



Setting Realistic Recovery Targets for Two Interacting Endangered Species, Sea Otter and Northern Abalone

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Abstract: Failure to account for interactions between endangered species may lead to unexpected population dynamics, inefficient management strategies, waste of scarce resources, and, at worst, increased extinction risk. The importance of species interactions is undisputed, yet recovery targets generally do not account for such interactions. This shortcoming is a consequence of species-centered legislation, but also of uncertainty surrounding the dynamics of species interactions and the complexity of modeling such interactions. The northern sea otter (*Enhydra lutris kenyoni*) and one of its preferred prey, northern abalone (*Haliotis kamtschatkana*), are endangered species for which recovery strategies have been developed without consideration of their strong predator–prey interactions. Using simulation-based optimization procedures from artificial intelligence, namely reinforcement learning and stochastic dynamic programming, we combined sea otter and northern abalone population models with functional-response models and examined how different management actions affect population dynamics and the likelihood of achieving recovery targets for each species through time. Recovery targets for these interacting species were difficult to achieve simultaneously in the absence of management. Although sea otters were predicted to recover, achieving abalone recovery targets failed even when threats to abalone such as predation and poaching were reduced. A management strategy entailing a 50% reduction in the poaching of northern abalone was a minimum requirement to reach short-term recovery goals for northern abalone when sea otters were present. Removing sea otters had a marginally positive effect on the abalone population but only when we assumed a functional response with strong predation pressure. Our optimization method could be applied more generally to any interacting threatened or invasive species for which there are multiple conservation objectives.

Keywords: *Enhydra lutris*, *Haliotis kamtschatkana*, predator–prey relations, reinforcement learning, species interaction, stochastic dynamic programming

Definición de Metas de Recuperación Realistas para Dos Especies en Peligro Interactuantes, *Enhydra lutris* y *Haliotis kamtschatkana*

Resumen: La falta de considerar las interacciones entre especies en peligro puede llevar a dinámicas poblacionales inesperadas, estrategias de manejo ineficientes, despilfarro de recursos escasos, y, peor aun, incremento en el riesgo de extinción. La importancia de las interacciones de especies no está en disputa, sin embargo los objetivos de recuperación generalmente no toman en cuenta a dichas interacciones. Este problema es una consecuencia de la legislación centrada en especies, pero también de la incertidumbre que rodea a dinámica de las interacciones de especies y la complejidad para modelar esas interacciones. La nutria marina (*Enhydra lutris kenyoni*) y una de sus presas preferidas, el abulón (*Haliotis kamtschatkana*), son especies en peligro para las que se han desarrollado estrategias de recuperación sin considerar sus estrechas interacciones depredador-presa. Utilizando procedimientos de optimización basados en simulaciones de inteligencia artificial, específicamente aprendizaje por reforzamiento y programación dinámica estocástica, combinamos modelos poblacionales de nutria y abulón con modelos de respuesta funcional y examinamos como afectan diferentes acciones de manejo a la dinámica de la población y la probabilidad de alcanzar

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las metas de recuperación de cada especie en el tiempo. Fue difícil alcanzar las metas de recuperación para estas especies interactuantes en la ausencia de manejo. Aunque se pronosticó que la población de nutrias se recuperaría, el logro de las metas de recuperación de abulón falló no obstante que las amenazas, como la depredación y captura furtiva, fueron reducidas. Una estrategia de manejo que conlleve una reducción de 50% en la captura furtiva de abulón fue el requisito mínimo para alcanzar metas de recuperación de abulón a corto plazo cuando había presencia de nutrias. La remoción de nutrias tuvo un efecto positivo marginal sobre la población de abulón pero solo cuando asumimos una respuesta funcional con fuerte presión de depredación. Nuestro método de optimización pudiera ser aplicado más generalmente a cualquier especie amenazada o invasora interactuante para la cual se hayan fijado múltiples objetivos de conservación.

Palabras Clave: Aprendizaje por reforzamiento, interacción de especies, *Enhydra lutris*, *Haliotis kamtschatkana*, programación dinámica estocástica, relaciones depredador-presa

Introduction

Whenever population dynamics of one species are affected by those of another, setting recovery targets is a challenge. The importance of species interactions in shaping ecological communities is undisputed (Soulé et al. 2005), yet listings and recovery activities under endangered species legislation continue to focus on individual species, even when they are known to interact strongly with other species (Clark & Harvey 2002). When listing of multiple species has occurred, it has been on the basis of shared habitat requirements rather than species interactions (e.g., Garry oak [*Quercus garryana*] ecosystems in Canada [Parks Canada Agency 2006]). Failing to account for strong interspecific interactions may lead to biased estimates of viability (Sabo 2008), the setting of unachievable targets, and inefficient use of conservation resources. Using decision theory and methods from artificial intelligence (Sutton & Barto 1998), we addressed allocation of conservation effort over time and under uncertainty to recover 2 interacting species simultaneously.

