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POLICY PERSPECTIVES

Conservation Challenges of Predator Recovery

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Abstract

Predators are critical components of ecosystems. Globally, conservation efforts have targeted depleted populations of top predators for legal protection, and in many cases, this protection has helped their recoveries. Where the recovery of individual species is the goal, these efforts can be seen as largely successful. From an ecosystem perspective, however, predator recovery can introduce significant new conservation and legal challenges. We highlight three types of conflicts created by a single-species focus: (1) recovering predator populations that increase competition with humans for the same prey, (2) new tradeoffs that emerge when protected predators consume protected prey, and (3) multiple predator populations that compete for the same limited prey. We use two food webs with parallel conservation challenges, the Northeast Pacific Ocean and the Greater Yellowstone Ecosystem, to demonstrate legal/policy conflicts and the policy levers that exist to ameliorate conflicts. In some cases, scientific uncertainty about the ecological interaction hinders progress towards resolving conflicts. In others, available policy options are insufficient. In all cases, management decisions must be made in the face of an unknown future. We suggest a framework that incorporates multispecies science, policy tools, and tradeoff analyses into management.

Introduction

Human activities have caused many predators to decline (Estes *et al.* 2011), in some cases leading to undesired effects that propagate through ecosystems (Estes *et al.* 2011; Ripple *et al.* 2014). Conservation efforts frequently focus on recovery of predators because they are charismatic and can affect communities in ways disproportionate to their biomass (Sergio *et al.* 2008). The success of predator protection programs has created a new set of challenges for natural resource managers (Yodzis 2001; Treves & Karanth 2003). In particular, unintended consequences of predator recovery may lead to conflict among objectives set up by multiple regulatory mandates. Using examples from marine and terrestrial ecosystems in the United States, we illustrate effects of predator-specific protections, including instances in which multiple managed species interact and cases where tradeoffs arise between protected predators and prey of commercial or recreational importance. We review available legal and policy tools for mitigating these conflicts, outline options to move forward with available science and policy tools, and highlight where existing science and policy are insufficient to address the problem.

The Endangered Species Act (ESA, 1973) and the Marine Mammal Protection Act (MMPA, 1972) are two core laws used to protect species in the United States. Both provide broad protections for individual species or populations, and make illegal the harassment, hunting, capturing, or killing of protected species. While protections are focused on individual species, both laws also recognize a broader ecosystem context. For example, the ESA requires designation and protection of critical habitat, and the MMPA states the primary objective of the management of marine mammals should be "to maintain the health and stability of the marine ecosystem." In some cases, these ecosystem considerations have allowed sufficient flexibility to manage multiple connected species

Table 1 Conflicts created by predator recovery, as seen in two simplified food webs

	Northeast Pacific marine mammal—Chinook			Greater Yellowstone Ecosystem		
Class of Conservation Conflict	Ecological conflict	Scientific Uncertainty	Policy conflict	Ecological conflict	Scientific Uncertainty	Policy conflict
1. Protected predator vs. human use	Pinnipeds vs. Chinook salmon	Do predators substantially reduce salmon fishery yields?	MMPA vs. human use	Wolf vs. elk	What is the relative importance of wolves, other predators, humans, and climate in controlling elk population productivity?	ESA vs. human use
2. Protected predator vs. protected prey	Orcas vs. Chinook salmon	What fraction of endangered salmon runs are eaten by orcas?	ESA vs. ESA	Grizzly vs. cutthroat	How much do grizzly bears contribute to mortality on cuthroat trout?	ESA vs. ESA
3. Protected predator vs. protected predator	Orcas vs. Pinnipeds	Would deterring or culling pinnipeds help orcas?	ESA vs. MMPA	Wolf vs. grizzly	What is the strength of competition between these two predators?	ESA vs. ESA

simultaneously, but in others, implementation of protections and recovery plans for large carnivores have missed important ecological connections.

We identify three broad classes of conflict that single-species predator conservation generates (Table 1). First, *protected predators versus human use* captures conflicts that occur when humans and predators compete for the same resource. Second, *protected predator versus protected prey* illustrates management challenges that arise from a protected predator consuming protected prey. The third category, *protected predator versus protected predator,* describes conflicts between two protected predators that share one or more prey species. In each case the policy driver of ecological conflict is clear: legal protections facilitate increases in selected predator species with limited authority to manage downstream effects.

