in that it explicitly organizes how costs and benefits to changing sex trade-off against one another to produce net payoffs to the individual. Although other authors have generated model structures that capture these dynamics to a greater or lesser extent (e.g., Alonzo and Mangel 2005, Molloy et al. 2007), here we formalize its use within a fisheries yield model. We use black sea bass (*Centropristis striata*) as an illustrative example of its usefulness in terms of the insights it can produce relative to the mechanisms that produce resiliency of the fishery to harvest, and the assessments points needed to adequately understand when over-fishing is occurring.

Our approach considers female size relative to the sizes of other fish in the population, the number of individuals at each size in the population, and male/male competition, although other elements of sex change can be incorporated. For example, many species may have endogenous cues that trigger sex change (e.g. Alonzo et al. 2004; Heppell et al. 2006), and while our example considers only exogenous cues, endogenous ones could be easily incorporated into the game theoretic framework. Our framework also allows each parameter to be modified or tested over a range of values if the data for a specific species is not available, or if one wishes to weight parameters differently. The flexibility inherent in our model may prove very beneficial for species in regions where fishing is very important, yet where managers lack the resources to perform formal stock assessments. For our implementation of the model, our inputs allow a female sea bass to determine her size relative to the largest in the population, how many individuals at each size exist in the population, and how she would fare in the male/male competition should she enter it. Also, by adding the fertilization rate to the male/male competition component of the model, we are able to determine how the decision to remain female or become male changes with varying values of k in the fertilization rate; where k is a proxy for the importance of males to the reproductive output of a population. At high values of k, a population can maintain its fertilization rate when there are few males in the population. At low values of k, losing one male can have detrimental effects on the reproductive output of a population. We determine the maximum sustainable yield (MSY), Biomass at F_{MSY} (B_{MSY}), number of males in the population, number of females changing sex, and average age at sex change. We evaluate the performance of a sea bass

population across a variety of exploitation rates (U) and fertilization rates (Brooks et al 2008). We then compared these to a non-sex changing stock under the same conditions.

2. Methods

Using data collected on black sea bass (Provost 2013), we first built an age and sex-based population projection model for a non-sex changing population. The model included age-specific natural mortality (M), age and sex-specific exploitation rates (U), and sex-ratio dependent recruitment (R). Individuals in age-class 2 and above were considered mature. Age-specific natural mortality was estimated as

$$\mathbf{M} = \mathbf{q}(age^c) \tag{1}$$

Each age-specific mortality value was used to create the mortality vector (M) for ageclasses 1-10. Exploitation rates for each age class were estimated from mark-recapture data collected by Provost (2013) and used to create the maximum exploitation vector for age classes 1-10 for both males (U_y) and females (U_x). In order to calculate R, egg production (E) was determined by,

$$E = \frac{\alpha F_m}{\beta + F_m} \tag{2}$$

where α is the maximum number of eggs produced by the population, F_m is the number of mature females in the population, and β is the value for F_m when $E = \frac{\alpha}{2}$.

Fertilization rate (f) was modified from Brooks (2008) so that

$$f = \frac{4km}{(1-k)+(5k-1)m}$$
(3)

where m is the proportion of mature males in the population and k is a steepness parameter which can range from 0.2 to 1.0. High values of k imply that a stock can maintain its fertilization rate when males are scarce (Brooks 2008). Recruitment (R) is then calculated as:

$$R = EfS_e \tag{4}$$

where S_e is the probability of an egg surviving to hatch. The recruits are added to the first age-class of the female population vector (**X**) with probability (p_x) or male population vector (**Y**) with probability (p_y). The two sex population vectors are added together to create the total population vector (**N**). Individuals that die from natural mortality (**NM**) or fishing mortality (**XU**_x + **YU**_y) are then removed from the population so that:

$$N_{t+1} = N_t - N_t M - X_t U_x - Y_t U_y$$
⁽⁵⁾

We started with 100,000 individuals in the population and ran the model under no fishing mortality until the population stabilized. The resulting stable age and sex distributions were used as the initial age and sex distributions for the model under fishing pressure. The model was run with mortality rates of 0.75^*M , M, and 1.25^*M , however, our results did not vary across these levels of natural mortality; all results presented are for models run where **M** is the natural mortality. We then calculated MSY, B_{MSY} , and male/female ratios for the population across varying values of k. U was modified in 5% increments to test MSY, B_{MSY} , and male/female ratios for the population at different