Applications of decision theory to solve complex environmental problems feature prioritization of regions with high biodiversity (Wilson et al. 2006), conservation of migratory species (Martin et al. 2007), and management of single endangered (Chadès et al. 2008; Chadès et al. 2011) and non-native invasive species (Firn et al. 2008; Regan et al. 2011). None, however, model interspecific interactions or examine how these interactions influence the effectiveness of optimal management scenarios. We used simulation-based optimization methods (Sutton & Barto 1998) to assess the feasibility of achieving recovery targets of 2 interacting species, the northern subspecies of sea otter (*Enhydra lutris kenyoni*) and one of its prey, northern abalone (*Haliotis kamtschatkana*). Both species are endangered (IUCN 2010) and included on Schedule 1 of Canada's Species at Risk Act. The sea otter is also listed as threatened under the U.S. Endangered Species Act.

Historically, distributions of sea otters and northern abalone overlapped in coastal habitats from Alaska (U.S.A.) to Baja California (Mexico) (Estes & VanBlaricom

1985). Sea otters eat a variety of prey (Tinker et al. 2006; Tinker et al. 2008); however, for some sea otters, abalone is a primary prey item (Costa 1978; Watson 2000; Tinker et al. 2007). Commercial hunting of sea otters until 1911 reduced their once-extensive distribution to isolated populations in Alaska (Kenyon 1969; Rotterman & Simon-Jackson 1988). Sea otter extirpation throughout most of its historic range likely led to dramatic changes in ecosystem structure (Estes & VanBlaricom 1985) and prey population dynamics and behavior (Watson 2000), including increased abundance of abalone and other shellfish. This in turn allowed the development of fisheries, including a commercial fishery for northern abalone (Estes & VanBlaricom 1985; Jubinville 2000). Commercial harvests of northern abalone in Canada began in the early 1900s and catches peaked in 1978. Between 1977 and 2002, the mean total northern abalone density at reference sites declined from 2.4 to 0.27 abalone/m² along British Columbia's central coast and from 2.2 to 0.34 abalone/m² in Haida Gwaii (Fisheries and Oceans Canada 2007). The fishery was closed in 1990 to promote recovery (Jubinville 2000). Despite the fishery closure and listing under SARA, northern abalone densities have continued to decline (Lessard et al. 2007). Illegal poaching is regarded as the key reason for the continued decline (Gardner et al. 2000; Jubinville 2000), but predation by expanding sea otter populations (Nichol 2007) is also regarded as a contributing factor.

Since sea otter reintroductions to coastal British Columbia and Washington in the 1960s and 1970s, annual population growth rates have ranged from 11% to 19%, the biological maximum (Estes 1990; Nichol 2007). At current rates of population growth and dispersal, sea otters will likely reoccupy all former parts of their range and exert renewed effects on prey dynamics. Despite this range expansion, the basis for reference points used to develop recovery targets for northern abalone is the historical abalone abundance data collected in the absence of sea otters (Sloan & Breen 1988). The densities at which northern abalone and sea otters coexisted before sea otter extirpations and the degree to which populations fluctuated naturally are debated (Fisheries and Oceans Canada 2007). Therefore, the feasibility of

achieving current abalone recovery targets in the presence of sea otter is unknown.

In the case of northern abalone, the immediate recovery goal in Canada is to halt the decline of existing populations (Fisheries and Oceans Canada 2007). The longer-term recovery goal is to increase the number and density of northern abalone to levels that are self-sustaining in Haida Gwaii, Queen Charlotte and Johnstone Straits, north and central coasts of British Columbia, Georgia Basin, and west coast of Vancouver Island. The 5-year recovery targets against which northern abalone recovery is assessed are to achieve mean densities of large adult (shell length >100 mm) northern abalone of $\geq 0.1/\text{m}^2$ at surveyed index sites in Haida Gwaii and north and central coasts of British Columbia and the presence of large adults at $\geq 40\%$ of surveyed index sites; ensure mean adult densities at newly established index sites in Queen Charlotte and Johnstone Straits do not decline below 0.06 and 0.02 abalone/ m^2 , respectively; and ensure mean adult densities along the west coast of Vancouver Island do not decline below 0.09 abalone/ m^2 (Fisheries and Oceans Canada 2007). No quantitative recovery targets have been articulated for sea otters. Rather, the recovery goal for sea otters in Canada is to sustain population growth and geographic range expansion. To achieve this, the management objective is to identify and, where possible, mitigate threats (e.g., oil spills) to sea otters and their habitat (Sea Otter Recovery Team 2007).