In general, the ESA and MMPA have a few safety valves, which allow "take" of protected species for a circumscribed set of reasons (Table 2). These options are limited, and none can address conservation conflicts driven by prioritizing some species over others in an ecosystem. However, where such conflicts are of sufficient policy importance to merit attention via rulemaking or analogous processes—for example, in the case of long-running and high-profile conflicts such as those we discuss in this article—resource agencies (primarily FWS and NMFS) have these avenues available to them.

Here, we illustrate the new challenges posed by recovering predators using the three classes of ecosystem conflict and well-documented, simplified food webs from two complex ecosystems: the Northeast Pacific and the Greater Yellowstone Ecosystem (Figure 1). We describe specific ecological and policy conflicts and science and policy tools available to address them. We close by suggesting options to move management forward.

Protected predators versus human uses

Both the Northeast Pacific and Yellowstone food webs have examples of conflicts between predators and human resource use (hunting, fishing) that arise from competition. From a policy perspective, both examples highlight how recovery of an endangered species can lead to a sociopolitical problem insofar as they create real or perceived competition with important stakeholder groups of hunters or fishermen.

The Northeast Pacific provides a globally recognized example of a conflict between predator populations and human utilization, specifically between marine mammals and fishermen (Trites *et al.* 1997). Commercial harvest of Chinook (king) salmon has declined from historic levels, in part to protect declining wild salmon populations, seven of which are ESA-listed (Figure 2a; Irvine & Fukuwaka 2011). Pinnipeds in this ecosystem were historically harvested, but are now protected by the MMPA. Pinnipeds in the Northeast Pacific, like many marine mammals around the globe, have rapidly increased following protection (Magera *et al.* 2013). Yet these substantial changes in predator biomass (and corresponding changes in fish consumption) have largely been omitted from fisheries management (PFMC 2008; Skern-Mauritzen *et al.* 2015). The extent to which predators reduce yields to fisheries remains an open question and an active area of research (Ruckleshaus *et al.* 2002;

Table 2 Available tools within the Endangered Species Act and the Marine Mammal Protection Act that can be applied to resolve policy conflicts created by recovering predators (Table 1). All tools require public notice-and-comment.

Safety valve	Description	Limitations
ESA		
§4(d) rule	Allows take of threatened—but not of endangered—species.	Rule must be "necessary and advisable" for the species' conservation. 16 USC § 1533(d). Litigation possible.
§10 Habitat Conservation Plans	Spatial and financial set-asides for habitat conservation; may allow take.	Plan must have adequate funding; take must be incidental, and cannot appreciably reduce likelihood of species survival/recovery; other limitations. See 16 USC § 1539(a)(2). Litigation possible.
§4 Distinct Population Segment listing/delisting	Allows listing or delisting of vertebrate populations, rather than entire taxonomic species.	For a population to be listed separately from the species as a whole, population must be discrete, significant, and imperiled. 61 Fed. Reg. 4722. Presumably, delisting a population of a species would follow similar limitations. Litigation likely.
§4 Delisting due to recovery	Species recovery is the goal of the ESA, and once a species is delisted due to recovery, take is no longer prohibited.	Where a species is no longer threatened or endangered, it may be removed from ESA protection by being delisted. 16 USC § 1533. Public notice-and-comment required. Litigation likely.
MMPA		
Waiver of moratorium on take	16 USC §1371(a)(3)(A) provides the Secretary of Commerce the authority to grant a waiver to the blanket moratorium on take of marine mammals under certain conditions.	Must be consistent with purposes of the MMPA, cannot be to the disadvantage of the species or stock. (Among other limitations). See 16 USC § 1372. Litigation likely.

Hilborn *et al.* 2012), but effects of pinniped predators on salmon are likely nonnegligible (Hilborn *et al.* 2012).

