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Synthesis

Should Ecosystem Management Involve Active Control of Species Abundances?

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ABSTRACT. We review four case studies in which there is a risk of extinction or severe reduction in highly valued species if we ignore either, or both, of two ecosystem control options. “Symptomatic control” implies direct control of extinction risk through direct harvesting or culling of competitors and predators. “Systemic control” implies treating the causes of the problem that led to an unnaturally high abundance in the first place. We demonstrate, with a discussion of historically observed population trends, how surprising trophic interactions can emerge as a result of alterations to a system. Simulation models were developed for two of the case studies as aids to adaptive policy design, to expose possible abundance changes caused by trophic interactions and to highlight key uncertainties about possible responses to ecosystem management policies involving active intervention to control abundances. With reasonable parameter values, these models predict a wide range of possible responses given available data, but do indicate a good chance that active control would reverse declines and reverse extinction risks. We find that controlling seal (*Phoca vitulina*) populations in the Georgia Strait increases juvenile survival rates of commercial salmon (*Oncorhynchus* spp.) species, but that commensurate increases in hake populations from decreased seal predation could be a compensatory source of predation on juvenile salmon. We also show that wolf (*Canis lupus*) control and moose (*Alces alces*) harvest bring about a recovery in caribou (*Rangifer tarandus caribou*) populations, where simple habitat protection policies fail to recover caribou before wolf predation causes severe declines. The results help address a common problem in disturbed ecosystems, where controlling extinction risks can mean choosing between active control of species abundance or establishing policies of protection, and allowing threatened species to recover naturally.

Key Words: *ecosystem management; predator control; trophic interactions*

INTRODUCTION

Many ecosystems throughout the world have been severely altered through habitat destruction, harvesting, and invasions by exotic species. A common problem among these disturbed ecosystems is the risk of extinction of one or more species caused by the cumulative effects of exploitation, or severe predation and competition with other species that are unnaturally more abundant because of ecosystem changes. The species at risk can be either commercially valuable, such as fish stocks, or valued purely for their existence. Habitat disturbances are often irreversible, or require long periods of time for habitat recovery to take effect. To reverse declines, natural resource management agencies are often forced to choose between controlling unnaturally high abundances to reduce extinction risks or establishing policies of protection to allow natural processes to reestablish. Advocacy for letting nature run its course has apparently been driven in part by intuitive models or beliefs about how dynamic interactions will restore some reasonable balance (e.g., Clements’ “climax community” concept (Clements 1928)), and in part by value judgments about how active intervention may be an instance where means do not justify ends. This model of community and ecosystem development has been challenged in light

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of repeated observations that ecosystems do not generally develop toward a single, predetermined state (Scheffer et al. 2001). Rather, self-organizing, positive feedback processes can produce an array of stable structures, each of which can be highly resilient and resistant to change (Peterson et al. 1999). Under this view, passive management efforts will not necessarily do anything to return ecosystems to former states, particularly if conditions no longer exist to tend systems toward those states.

Reserves and protected areas can be placed strategically to provide essential conditions at important stages of animal life histories, such as enhancing recruitment of marine species by protecting highly productive areas, or providing nesting habitat for migratory birds. Reserves can also provide perpetual refuges away from human impacts, which is a common goal of large national parks. A common theme in ecosystem management is to lower exploitation rates, and allow ecosystem processes to return to a natural balance. This directly targets the perceived source of the problem, but may not be sufficient to remedy damage caused by exploitation of habitat and the effect that has on valued species. There can be cases where ecosystem management may also require direct and even complex controls of competing and predatory species in order for natural processes to reestablish. Given the history of failure in this area, it is not surprising that agencies can be reluctant to intervene in this way, but ecosystem modeling continues to progress, and can do a reasonable job of predicting undesirable side effects (e.g., see the discussion by Yodzis (2001) about culling marine mammals to enhance fisheries production). These predictions can be used to design adaptive policy scenarios that can be used in management experiments to reduce uncertainties about these outcomes (Walters 1986, Walters and Holling 1990).