Separate recovery strategies have been prepared for sea otters (Nichol 2007) and northern abalone (Lessard et al. 2007) under SARA, although conflicts between recovery goals for both species are recognized (Gardner et al. 2000; Watson 2000; Gerber et al. 2004). Recovery teams for both species acknowledge that meeting recovery targets for northern abalone could require control of sea otter abundance (Gardner et al. 2000; Sea Otter Recovery Team 2007). Although the key management action under consideration by the northern abalone recovery team is enforcing regulations against abalone poaching, sea otter control and abalone population enhancement are also being considered. We sought to determine the abundances at which these 2 species are likely to coexist under various management scenarios.

Methods

To determine whether recovery targets for sea otter and northern abalone are achievable simultaneously, we built a stochastic population model for each species; specified hypothetical functional relations between the species; identified the actions that could be applied to achieve recovery targets; specified a reward function based on defined recovery targets; simulated the relation between the interacting population models and management actions

to identify the optimal recovery strategy; and performed sensitivity analyses on all major model assumptions.

Stochastic Population Models

We modeled the sea otter population of the Pacific Rim National Park (PRNP) (west coast of Vancouver Island) following Gerber et al.'s (2004) model of a sea otter population in neighboring Washington state, which suggested Beverton-Holt or Ricker models are appropriate. We used a stochastic Ricker model,

$$N_{t+1} = N_t e^{r(1 - \frac{N_t}{K})} - J_t(f, i)N_t, \quad (1)$$

where K is carrying capacity, N_t is population size at time t , and r is intrinsic growth rate. In the PRNP, Gregr et al. (2008) estimated the area of suitable sea otter habitat as 1036 km^2 and the carrying capacity as 4073 individuals. We used an intrinsic growth rate (r) of 0.191, which we based on observed rates of population growth following reintroduction of sea otters on the west coast of Vancouver Island (Nichol 2007). The stochastic term $J_t(f, i)N_t$ is sea otter mortality due to oil spills. Whereas sea otters are killed by predators such as killer whales (*Orcinus orca*), sharks (Selachimorpha), and Bald Eagles (*Haliaeetus leucocephalus*) (Estes et al. 1998), oil spills pose the single largest threat to sea otter populations (Ralls & Siniff 1990; Nichol 2007). In our sea otter population model, we used a stochastic process to simulate death by oil spills which occurred with a probability of 0.1 each year and oil-spill intensity varied uniformly from 0.23 to 0.42 and reduced the population of sea otters by 23–42% (spill parameters were based on observed oil spills in Washington state [Gerber et al. 2004]). Oil spills represented a catastrophic event that affects the sea otter population in British Columbia. Catastrophic events could also have been disease outbreak or toxic algal blooms, for example (Estes et al. 2003).

We assumed an initial population of 100 individuals, and the simulations of our sea otter model predicted a maximum expected census of 3251 otters (Supporting Information) in the PRNP.

We based a stage-structured matrix model for northern abalone on carapace lengths (8–135 mm) and density estimates collected from 2001 to 2002 during underwater visual surveys of index sites in southeast Haida Gwaii and the central coast of British Columbia (Zhang et al. 2007; Hankewich & Lessard 2008; Hankewich et al. 2008). Data were collected in areas where sea otters were largely absent; however, illegal and unreported harvest may have occurred in some survey sites. We modeled the density of males and females assuming an equal sex ratio (Breen & Adkins 1982; Sloan & Breen 1988) and no sex-specific differences in growth or survival (see Supporting Information for model details).