Similar competitive interactions between predators and humans also occur on land. The gray wolf is well-known for conflicts with humans (Bergstrom *et al.* 2014). The extirpation and subsequent reintroduction of wolves to Yellowstone in 1995 has been exceptionally well documented. Twenty years after reintroduction, wolves have been delisted in Idaho and Montana, but remain listed as a nonessential experimental population in Wyoming. Rebounding wolf populations have increased wolf predation on livestock, costing ranchers tens of thousands of dollars annually (Muhly & Musiani 2009). Wolves may also affect recreational hunts of elk in states bordering Yellowstone. In 1992, the northern population of Yellowstone elk reached a peak of 19,000 individuals and approximately 4,500 elk were taken by hunters (Figure 2b, Eberhardt *et al.* 2007). The number of elk killed by wolves exceeded that taken by hunters in 2005, and by 2012 when elk numbers declined to <4,000 animals, recreational hunts were eliminated (Vucetich *et al.* 2005; Varley & Boyce 2006). A key scientific uncertainty is how much of this dramatic change in elk abundance was caused by changes in hunting, predation by wolves, or prolonged drought, respectively (Vucetich *et al.* 2005). Predicting and understanding the elk population's response to the management lever of reduced hunting depends on the relative importance of hunting, predation, or food supply in determining elk population growth.

Both the Northeast Pacific and Yellowstone examples represent an opportunity to align predator consumption rates with statistical models that inform management decisions. The science needed to begin this effort is available now. Ongoing monitoring of predator populations—even after they recover—will be required to improve estimates of predator consumption rates and to track changes in diet patterns through time. However, currently available data should be sufficient to begin exploring tradeoffs between human use and predators in a management context.

Given policy preferences in favor of protected species and the safety valves outlined above (Table 2), a key question is: how could management efforts include ecosystem effects of species conservation under current law? The answer depends on the policy context and the extent to which predators are responsible for reduced human harvest. In the Northeast Pacific, if scientific analyses can estimate pinniped depletion of salmon populations, a likely policy safety valve would involve pursuit of a waiver of the MMPA's moratorium on take (Table 2). Culling pinnipeds is legally feasible, but may not be socially acceptable. In the Yellowstone ecosystem, wolves and elk in Idaho and Montana are managed for hunting. In Wyoming, the nonessential experimental wolf population effectively allows for