levels of exploitation; i.e. we tested each population at 0.05xU, 0.1xU, and so on. For B_{MSY} , Biomass was calculated using the allometric relationship

$$w_a = v_1 l_a^{\nu_2} \tag{6}$$

where w_a is weight at age a and l_a is length at age a and v_1 and v_2 are species specific parameters. Length at age was modeled via the von Bertalanffy (1938) equation

$$l_a = L_{\infty} (1 - e^{-K(a - t_0)}) \tag{7}$$

Parameters were estimated from data collected for black sea bass (Provost 2013). All parameter values used to initialize the model can be found in Table 1.

We then calculated MSY, B_{MSY} , and male/female ratios for a protogynous stock using the same population model described above, but also allowing females to change sex according to a game theoretic, locally greedy goal. We computed a 'Gain matrix' in our game theory model for the expectation of reproduction at a given size, limited by *E*. This value represented the highest reproductive value that could be achieved by an individual female in a given age class. We then also defined a 'Loss matrix', which described how to modify the 'Gain matrix' by fertilization rate and the relative abundance of each sex at each size. Male/male competition is included in this matrix as the ratio of an individual's current size to a weighted average of the size of all other males, modified by *f*. The 'Payoff matrix' is therefore the 'Loss matrix' subtracted from the 'Gain matrix.' This value is the actual expected reproduction for an individual of a given size and can only change as the 'Loss matrix' changes. If a female's loss from becoming male is less than the loss from remaining female, then and only then will she change sex. We then removed those individuals that changed sex from the female population vector and added them to the male population vector. This allowed us to calculate the average age at which the protogynous population was expected to change sex across varying fishing pressures and values of k. By considering many values of k, we can test the effects of fishing at various levels of male/male competition and across many fertilization rates. We then compared MSY, B_{MSY} , and male/female ratios for the non-sex changing and sex changing stocks.

3. Results

We started the population at 100,000 individuals at a stable age and sex distribution and ran each model under varying values of exploitation and *k* for 20 years. The following results represent a comparison of MSY, B_{MSY} , and proportion of males in the population for non-sex changing and sex changing stocks at the 20th year. Non-sex changing stocks produced a slightly higher MSY for all values of *k* (Table 2; Figure 1). MSY for the non-sex changing (MSY(G)) stock ranged from 9404 to 75,970 while MSY for the sex changing (MSY(P)) stocks ranged from 8786 to 75,388 (Table 2). Each stock produced the lowest MSY when *k*=0.2 and the highest MSY when *k*=1. The highest difference (as a percent) in MSY was at *k*=0.2 where the difference was 7%. The lowest difference (as a percent) was at *k*=0.5 where the difference was 0.02% (Table 2).

Sex changing stocks produced a higher B_{MSY} ($B_{MSY}(P)$) across all values for k, and ranged from 367 to 28,400 (x1000 kg) and the B_{MSY} for the non-sex changing stock ($B_{MSY}(G)$) ranged from 36,45 to 27,817 (x1000 kg) (Table 2; Figure 1). The smallest B_{MSY} for each stock was when k=0.2 and the largest B_{MSY} was when k=1. The greatest difference in B_{MSY} was when k=0.4 where the difference (as a percent) was 5.7% (Figure 2). B_{MSY} at k=0.4 were the most different with the gap narrowing as k changed from that point in either direction. The smallest difference in the populations was when k=0.2 where the difference was 0.74% (Table 2). While B_{MSY} was still higher for sex changing population, there was a steep decline in the difference in B_{MSY} between k=0.4 and k=0.2 (Figure 2). This is likely due to the sex changing population not being able to compensate for the loss of males as well when k is very low (i.e. where males matter the most).