Poaching of abalone is a key threat to recovery of this species (Gardner et al. 2000; Jubinville 2000). Effectiveness of antipoaching measures increases as the amount of money spent on enforcement increases (Hilborn et al. 2006), but these measures are unlikely to ever be 100% effective. We assumed poaching occurs stochastically with a removal rate of 17–23% per year (Zhang et al. 2007). However, when abalone density reaches an arbitrary critical threshold (0.01 abalone/ m^2), we assumed poaching occurs only at a very low intensity (1%). This assumption simulates reduced fishing effort in depleted populations. In the absence of sea otter predation and illegal harvest, the simulation of our matrix population model predicted that northern abalone could reach their carrying capacity within 30 years. Under current estimates of illegal harvest and absence of predation the simulations predicted total density would decline to 0.15 abalone/ m^2 and adult density to $0.05/m^2$ over 100 years (Supporting Information).

Functional Responses

Despite decades of research on both species, there is little detailed information on how sea otters and abalone interact. Tinker et al. (2008) provide one of the few studies that include parameters on the feeding behaviors of sea otters and show that sea otters exhibit a range of feeding strategies from specialized to general, depending on the availability of prey. To account for the uncertainty surrounding the sea otters' feeding strategies, we modeled the interaction between sea otters and abalone with 3 common types of functional responses: linear, hyperbolic, and sigmoid (Holling 1959). We assessed how these predation behaviors may affect abalone density and potential optimal management strategies. Given uncertainty, we explored a range of functional responses that cover the possible species interactions. We based the underlying assumption used to derive our functional responses on the maximum number of abalone eaten per day per sea otter. We used the average energetic requirements of adult sea otters in California (12412 KJ/day [Yeates et al. 2007]) and the caloric content of abalone of size 11–15 cm (704 KJ [Yeates et al. 2007]) to derive the maximum number of prey eaten (P_{max}) of 18 abalone/day. It is possible that the caloric needs of sea otters in colder climates, such as our study region, are higher. This upper limit therefore represents a conservative value of the energy requirements of sea otters. Parameter P_{max} provides an upper bound for all the functional curves we propose (see Supporting Information for model details).

Conservation Objectives and Actions

The first step in evaluating the effectiveness of fixed management strategies and developing a procedure for optimizing management actions is to define conservation

objectives. We identified strategies that would maximize the abundance of both species over time. To achieve our conservation objectives with management strategies that are either fixed or vary over time, we considered 5 management actions: introduce sea otters, enforce abalone antipoaching measures, control sea otters, one-half antipoaching and one-half control sea otters (defined below), and do nothing. We considered the action introduce sea otters to determine whether waiting for the recovery of abalone before introducing sea otters helped achieve our recovery goal. Antipoaching efforts reduced illegal harvesting by 50% on average ($\sim U(0.43, 0.57)$) during the time they are implemented. We considered the direct removal of sea otters (Gardner et al. 2000), for example, through the reinstatement of First Nations' subsistence hunting. The action control sea otters removed the number of otters above 60% of their carrying capacity. We also considered the action one-half antipoaching and one-half control sea otters to assess whether taking these 2 actions simultaneously but at half the level of effectiveness would yield greater benefit than either one alone. Finally, we considered the option of doing nothing (i.e., no recovery actions taken for either species).

Optimization Model

To derive the best multispecies conservation strategy for abalone and sea otters, we designed a simulation model that incorporates the population dynamics of each species, their interaction, and how management decisions affect their abundance. We solved the corresponding Markov decision problems with 2 optimization procedures from artificial intelligence: reinforcement learning and value iteration, also known as a stochastic dynamic-programming procedure (Sutton & Barto 1998). Whereas reinforcement learning is suitable for time-delayed management problems, value iteration assumes management effects are immediate. In our case, both optimization procedures led to similar strategies, but the reinforcement-learning procedure took longer to converge to the solutions (see Supporting Information for modeling details and MATLAB code). The optimal strategies derived can be evaluated on the basis of their performance. We used the expected sum of rewards over a finite time horizon as a performance criterion of our optimization problem (see Supporting Information for definition of rewards).

For the initial state of our model, we assumed sea otters were absent from the system and the entire abalone population was at an average density of $0.21/m^2$ (Zhang et al. 2007). Alternative starting densities did not affect long-term management results. We examined the performance (e.g., expected sum of rewards and corresponding abalone density and sea otter abundance) of the optimal strategy versus 4 fixed strategies: abalone antipoaching measures only; antipoaching measures and removal of sea otters when 60% carrying capacity threshold is met; and