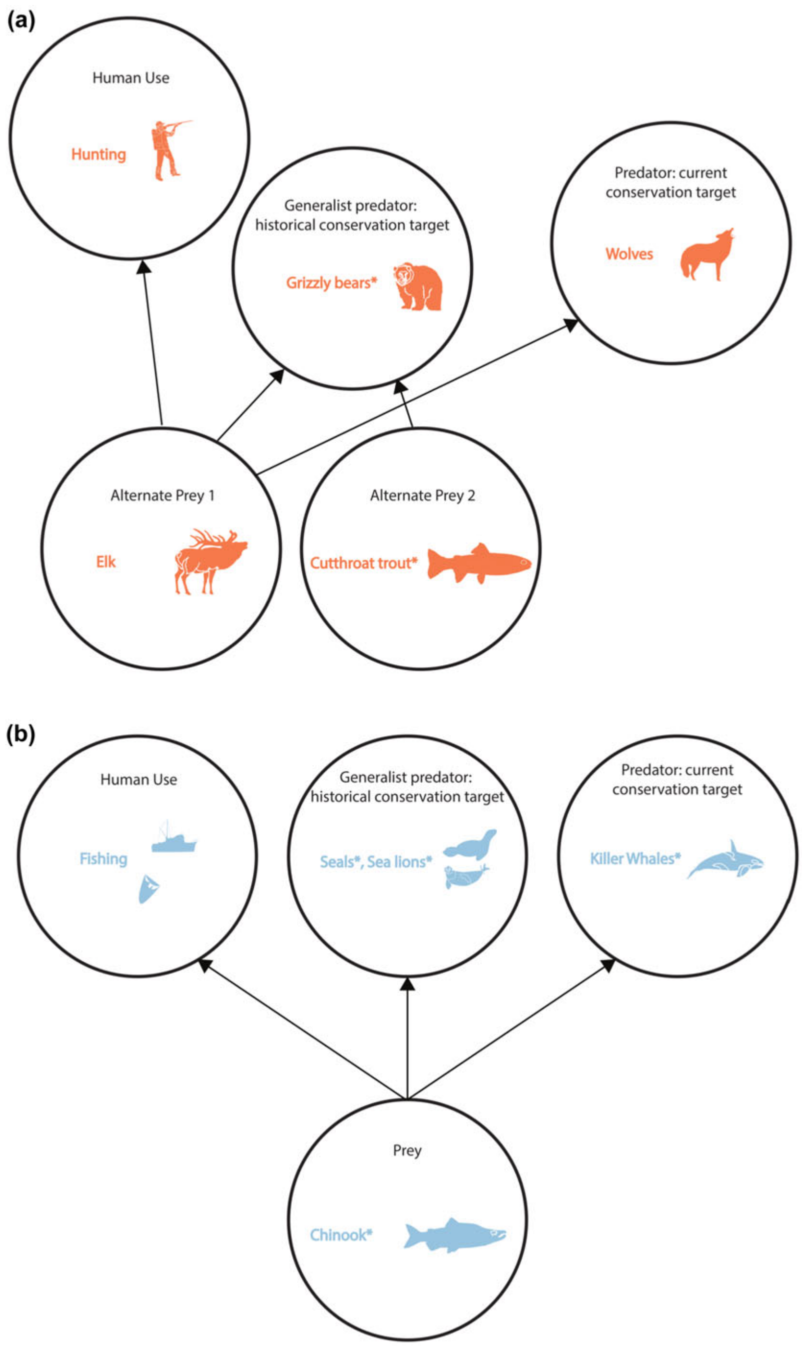

Figure 1 Diagrams of simplified 3-predatorfood webs in (a) the Yellowstone Ecosystem (red) and (b) the Northeast Pacific Ocean (blue). Species with an asterisk have protected status, or are threatened, endangered, or historically depleted. Additional prey species exist for both predators; only those of particular commercial importance or conservation concern are represented here.

the same flexibility as a threatened species designation (Table 2). An existing take exception provides a process by which a State or Tribe can apply for a take permit "if wolf predation is having an unacceptable impact on wild ungulate populations" (72 Fed Reg 75366 12/11/08).

Protected predators versus protected prey

The complexity of managing ecosystems as predators recover increases when both predator and prey are protected. Legislative mandates typically do not address tradeoffs that arise from predator–prey interactions. Despite the ecosystem aims in the ESA and MMPA, both are primarily single-species management tools.

In the simplified Northeast Pacific food web, killer whales consume salmon. A conservation conflict arises from Southern Resident killer whales (an Endangered DPS under the ESA) eating ESA-listed Chinook salmon (Figure 1). Across the Northeast Pacific, total abundance