Active control programs are commonly advocated only for exotic species that present obvious threats to natural ecosystem structure. We believe that resource demands and political pressures will force agencies to implement spatially and temporally complex policies of protection, enhancement, harvest, and various other controls, regardless of our understanding of the side effects. We believe these agencies can identify where precautionary active control of overabundant competitors and predators of target species can at least hasten recoveries and reduce extinction risks in the interim. We suggest that the practice of ecosystem management may at times require active food web manipulation policies when simple protection from further human disturbance appears likely to fail.

The cases we examine here all have the potential to defy the intended purpose of management actions, which are aimed at recovering a focal species perceived to be at risk of extirpation or extinction. Some manipulations, although aimed at increasing abundances of target species, can actually reduce abundances because of unexpected increases in predators and competitors. Yodzis (2001) rightly points out that predator management should be sensitive to cases where removal of a top predator may lead to an increase in abundance of another species that preys on the target species. We show additional cases where control of a top predator can also lead to an increase in densities of direct competitors of the target species. Another possibility is that bottom-up enhancement of target species' conditions can also favor conditions for competitors or predators of that species. We have chosen these cases because they cover a range of situations involving the aforementioned causes and side effects. The cases also represent recovery goals for commercial as well as existence-valued species. Table 1 summarizes how the systems were altered, what the intended solutions are, and how things may go wrong.

Simulations were used to expose possible abundance changes caused by trophic interactions, and to highlight key uncertainties about possible responses to ecosystem management policies involving active intervention to control abundances. Simulation results are provided for two of the four cases discussed. The two other cases are discussed with respect to the results of past management experiments not explicitly reproduced in this paper. In both simulated cases, we find evidence that a short-term reduction in predator numbers provides either a brief respite in a decline of a target species, or accelerates the recovery of a target species during a concurrent long-term habitat improvement policy. The models are based not on direct management experience (or past adaptive management experiments) aimed at testing active intervention policies, but on highly fragmentary and often anecdotal data on historical system changes; as such, they must be viewed only as reasonable hypotheses to be considered in adaptive policy design exercises. In only one of our case examples (the Grand Canyon) has a model actually been used

Table 1. Summary of case studies.

Case	Alteration	Outcome	Solution	Concern
Salmon in the Strait of Georgia, British Columbia	Seals protected and salmon overharvested	Predation on juvenile salmon	Cull seals to increase juvenile survival	Lowering seal abundances may lead to an increase in the abundance of known predators of juvenile salmon (hake)
Caribou in North American boreal forests	Loss of old-growth forest	Predation by wolves following moose colonization	Protect old-growth forest to prevent further degradation	Wolves may continue to prey on caribou, if moose continue to support wolves
Humpback chub in the Grand Canyon	Exotic predators and competitors introduced, and water temperature lowered	Some exotics are productive in cold water, and prey on chub	Raise water temperature	Other exotics are more productive in warmer water, and will prey on native fishes as well
Lean lake trout in the Great Lakes	Exotic piscivores used to control other exotic invaders	Exotics compete with lean lake trout	Close fishery of leans and harvest native competitors	Native piscivores will respond to loss of one competititor and out-compete focal species

in Adaptive Environmental Assessment and Management (AEAM, Holling 1978) workshop processes to help organize policy debate among management stakeholders, and to promote development of an experimental management plan.