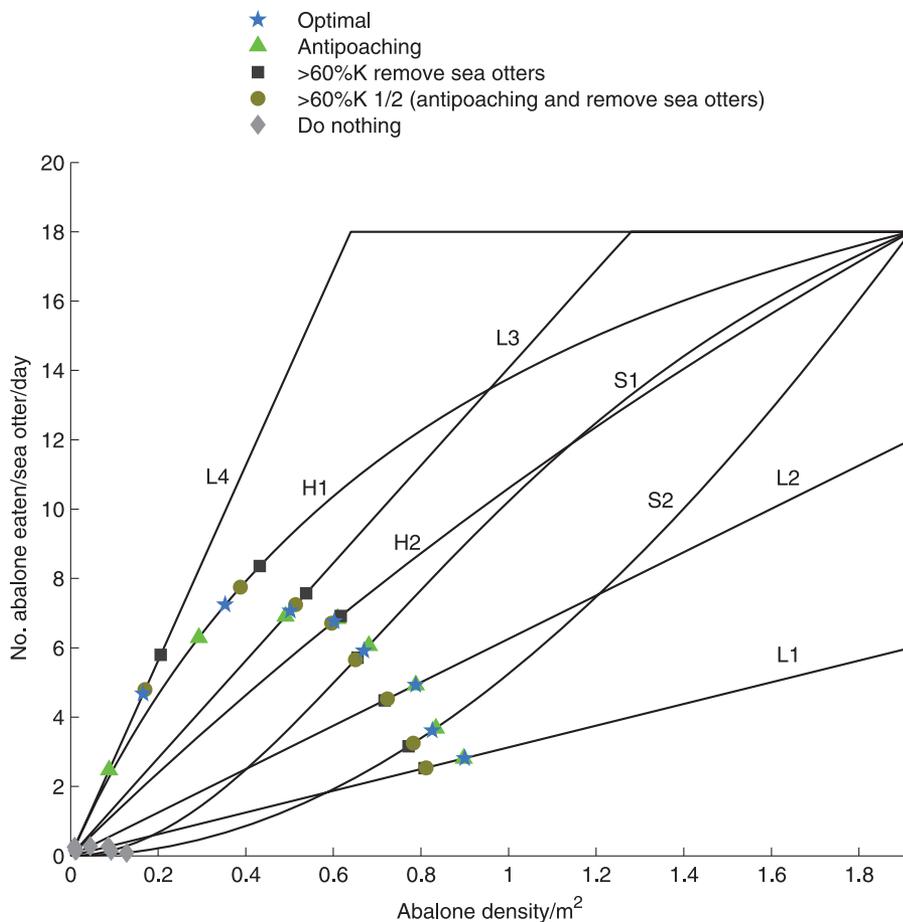


Figure 1. Simulation results of optimal and fixed strategies for different functional responses of sea otters to the density of their prey, northern abalone (K , carrying capacity). Symbols represent the expected density of northern abalone under alternative functional responses and management strategies.

half-efficiency antipoaching measures and removal of sea otters above the threshold; and do nothing. We simulated optimal strategies over 100 years to assess the dynamic of the system and the effect of management actions. We also ran sensitivity analyses on the carrying capacity and intrinsic growth rate of the abalone population model to determine the effect of these 2 parameters on our results.

Results

The sea otter population reached 75% of its carrying capacity with occurrence of oil spills in the absence of sea otter removal for all functional responses (Fig. 1). When sea otters were removed sea otter populations were maintained at 50–70% carrying capacity (Supporting Information). In the absence of management (i.e., do nothing), the density of abalone was predicted to decrease to 0.02–0.09 abalone/m² for the entire population and to 0.002–0.01 abalone/m² for adults only (Figs. 1 & 2 & Supporting Information). With management, the maximum density for adult abalone occurred with linear functional response (L1), under which it was assumed the lowest rate of predation by sea otters of all functional

responses, and the density of abalone reached 0.23 adult abalone/m² (Fig. 2a & Supporting Information). In contrast, under the highest predation pressure, hyperbolic H1 and linear L4, an adult density of 0.078 and 0.035, respectively, was predicted. Thus, under optimal management and in the presence of sea otters, the density of abalone was predicted to be between 0.035 and 0.23 adults/m².

For the entire abalone population, the best outcome was with the linear functional response: total population density of 0.9 abalone/m². Total abalone density gradually declined as the level of predation within the functional responses increased and was 0.35 abalone/m² for hyperbolic H1 and <0.17 for linear functional response L4, the lowest abalone density scenario (Fig. 2b). Although the optimal strategies always achieved a higher expected performance than the fixed strategies, taking any management action (fixed or optimal) was better than the do-nothing strategy irrespective of the assumed functional response (Figs. 1 & 2).