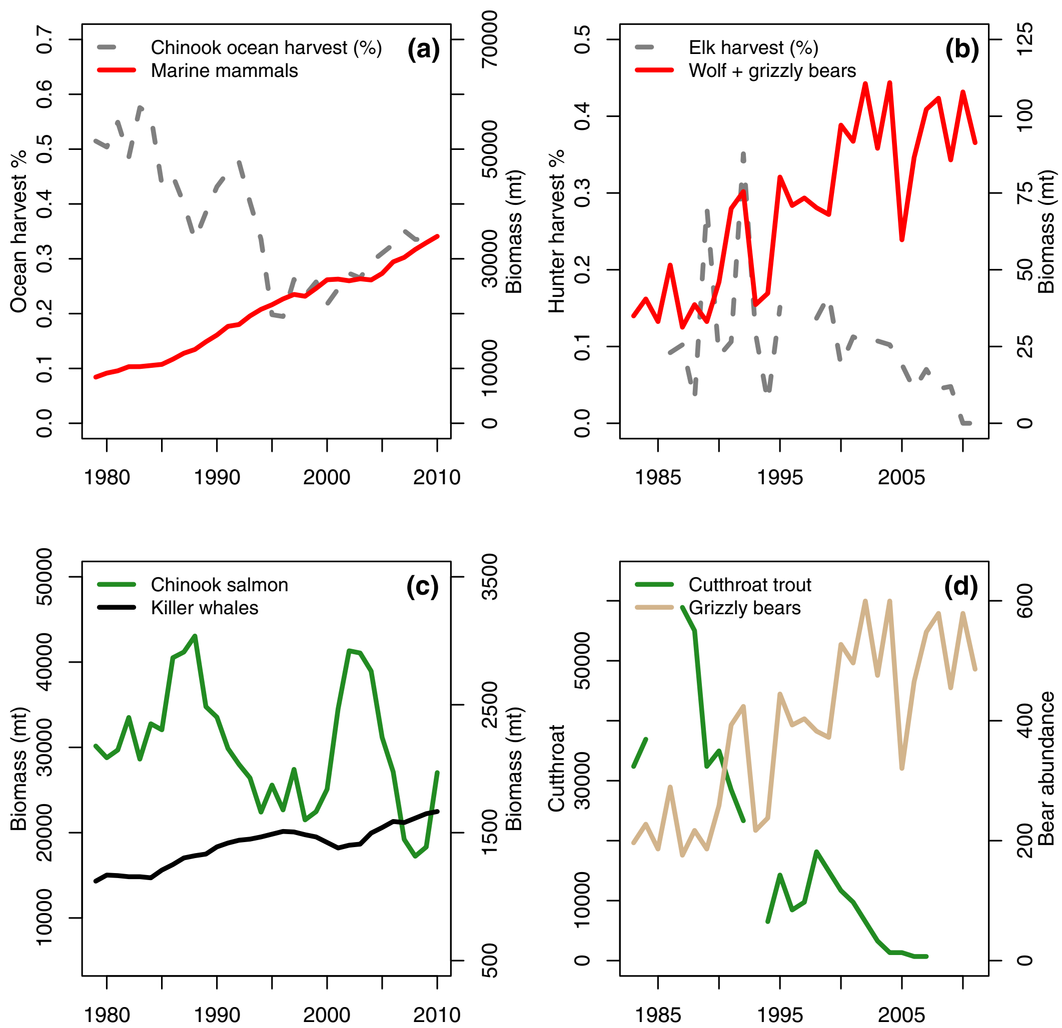

Figure 2 Time series of Chinook ocean harvest from commercial fishing and marine mammal biomass (pinniped, resident killer whale) in the Northeast Pacific Ocean (a), time series of predator biomass and elk harvest rates on the northern range elk herd of Yellowstone National Park (b), time series of ocean abundance of Chinook salmon and their killer whale predators in the Northeast Pacific Ocean (c), and time series of cutthroat trout at Clear Creek on Yellowstone Lake, and grizzly bear abundance in the Greater Yellowstone Ecosystem (d).

of killer whales has increased gradually as total Chinook salmon has declined (Figure 2c). This conflict is complicated because only a subset of each species (killer whales, Chinook salmon) is listed under the ESA. Chinook are the preferred prey of Southern Resident killer whales (Hanson *et al.* 2010), however the proportion of those Chinook prey that are endangered, threatened, or of hatchery origin is unknown.

A clear terrestrial analogue involves grizzly bears in the Yellowstone ecosystem. Grizzly bears were listed as threatened under the ESA in 1973. Bear numbers in Yellowstone increased steadily over the last three decades (Haroldson *et al.* 2012), however the exact rate is debated (Doak & Cutler 2014). Recent efforts to delist Yellowstone grizzlies have failed (see *Greater Yellowstone Coalition Inc v. Servheen*, 665 F.3d 1015 [2011]), and the Yellowstone Grizzly DPS remains threatened.

Grizzly bears consume many seasonally abundant prey items, including elk, pine nuts, grasses, and berries (Fortin *et al.* 2013). One historically important prey for grizzlies was Yellowstone cutthroat trout. Cutthroat declined after invasive lake trout were introduced to Yellowstone Lake in the mid-1990s, and are now rarely observed in grizzly diets (Fortin *et al.* 2013; Figure 2d). Given its population declines, cutthroat remains an important conservation focus in Yellowstone (though FWS determined ESA protection was not warranted, 71 Fed Reg 8818 02/21/06).

Hence, Yellowstone provides an example of predator (grizzly) and prey (cutthroat) simultaneously meriting conservation focus, and creating policy conflict. Even if only small numbers of cutthroat are consumed per capita by grizzlies (e.g., too few to be frequently observed in studies of bear diets), this level of predation could equate to sizable mortality on a small population of Yellowstone cutthroat.

In both the Yellowstone and Northeast Pacific ecosystems where protected predators consume protected prey, policy mandates simultaneous recovery of predators and prey with limited authority to explicitly include species interactions. As with the pinniped-versus-human-use example, key scientific parameters remain poorly understood, but it is clear that single-species approaches have limited authority to balance objectives for two species, let alone whole ecosystems. Simple multispecies models that include predation interactions may be useful in simultaneously setting achievable recovery goals for both predator and prey (or evaluating ranges of both species' abundances under alternative management actions).

If modeling can help guide sensible policy, that policy must then be implemented under the existing legal regimes of the ESA and MMPA. For Southern Resident killer whales and listed Chinook, a synoptic management strategy would ensure a population of listed Chinook sufficient to ensure the lineage's survival and to feed the killer whales. However, complex factors affect Chinook populations, including dams, fishing, hatchery practices, habitat, and predators. If recovering Chinook populations were simple, and immediately within NMFS's power, it would have been done already. Further, none of the safety valves of the ESA or MMPA appear to help: reducing numbers (via take) of protected predator or prey species would not address the problem. Instead, it seems clear that where both predator (killer whale) and prey (Chinook) are imperiled, larger ecosystem-scale productivity drivers are likely involved, and current laws do not have the regulatory authority to change such drivers.