Case Examples Where Passive Policies May Fail

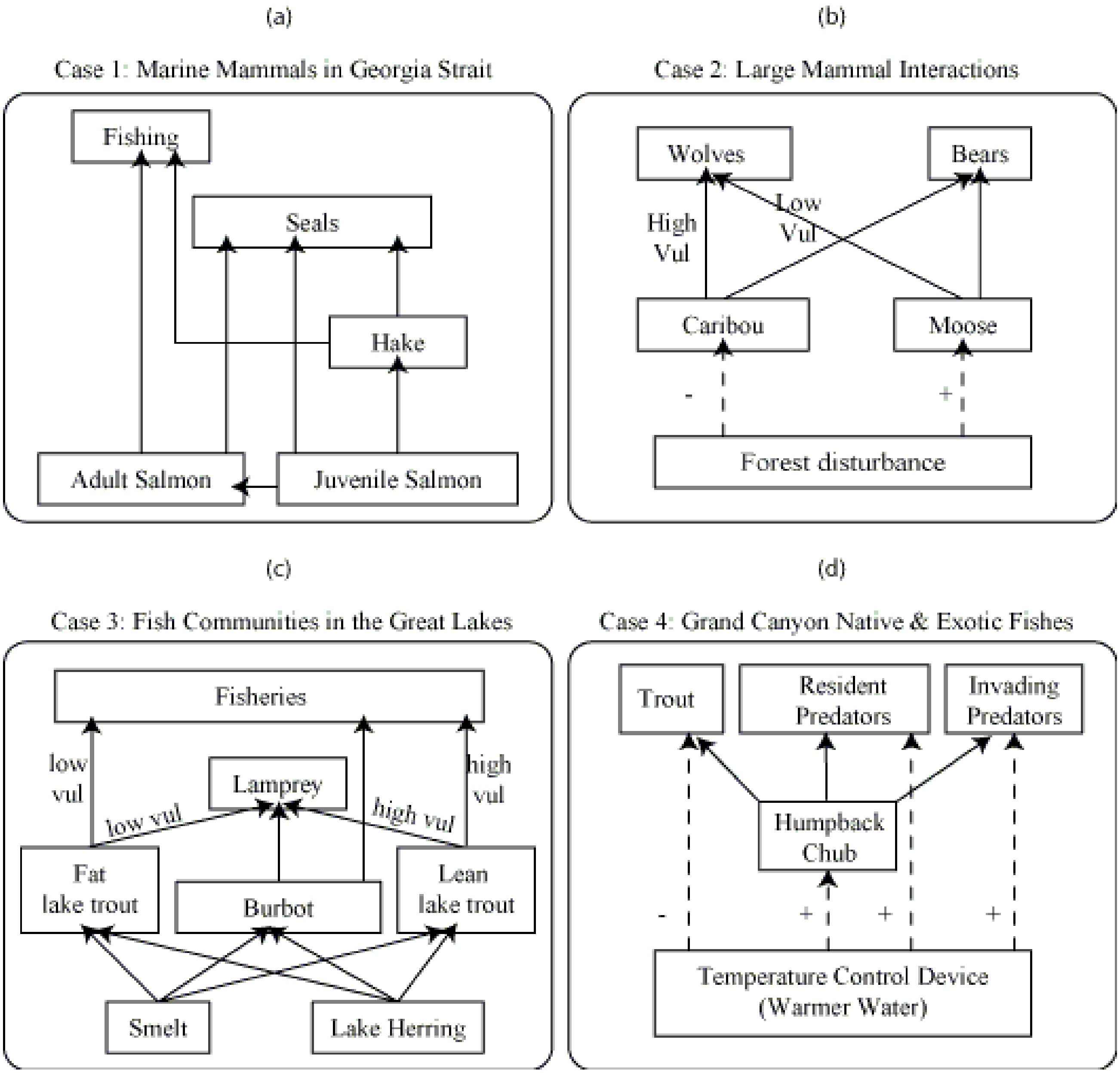
Figure 1 shows a diagram of trophic interactions for each case example. We include only those species where noticeable trophic effects have been observed empirically. The solid arrows indicate the direction of energy flow, whereas the dashed arrows indicate an indirect positive or negative effect on the productivity of a species. The interactions are discussed in detail under the heading of each individual case study.

Case 1: Marine mammals and fishes in the Strait of Georgia, British Columbia

During the 1960s, 1980s, and 1990s, severe declines were observed in a variety of fish species in the coastal waters of British Columbia, most prominently in the Strait of Georgia (SOG). In some species, such as herring (*Clupea pallasii*), lingcod (*Ophiodon elgongatus*), and rockfishes (*Sebastes* spp.), these declines have been attributed mainly to excessive fishing (Ketchen et al. 1983, Cass et al. 1990, Schweigert 1993), but the main proximate causes of declines of coho salmon (*Oncorhynchus kisutch*) and chinook salmon (*Oncorhynchus tshawytscha*) appear to be decreased juvenile marine survival rates. There has been an increase in the mortality rate of fish between the time of migration to sea from natal streams and when fish reach harvestable sizes (Walters and Ward 1998, Beamish et al. 2000). The source of this increased mortality has not been identified.