The optimal strategies computed for different functional responses had a similar structure. In the absence of sea otters and for any density of abalone, the first management action was to introduce sea otters. We found no benefit in waiting for the abalone population to recover

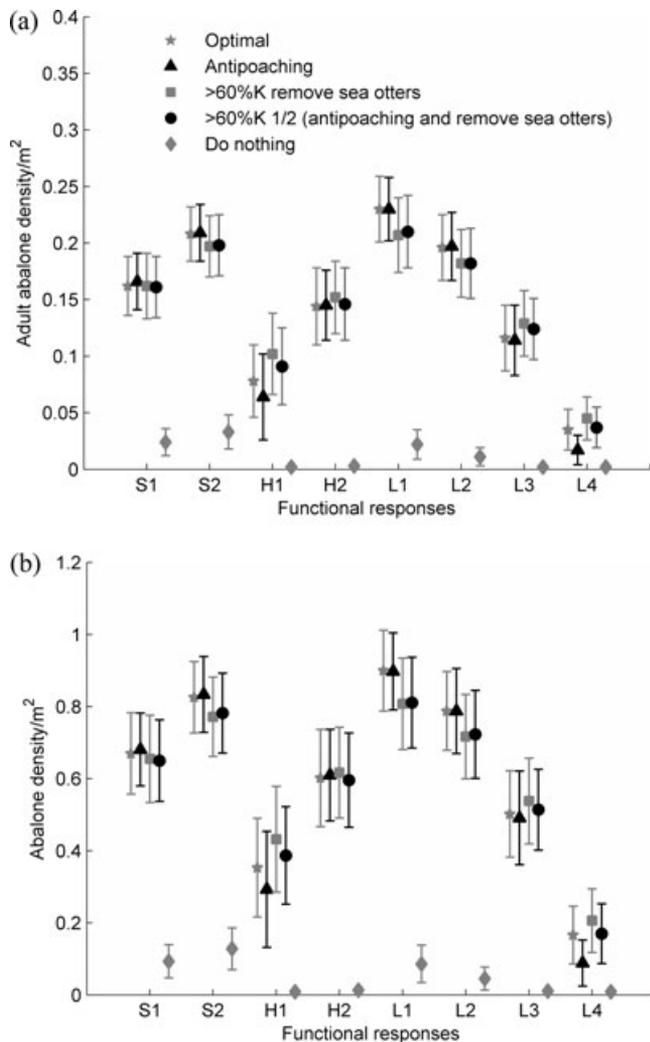


Figure 2. Abalone densities achieved for (a) the adult population only and (b) the entire population under optimal and fixed management strategies for sigmoid functional responses (S1, S2), hyperbolic functional responses (H1, H2), and linear functional responses (L1–L4) (also presented in Fig. 1) (K , carrying capacity).

before introducing sea otters because the objective was to recover both species simultaneously as fast as possible. When sea otters reached 60% carrying capacity, we allowed removal of sea otters. For most functional responses (linear L1–L3, sigmoid S1 and S2, and hyperbolic H2), this management action contributed little or not at all to reaching recovery targets for northern abalone. For high predation rates (linear and hyperbolic functional responses L4 and H1), removing sea otters was a component of the optimal strategies only when density of the total abalone population fell below 0.4 abalone/m² (Fig. 1).

When we simulated an optimal strategy over 100 years for functional response hyperbolic H1 (Fig. 3), the op-

timal strategy consisted of introduction of sea otters followed by antipoaching measures to reduce illegal harvest by 50%. When the abundance of sea otters was below 2000 individuals, antipoaching measures increased the abalone density to 0.7 abalone/m² for the total population and 0.2 abalone/m² for adults >100 mm after 25 years. Above 2000 individuals, sea otter predation reduced total abalone density to 0.3 abalone/m² and adult density to 0.05 /m². When sea otters are affected by oil spills (Fig. 3), their abundance decreased sharply and in response to the decreased predation pressure the abalone density increased.

Under the best management scenario, combined increases in carrying capacity of 0.2 and intrinsic growth rate of 0.05 across all habitat types increased the total abalone density by 0.09/m² at low to medium predation levels (linear functional responses L1–L3). However, an increase in the carrying capacity and intrinsic growth rate had little effect on abalone density for predation rates above that predicted by linear functional response L3. Increasing the abalone intrinsic growth rates allowed the abalone population to recover faster under predation pressure than increasing the carrying capacity. Likewise, reducing the growth rate and carrying capacity decreased the abalone density to 0.09 /m² for linear functional responses L1–L3 (Supporting Information).