Yellowstone is experiencing similarly conflicting single-species management goals, although cutthroat are not protected under the ESA. As with Chinook and killer whales in the Northeast Pacific, the effect of grizzlies on cutthroat populations is uncertain because observed encounter rates are low, compounding a policy conflict with scientific uncertainty. Any solution to this conflict does not lie in easing ESA protections, but rather in safeguarding the future of both predator and prey species by managing larger scale threats and invasive species (lake trout, climate change). Meanwhile, monitoring and modeling to capture scientific uncertainty would help ensure future management is grounded in data that speak to precise policy questions.

Protected predators versus protected predators

Competition between protected predators is a third type of conflict created by predator-focused management. In both the Northeast Pacific and Yellowstone food webs (until the recent delisting of wolves in all states except Wyoming), each ecosystem had multiple protected predators competing for the same prey.

In the Northeast Pacific, pinnipeds and killer whales both prey on Chinook salmon, creating a conflict in single-species management goals. In contrast to killer whales which are Chinook specialists, pinnipeds have broader diets. Chinook may represent a small fraction of individual diets, but the effect of predation may be significant because of large populations of seals and sea lions (Lance *et al.* 2012).

In Yellowstone, protected wolves and grizzlies both consume elk, again creating conflict via indirect competition. Wolf diets are dominated by elk (Stahler *et al.* 2006), while grizzlies rely on elk seasonally (Fortin *et al.* 2013). Predation on elk calves has increased in recent years, and is now the primary driver of low elk calf survival (Middleton *et al.* 2013). Grizzlies could negatively affect wolves if grizzly predation leads to smaller elk herds (Figure 3b) and the opposite may be true if wolf populations more strongly control elk dynamics.

Both ecosystems highlight a need to understand competition between protected predators that share the same prey resource, however the policy options to resolve each conflict are different. In the Northeast Pacific, permitting take of pinnipeds via a moratorium waiver might benefit endangered Southern Resident killer whales. However, the outcome of culling pinnipeds is difficult to predict because the interaction between killer whales and pinnipeds is indirect (Yodzis 2001). In the Yellowstone ecosystem, because both wolves and grizzlies are protected by the ESA, policy options are less clear. In theory, a 4 (d) rule could be pursued to allow take of one species in specified areas, along with a Habitat Conservation Plan that protected habitat elsewhere. As in the pinniped example, predicting the impact of take would be difficult. Further, there is no guidance on prioritizing one species over another when they have similar levels of protection. Regardless, building scientific understanding of how each predator affects elk population dynamics and how feedbacks among all three species could affect recovery trajectories of grizzlies and wolves is necessary to understand how to improve recovery goals for both species.

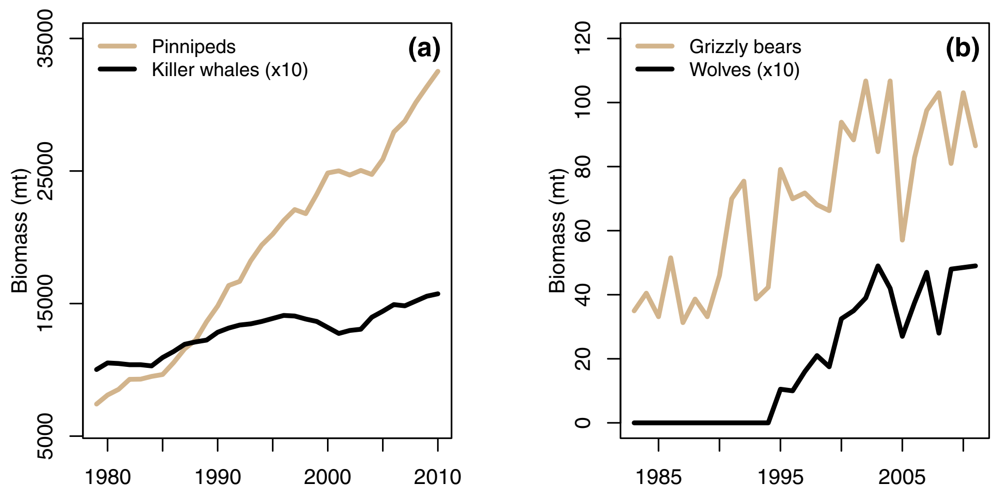

Figure 3 Time series of competing top predators: pinnipeds and fish eating killer whales in the Northeast Pacific Ocean, and time series of wolves and grizzly bears in the Greater Yellowstone Ecosystem.