There have been various oceanographic changes over this period, most prominently the warming of waters associated with strong *El niño* events and changes in North Pacific air–water circulation patterns. It is thought that warming sea water may decrease juvenile salmon survival rates (Mantua et al. 1997, Welch et al. 1998, Hare et al. 1999, Ware and Thompson 2000). Up until 1970, the Department of Fisheries and Oceans ordered a bounty on harbor seals (*Phoca vitulina*). There are no published reports on the exploitation rates for harbor seals; however, we have witnessed a substantial increase in abundance since the first population estimate in 1973 (Olesiuk 1999). There has also been a dramatic increase in abundance of marine mammals, particularly harbor seals and

Fig. 1. Graphical representation of interactions between predators, prey, competitors, and human alteration. Solid arrows represent the direction of energy flow. Dashed arrows represent indirect effects on species abundances (positive and negative effects as indicated). (Vul = vulnerability.)



California sea lions (*Zalophus californianus*), as a result of marine mammal protection acts (Olesiuk 1999). These species are known to consume the fish species that have declined (Olesiuk et al. 1990). Valued commercial and recreational fisheries are in direct conflict with seal protection policies. Fisheries values would obviously benefit from reducing mortality caused by seal predation, but the compensatory effects are not well understood. This situation may benefit from experimental control of seal abundances using an adaptive management approach.

Fishing for ground fish in the SOG was carried out using long-line and trawl gears in a few selected areas, targeting lingcod, Pacific cod (*Gadus macrocephalus*), and rockfish species. Fishing for salmon has both commercial and recreational components for all five Pacific species, and fishing mortality rates have remained relatively constant. It is not clear which factor is responsible for the decline in marine survival rates for juvenile coho salmon, or whether a reduction in harbor seal abundances would reverse this trend. More recently, fishing mortality has declined because of the closure of the coho salmon fishery in British Columbia. For the purposes of this model, we ignore the highly migratory species, such as sockeye (*Onchorhynchus nerka*) and pink salmon (*Oncorhynchus gorbuscha*). The herring (*Clupea* spp.) fishery is a commercial gillnet and seine fishery. Before 1970, Pacific herring were reduced for fishmeal, and after the collapse in the late 1960s, a more valuable roe fishery developed. The Pacific hake (*Merluccius productus*) fishery did not commence until 1975 in the SOG, and the most recent fishery development is the krill (*Euphasia* spp.) fishery that started in 1997. Krill are the major component of the aggregated carnivorous zooplankton group, and a primary diet item for many zooplanktivorous fishes, including hake and herring.

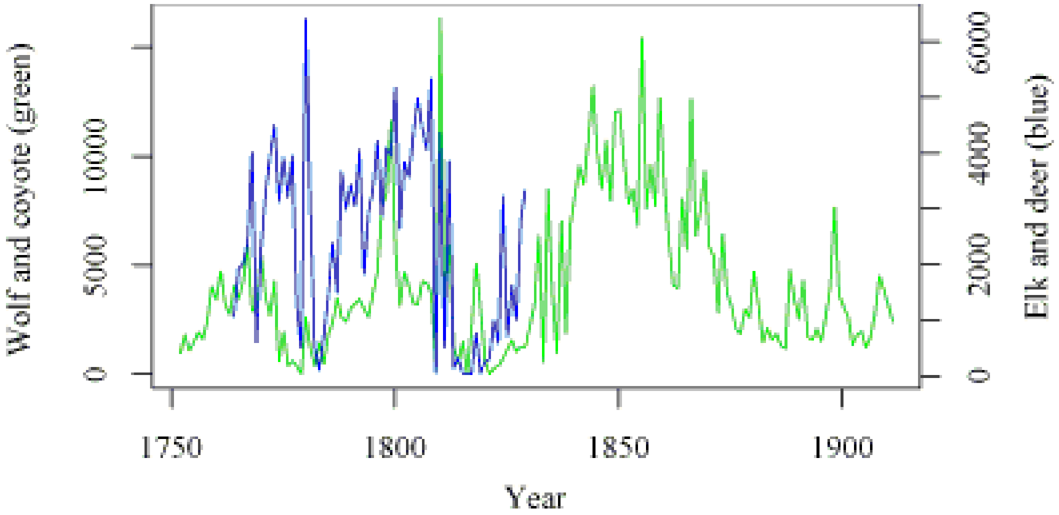
Ecosystem trophic models (Walters and Martell 2004) indicate that the changes in salmon mortality rates in the SOG can be at least partly explained by the measured changes in marine mammal abundance (Dalsgaard et al. 1998). In some localized areas, particularly downstream from salmon hatcheries during periods when naïve hatchery salmon juveniles are migrating to sea, marine mammal predation is obvious and highly visible to the public (Yurk and Trites 2000). It is quite possible that marine mammals are far more abundant in the SOG today than they have been over the past few millennia; their numbers may have been reduced considerably by harvesting (and culling to protect fishing opportunities) by First Nations peoples (Wallace 1998). At current marine survival rates, about 30% of the 100–200 coho and chinook spawning runs to streams around the SOG are at risk of extinction within the next two decades (Beamish et al. 2000)