Discussion

Failure to account for interactions between species could lead to inefficient management strategies, waste of scarce resources, and at worst species extinction (Hatfield 2001). The short-term goal for northern abalone is to halt further decline. In the PRNP this means maintaining adult population density above 0.09/m². Our results suggest that under current estimates of poaching of northern abalone and recovery of the sea otter population, achieving this target is highly unlikely without management. A management strategy entailing a 50% reduction in poaching of northern abalone was a minimum requirement to reach short-term recovery goals for northern abalone in the presence of sea otters. This result held across a range of possible functional responses between both species and different growth parameters. In addition, removal of sea otters had a marginal positive effect on the abalone population only when we assumed a functional response with strong predation pressure (linear and hyperbolic functional responses L4 and H1) (Fig. 1). This result suggests improving enforcement of antipoaching measures should be the highest priority if the objective is to achieve the short-term recovery target for northern abalone. Other management options for northern abalone are being considered (e.g., population supplementation), but empirical evidence of their effectiveness is not yet available.

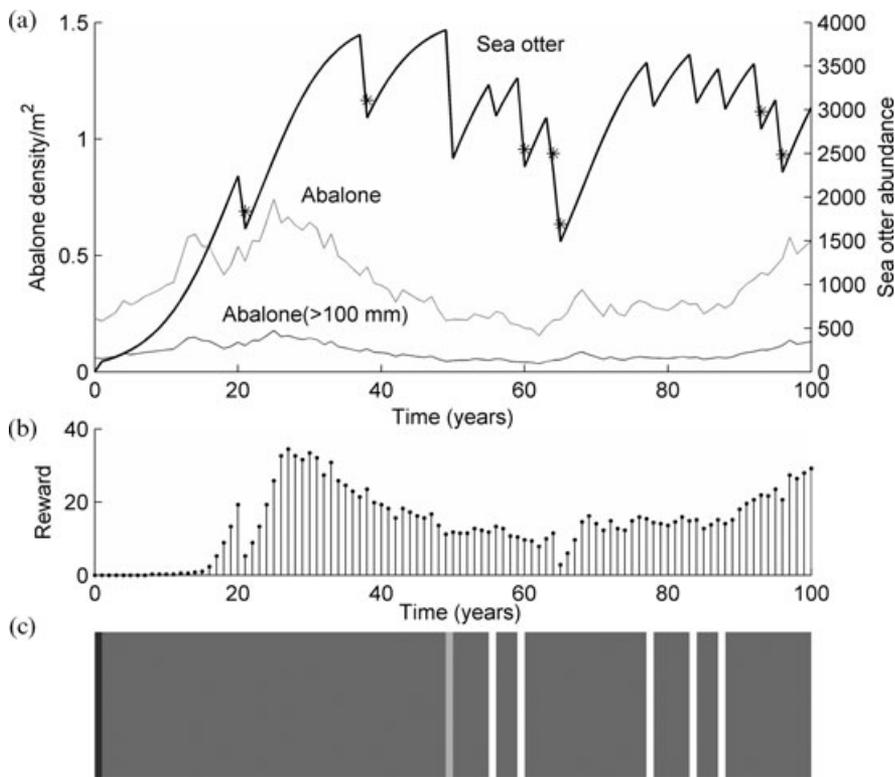


Figure 3. A simulation of the dynamic between sea otters and abalone (a) with a stochastic occurrence of oil spills () assuming the hyperbolic 1 functional response (Fig. 2) and (c) with optimal management undertaken over time that is based on the state of both species represented in (a) (black, sea otters introduced; dark gray, antipoaching measures; light gray, removal of sea otters; white, antipoaching measure and removal of sea otters at half efficiency [see text]). (b) When both species reach an equivalent level of density or abundance a positive reward is obtained and represents the performance of the optimal management regarding our conservation objectives.*

The choice of functional response had the largest effect on the density of abalone in the presence of sea otters (Supporting Information). We accounted for the range of foraging behaviors of sea otters by examining a range of functional responses that are likely to incorporate most feeding behaviors that have from weak to strong influences on abalone mortality. Results of our sensitivity analyses showed that changes in the abalone intrinsic growth rate, an uncertain parameter, were less influential than the assumed functional response on management outcomes (Supporting Information).