Discussion

Our case studies of conservation conflicts created by predator recoveries show that predator recovery does not necessarily equate with ecosystem recovery. Instead, laws designed to protect and recover individual species have led to conflicts with other species and humans that share the ecosystem. Relieving these conflicts may be possible over short (<5 years) or longer time scales (>5 years). In some cases (pinnipeds vs. Chinook), developing multispecies models that could inform salmon management is possible in the short term, and policy tools exist to help resolve existing conflicts (permitting take of pinnipeds under MMPA). In other cases (wolves vs. grizzlies), additional long-term monitoring or model development will be required to evaluate tradeoffs between predators. Existing policy tools may be insufficient to manage downstream effects of recovering predator populations, in particular for ESA-listed predators with large home ranges, which may preclude the use of Habitat Conservation Plans.

We highlighted the Northeast Pacific and Yellowstone ecosystems because they have parallel management and conservation challenges. However, multispecies conservation conflicts are common to many systems. For example, Atlantic cod fisheries conflict with large populations of grey and harp seals on the east coast of North America (Yodzis 2001). Protected pinnipeds in Puget Sound predate on threatened steelhead runs (Hard *et al.* 2007) and rockfish (Ward *et al.* 2012). On California's San Clemente Island, an endangered shrike is consumed by a threatened island fox, and both the shrike and fox are eaten by golden eagles which are protected under the Migratory Bird Treaty Act (MBTA) and the Bald and Golden Eagle Protection Act.

Similar safety valves to those possible in our case studies have also been applied in other ecosystems. In the US Pacific Northwest forests, the MBTA protects an expanding barred owl population, while the ESA protects a declining population of spotted owls. Competitive dominance of the barred owl over the spotted owl for food and nest locations is contributing to spotted owl decline (Gutierrez *et al.* 2007). While the management goal is the persistence of both raptors, the culling of barred owls to protect spotted owls was made possible with a permit under the MBTA. In another recent example, NMFS has proposed to remove recovered humpback whales from ESA protection by establishing 14 DPSs around the globe and delisting 10 of them (80 Fed Reg 76 4/21/2015).

To resolve conflicts created by competition, predation, and human harvest where existing policy vehicles are insufficient, new strategies are required. One potential option is to develop multispecies recovery plans for tightly linked ESA listed species. Multispecies plans have already been used to protect groups of plant species occupying similar habitat, although with questionable success rates (Clark & Harvey 2002). Reenvisioning multispecies recovery plans to include multispecies models and associated tradeoff analyses may aid in setting recovery goals for a predator and its prey, or for two predators simultaneously. This approach would build from an explicit consideration of tradeoffs among predators and other objectives (such as prey abundance, prey harvest levels, abundance of another predator). Tradeoffs may be linear or nonlinear, and there may exist combinations that maximize both goals at minimal cost to either one (Lester *et al.* 2013). For predators that are not listed under the ESA, economics may also be considered. For example, in states where wolves are delisted, economic costs to ranchers for lost livestock or reduced productivity due to wolves, payments made to compensate for those factors, and reduced opportunities for recreational elk permits could be weighed against revenues generated from ecotourism and recreational hunting permits for wolves. In a risk analysis framework, the costs of monitoring, restoring, and managing predators, prey, and/or their habitat could also be included. Cultural considerations beyond economics are essential components of such analyses (Poe *et al.* 2014).

Human–wildlife conflicts have a long history in the United States (e.g., Bergstrom *et al.* 2014). Management conflicts created by two protected species that interact are newer, but rapidly increasing. Resolving these conflicts will require managers to prioritize among competing objectives. In some cases, available policy options will be limiting, and in others monitoring and model development is necessary before existing policy tools can be pursued. This interaction between science and policy is challenging, but must be considered to move forward successful management approaches in complex socioecological systems.

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Supporting Information

Additional Supporting Information may be found in the online version of this article at the publisher's web site:

Detailed explanation of data sources for figures

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