Case 2: Large mammal interactions in northern boreal forests

Three key players in the large mammal communities of the boreal forest are moose (*Alces alces*), woodland caribou (*Rangifer tarandus caribou*), and wolves (*Canis lupus*). Moose prosper in successional (deciduous) vegetation communities following disturbance by fire and logging (Schwartz and Franzmann 1991), whereas caribou seek the lichen forage that develops in older forest stands (Servheen and Lyon 1989). Forest harvesting throughout the boreal has decreased the age structure of forests, and created more moose habitat, leading to the current caribou conservation problem. Over most of the boreal forest region, wolves depend (in winter) mainly on moose, and there is evidence of a very long-term, large-scale natural predator–prey cycle between these species (Peterson et al. 1984). Turchin (2003) shows evidence of periodic trends in ungulate and wolf populations in North America, Scandinavia, and Russia. Hudson's Bay Company records of wolf, coyote (*Canis latrans*), elk (*Cervus elaphus*), and deer (*Odocoileus* spp.) pelts show a cycle period of between 30 and 50 years (see Fig. 2). As the length of a cycle is set by the relative rates of prey production and predator mortality (May 1981), we can expect the period to vary somewhat with regional differences in those rates. Peterson et al. (1984) show a cycle period of approximately 38 years for moose and wolves on Isle Royale, which is within the expected range of what we would predict from simple predator–prey models, given the intrinsic population growth rates and survival rates observed for moose and wolves. That is roughly half the period that would be expected from a caribou–wolf cycle. Scandinavian reindeer herds show trends on the order of 70 years (Turchin 2003), as did the Nelchina herd in Alaska (van Ballenberghe 1985). In recent decades, there have been alarming declines in woodland caribou populations, associated with declines in juvenile survival rates.

There has been bitter public debate, at least in British

Fig. 2. Hudson's Bay Company records of wolf and coyote, and elk and deer pelt returns (from Turchin (2003)).



Columbia, about whether to actively intervene with wolf control in the forest areas frequented by these herds. Wolf control programs have typically produced immediate, sometimes dramatic increases in juvenile survival rates of wolves and caribou, but have been followed by strong compensatory responses in wolf populations (Bergerud and Elliot 1998, Hayes and Harestad 2000b). It is also argued that wolf controls result in an increase in bear (*Ursus* spp.) predation, as bears are harassed less frequently by wolves, but because compensatory predation by bears is typically delayed by several years (Bergerud and Ballard 1988), the short-term benefits of a wolf control program would still be realized. Additionally, because bear predation on woodland caribou mainly occurs shortly after parturition when wolves are typically absent, there is little reason to believe that wolves and bears compete during that phase of caribou life history.