Historical densities of sea otters and northern abalone are unknown. What is clear is that baselines for the recovery of abalone are based on data collected after extirpation of sea otters. Explicitly modeling the interactions between sea otters and abalone illustrates the effect of sea otter predation on the density of abalone. In the absence of predation and with antipoaching measures, our results suggest densities of 0.32–0.6 adult abalone/m² are possible (Supporting Information). With predation by sea otters, abalone densities fell below 0.23/m². This result suggests that as long as sea otters are present, northern abalone are unlikely to reach densities observed during the pinnacle of the northern abalone fishery, the historical abundances used as reference points for setting northern abalone recovery targets under SARA. Irrespective of the starting density of abalone, once sea otters start feeding on abalone, an equilibrium density of adult abalone of 0.035–0.23 abalone/m² is expected.

In the absence of data that would allow formal modeling of the interaction between sea otters and abalone, we assumed a range of possible functional responses that demonstrated that under substantial uncertainty one can derive guidelines for the management of strongly interacting endangered species. To do this, we used simulation-based optimization methods, namely reinforcement learning and stochastic dynamic programming (Sutton & Barto 1998). Reinforcement learning can reduce the exploration search space and focus on the exploration of most likely situations. Given their relative ease of implementation and successful use in other situations (Sutton & Barto 1998), we hope reinforcement-learning methods will become more widely adopted in conservation. The main disadvantage of reinforcement-learning techniques is the slow convergence toward optimal or near-optimal strategies. Most reinforcement-learning methods give satisfactory results, but when several management actions have similar outcomes the resulting strategies are difficult to analyze due to the similar effectiveness in achieving targets of alternative actions. In our case, results of stochastic dynamic programming and reinforcement learning suggested similar management strategies. However, when >2 species are studied and as the number of states becomes too large to be solved with stochastic dynamic programming, reinforcement-learning techniques may provide an alternative (Nicol & Chadès 2011). Our interaction model focused on 2 species. However, both species evolved in a complex

ecosystem with other species, such as sea urchins and kelp, which also interact directly or indirectly with our study species (e.g., Estes et al. 2010; Watson & Estes 2011). Although we included stochastic noise in our models to account for effects of unknown interactions, we could not model with precision such detailed ecosystem interactions because data are lacking.

We assumed our conservation decisions had equal financial costs. In practice, resources are constrained and incorporating economic costs in our analyses could lead to different optimal management strategies. For example, reducing poaching would likely cost more than allowing a traditional hunt of sea otters by First Nation communities. We also assumed both species were valued similarly, but our utility function encouraged recovery of abalone over sea otters (reward function [Supporting Information]). Whereas our model aimed for recovery of both species, society may not value both species equally. In particular, controlling a charismatic species such as sea otters may be an unpopular conservation measure. Societal or economic values can be easily incorporated in our framework through the definition of the reward function (Nicholson & Possingham 2006).

Frameworks such as ours are useful for considering and setting recovery targets and evaluating the success of different management strategies. As our understanding of species interactions expands, simultaneous management of multiple threatened species is likely to occur more often. For example the population dynamics of threatened killer whales may be limited by a single species of commercially important salmonid (Ford et al. 2010; Williams et al. 2011), which is also of conservation concern. Understanding trophic interactions is crucial to informing politically charged debates around commercial whaling. The assertion that whales are responsible for declining fish stocks has been used widely to advocate for whaling (Gerber et al. 2009). Through the modeling of trophic interactions, Gerber et al. (2009) demonstrate that even eradication of whales has a negligible effect on fish biomass compared with small changes in fishing rates.

Our framework can inform management of interacting species because it assesses the probability of success of management actions in achieving multiple objectives. It is also a practical way to evaluate the potential success of management actions because it explicitly accounts for a species' functional response to predation and the uncertainty surrounding the response. We assumed we were able to perfectly observe the status of each species, whereas in reality information on the current state of species is incomplete (Chadès et al. 2008). For example, it is well-known that abalone are elusive. We suggest future work account for the inability to perfectly detect interacting species (MacKenzie & Kendall 2002; Chadès et al. 2011). Our framework can also be used to model the complex trophic interactions between non-native in-

vasive species and native endangered species (Collins et al. 2009). Investigations into the functional relations between interacting species will aid the development of realistic recovery targets and avoid setting unachievable management goals.

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Supporting Information

Northern abalone population model (Appendix S1), functional responses (Appendix S2), optimization models and MATLAB programs (Appendix S3), abalone population parameters (Appendix S4), simulation results (Appendix S5), simulation results for different values of abalone intrinsic growth rate and carrying capacity (Appendix S6), and other supplementary information (Appendices S7–S12) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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