The higher B_{MSY} , despite lower MSY, for the sex changing population reflects the higher proportion of males in that population than in the non-sex changing population (Figure 3). The sex changing population had a higher proportion of males in the population for all values of *k* and *U* (Figure 3). The difference in the proportion of males in the population increased with an increase in exploitation and a decrease in *k*. The number of females that changed sex in the sex changing population decreased as *k* increased, reflecting the relative importance of males to the fertilization rate as *k* decreases (Figure 4). For low *k* values, more males are required to maintain the fertilization rate, thus females changed sex at twice the rate for the lowest value of *k* than they did at the highest (Figure 4). The age at sex change decreased as the exploitation rate increased, reflecting the population's flexibility in the timing of sex change in order to compensate for the loss of large males. At low values of *k*, the average age at sex change in our study decreased more rapidly as exploitation increased than it did for higher values of *k* (Figure 5).

4. Discussion

Exploitation of hermaphroditic fish populations is common worldwide, and these species make up a large proportion of the fisheries serving poorer nation-states (e.g., Carribean; Chiappone et al. 2000; Caballero-Arango et al. 2013). Such fisheries are prone to overfishing in part due to data scarcity, and the lack of species-specific catch and effort regulations (Chiappone et al. 2000). Methods exist to evaluate the population status of data-poor species (Bednarek et al. 2011), however standard fisheries models cannot account for the effects of sex change in their results. Existing fisheries models suggest that there cannot be a one-size-fits-all model to evaluating the sustainable harvest of sexchanging species (Alonzo and Mangel 2005; Heppell et al. 2006; Molloy et al. 2007), which places a heavier burden on managers working to conserve such species in that they are required to customize models for each situation. We developed game theoretic methods to modeling sustainable yield as a way to flexibly incorporate species' life histories, and illustrated the insights such a model can provide using black sea bass. This approach is very beneficial when considering data-poor species such as the protogynous tiger grouper (*Mycteroperca* tigris) where the species is heavily exploited, yet even basic reproductive biology is not well known (Caballero-Arango et al. 2013).

Our results suggest that black sea bass stock yielded a slightly lower maximum sustainable yield (MSY) but a higher biomass than an otherwise identical non-sex changing stock. This higher biomass at MSY for the sex changing stock is due to the higher numbers of male fish in the population, as male black sea bass are larger than females of the same age (Provost 2013). As males were fished out of the population, the sex changing female stock was able to replace them. The sex changing stock replaced males more readily when maintaining the fertilization rate required more males in the population (low k). Sea bass did not replace individuals lost to harvest nearly as quickly when $k \ge 0.5$. This finding, along with those of Brooks et al. (2008), illustrates the importance of understanding how much males contribute to reproductive success for a population of concern. We showed that a protogynous population with low values for k would decrease its age-at-change more rapidly than those with higher values for k. This result suggests exploitation will affect stocks with a lower value for k more drastically that those with a high value.

Fertilization rate and the importance of males in this rate (k) can be difficult to measure, particularly for data poor species. However it is essential to understanding population dynamics and the effects of fishing on protogynous species. Even if it cannot be directly measured, these parameters may be inferred from the reproductive behavior of a species. One would assume species that spawn in large groups would have relatively high values of k because losing one male will not be very detrimental to the population (Brooks et al. 2008). One would also assume that species that spawn in pairs would have a very low value for k because losing a male could have detrimental effects on the population's fertilization rate. This has been shown in the protogynous reef fish Thalassoma bifasciatum, which has two distinct mating systems; group mating and paired mating. Marconato et al. (1997) determined that the fertilization rates for the portion of the population that used group spawning were much higher than for those mating in pairs. This result suggests that losing a male from the group-spawning portion of the population would not be nearly as detrimental to the entire population as losing one of the paired males. Our results reflect this. For high values of k, we observed the lowest amount of

sex change and for the lowest values of k we observed the highest amount of sex change. Understanding the breeding behavior of a protogynous species will allow researchers to estimate k and better understand the impacts of fishing on the fertilization rate and on the stock as a whole.

Increased exploitation increased the difference in male proportion of the population between non-sex changing and sex changing stocks, and decreased the average age at sex change for the sex changing stock. This result is due to the compensatory mechanism of flexible timing at sex change. For species with a fixed ageat-change, the proportion of males drastically declines with an increase in exploitation (Alonzo and Mangel 2004; Heppell et al. 2006). For species with plasticity in their age-at change, populations may remain relatively stable under higher rates of exploitation (Alonzo and Mangel 2005). While adjusting the age at which the stock can change sex can compensate for lost males, it does create a situation where the average size of the population decreases with an increase in exploitation. It has been shown for protogynous stocks that populations under heavy fishing pressure may have similar sex ratios to those stocks of the same species under lighter fishing pressure (Götz et al. 2008). However, these studies have also shown that stocks under heavier fishing pressure have a smaller average body size and a smaller size-at-change than those under lighter fishing pressure (Hamilton et al. 2007; Götz et al. 2008). The findings of these studies are reflected in our results as well. While the sex ratio for our sex changing stock remained fairly constant across varying rates of exploitation, the age-at-change decreased drastically. If stock assessments were to collect data on the age or size-at-change for sex changing stocks, it could alert managers to fishing rates that may be dangerously high. Many collect data on

sex ratio, few collect data on age-at-change (Provost 2013). While sex ratio can allow managers to detect problems in non-sex changing populations or sex changing populations with a fixed age-at-change, it is not as helpful for sex changing stocks with flexible age-at-change.

Our game theoretic approach accommodates stocks with fixed age-at-change and/or stocks that cue on exogenous factors before changing sex. Our implementation here included competition as a function of the size relative to the population and weighted by the number of individuals in each size class. Some models considering exogenous cues for sex changing fish have simply assumed that a fish will change sex when it reaches a given size relative to the largest in the population (e.g. Mollov et al. 2007). Other models have included expected reproductive output as a cue for sex change, however, they limited their findings to a single species-specific case (e.g., Alonzo and Mangel 2005). While these assumptions may hold true for some species, such a case-bycase approach to examining the effects of exploitation on sex changing fish would not be of broad use. If the assumptions above were true for a species of concern, our game theoretic framework would accommodate that assumption by simply adjusting the 'Loss' matrix' to fit the assumptions. This framework also provides an opportunity to determine the effects of exploitation on the assumptions themselves. The results of our approach are similar to those produced by more species-specific models in that they both predict that sex changing stocks that use exogenous cues are as robust to exploitation as non-sex changing stocks. Our results also predicted that stocks of sex changing fish, while maintaining similar sex ratios, tend to have smaller individuals and smaller size-atchange. This matches the empirical results observed for sex changing stocks (Hamilton et al. 2007; Götz et al. 2008). Having such a flexible, non-species specific model to examine the effects of fishing will be vital to managing sex changing species.

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Figure 1. Biomass yield (a-c) and total yield in numbers of fish (d-f) at varying exploitation rates (U) for k=0.3 (a & d), k=0.5 (b & e), and k=0.9 (c &f). The solid line represents the values for the sex changing stock and the dashed line represents values for the non-sex changing stock in all graphs.

Figure 2. Difference in B_{MSY} as a percent of the total difference between B_{MSY} for a sexchaning stock and B_{MSY} for the non-sex changing stock at varying values of *k*.

Figure 3. Difference in the proportion of males in the population of the sex changing stock and the non-sex changing stock at varying exploitation rates (U). The solid line is for values when k=0.3, the dashed line represents values when k=0.5, and the dotted line represents values when k=0.9.

Figure 4. The percentage of females that changed sex in the sex changing population at varying values of k, calculated as the number of females that change sex divided by the number of mature females.

Figure 5. The average age at sex change for the sex changing stock at varying rates of exploitation (U). The solid line is for values when k=0.3, the dashed line represents values when k=0.5, and the dotted line represents values when k=0.9.

Parameter	Parameter value	Source and definition
Mortality	i arameter value	
a	0 694	Parameter for Lorenzen model(NESC 2012)
q	[0.5, 1, 2, 1, 0]	A go of individual fish
age	[0.3, 1, 210]	
c	-0.41/	Parameter for Lorenzen model(NFSC 2012)
Exploitation		
$\boldsymbol{U}_{\boldsymbol{y}}$	[0, 0.42, 0.54, 0.63, 0.63, 0.63,	Maximum exploitation of females. Estimated from mark
-	0.63, 0.63, 0.63, 0.63]	recapture data on black sea bass (Provost 2013).
Ur	[0, 0.42, 0.11, 0.28, 1, 1, 1, 1, 1, 1,	Maximum exploitation of males. Estimated from mark
x	1.]	recapture data on black sea bass (Provost 2013).
Recruitment	2	
<i>α</i>	2 800 000	Maximum number of eggs that can be produced by the
U.	2,000,000	nomilation
0	50 000	Number of moture females required to produce helf of the
р	30,000	multiple of mature remains required to produce that of the
	48,040	maximum number of eggs.
F_m	48,040	Number of mature females.
k	[0.2, 0.31.0]	Steepness parameter for fertilization rate (Brooks et al. 2008)
т	0.34	Proportion of mature males in the population.
S_e	0.05	Survival of eggs.
Biomass		
\mathcal{V}_{I}	0.0649	Species specific parameter for estimating weight at age.
1		(Froese and Pauly 2012)
Va	2 468	Species specific parameter for estimating weight at age
<i>v</i> ₂	2.400	(Frages and Pauly 2012)
		(Floese and Fauly 2012)

Table 1. Parameter values used in the model and for equations 1-6.

k	$B_{MSY}\left(G\right)\left(x\ 1000\ kg\right)$	B _{MSY} (P) (x 1000 kg)	MSY (G)	MSY (P)	
0.2	3645	3672	9404	8786	-
0.3	8554	8988	22,666	22,317	
0.4	12,573	13,287	33,780	33,664	
0.5	15,957	16,818	43,092	43,082	
0.6	18,906	19,806	51,414	51,212	
0.7	21,542	22,378	58,685	58,433	
0.8	23,873	24,619	65,109	64,768	
0.9	25,951	26,540	70,833	70,379	
1	27, 817	28,401	75,970	75,388	

Table 2. B_{MSY} and MSY for gonochoristic (G) and protogynous (P) stocks at varying values of k.



Figure 1.



Figure 2.



Figure 3.



Figure 4.



Figure 5.

CONCLUDING REMARKS

The overarching goal of the research presented in this dissertation was to examine how simple modifications to mathematical models that are widely used in a conservation context can be used to aid management of complex conservation situations. Managing species involves spending considerable monetary and political capital, and management decisions should be based on accurate and accessible models. Here I have shown novel ways that foundational models in ecology (matrix population models and functional response), conservation (population viability analysis) and evolutionary biology (game theory) can be used to aid decision making for complex conservation problems.

In chapter 1, I showed that combining two matrix-based population viability analysis (PVA) models with a functional response provides suggestions for managing invasive/problem predators. I show that, in a conservation situation where predators are being managed for the sake of their prey, that my approach disagrees with a standard PVA, which suggests management on how to reduce the predator population. My coupled predator-prey model provides a flexible yet comprehensive approach to exploring a range of management actions designed to benefit native prey species. The results show that the need for such a model is real, and can potentially save managers (and stakeholders) considerable monetary and social capital by more effectively identifying the most efficient management options given the situation.

In the second chapter, I show how a simple addition to standard PVA models can determine the probability of a management action accomplishing its conservation goal. This addition explicitly recognizes that real-life management is a one-shot occurrence, and thus it is more appropriate to visualize the outcome of management actions as probabilities and not as simple changes in mean values or shifts in distributions. This method is as simple as counting, on a rub-by-run basis, the result of the PVA model. This method is not meant to supplant PVA models, only to enhance them. This approach to evaluating the outcome of PVAs can improve the use of PVA models and provide greater insight into what is driving their results. My hope is that this simple extra step will be used in future decision making based on PVA.

In chapter 3, I used game theory to model the sex changing behavior of a hermaphroditic fish, and evaluated the effects of fishing. I showed that a hermaphroditic fish with a flexible age or size at sex change can be as robust to fishing as a non-sex changing species. I also showed that, while the sex ratio can be well maintained by a sex changing stock under heavy fishing pressure, the average size of the population decreases with increased fishing pressure. I also showed that understanding the breeding biology of hermaphroditic species is vital to understanding the effects of exploitation on them. At low values of k (parameter in the fertilization rate), size at change decreased more rapidly than for high values. The number of fish changing sex was twice as high for low values of k than for the highest value. Having such a flexible, non-species specific model to examine the effects of fishing will be vital to managing sex changing species. Hopefully, this work will show the importance of keeping track of age-at-change and other measures of health for sex changing stocks when making formal stock assessments.