In the caribou–moose–wolf system, there are reasons to believe that the “balance of nature” paradigm will not apply. Population dynamics models predict only a limited range of conditions under which caribou can persist if a moose population enters the predator–prey system. Models must assume that wolves ignore caribou at low densities, are incapable of finding them, or only eat the old and dying. There is no dispute that some of this behavior is in effect, but rates of decline suggest these behavioral reprieves do not predominate. Figure 1(b) illustrates the trophic interactions between caribou, moose, and their predators. A wolf population requires a minimum amount of prey biomass to sustain itself. Although caribou are known to be more vulnerable to wolf predation than moose (Haber 1977), wolves tend to sustain themselves primarily on moose because they remain within wolf territories year round, and provide more biomass per kill. Because caribou have lower net birth rates than moose, they cannot maintain net population growth as wolves increase in response to moose productivity. It is the wolves’ numerical response to moose that contributes most significantly to the decline of caribou (Messier 1994). We predict that caribou populations will decline or even go extinct when wolves can continue to increase in response to moose productivity (Seip 1992, Dale et al. 1994, Messier 1995, Bergerud and Elliott 1998, Lessard 2005).

Case 3: Native and exotic fishes in the Grand Canyon

After the construction of Glen Canyon Dam, the Colorado River in the Grand Canyon changed dramatically from a warm, turbid, and violently seasonal ecosystem to a cold, clear, and diurnally violent ecosystem associated with change in flows driven by demand for electrical power. Even the diurnal changes were dampened considerably after 1990. Biological production in the natural system was driven by allochthonous carbon sources, most of which now precipitate out in Lake Powell. Since construction of the Glen Canyon dam, only the upstream reach from the dam to the Paria River has extremely high primary production. A suite of cyprinid and catostomid species originally dominated the river's fish community. Now it is dominated in upstream reaches by exotic rainbow trout (*Oncorynchus mykiss*) and brown trout (*Salmo truta*), and in lower reaches, by warm-water exotic fish species. One remaining native fish, the humpback chub (*Gila cypha*), is listed as endangered, and has been declining in abundance by nearly 10% each year over at least the past decade (Walters et al. 2000). Over the past decade, Grand Canyon scientists and management stakeholders have attempted to use ecosystem modeling in AEAM workshops as a tool to promote communication, expose key uncertainties, and identify alternative management strategies (Walters et al. 2000). The resulting Grand Canyon ecosystem model, and related mini-models for specific populations, has resulted in recommendations for a long-term adaptive management plan involving a "titration" approach, where progressively more severe and costly interventions may be tested along the way to discovering a policy that results in humpback chub recovery.

The remaining humpback chub population has a potadromous life cycle, with spawning and juvenile rearing taking place mainly in one tributary (Little Colorado River, LCR) and adult residence mainly in the Colorado mainstem (Valdez and Ryel 1997). At present, there is apparently no successful juvenile rearing in the mainstem, most likely because of poor growth in cold water and predation by trout near the LCR confluence (Marsh and Douglas 1997). In 2003, the first step in the adaptive management titration experimental plan was implemented, with a relatively inexpensive "mechanical removal" (electrofishing) program to reduce trout abundance near the LCR confluence by 90%, and this exotic control program will likely be extended to other areas and fish species in the Grand Canyon National Park. Debate about further measures to stop the humpback chub decline centers on habitat restoration measures (such as a temperature control device on Glen Canyon dam) to make the mainstem near LCR a more favorable environment for juvenile humpback chub. The main concern in this debate is whether the beneficiaries of habitat restoration will be native fishes or a suite of exotic warm-water fish predators (channel catfish (*Ictalurus punctatus*), carp (*Cyprinus carpio carpio*), striped bass (*Marone saxatilis*)) that could have even more severe impacts on humpback chub juvenile survival than the trout apparently have already. Figure 1 (d) illustrates how predators of the chub benefit directly from the warming of the water, and thus can potentially increase in numbers sufficiently to counter any benefits realized in chub recruitment.

Case 4: Fish communities in the Great Lakes

The Laurentian Great Lakes have experienced massive changes in fish community structure caused by overexploitation of native species and the invasion of exotic species (Crowder 1980). The exotic sea lamprey (*Petromyzon marinus*) played a major role in the reduction of the native piscivores. This contributed to local extinctions of the apex predator, lake trout (*Salvalinus namaycush*), in each of Lakes Ontario, Erie, Huron, and Michigan (see Figure 1c). There has been a great deal of adaptive management modeling work on the Great Lakes ecosystems since the late 1970s (Milliman et al. 1987, Kruger et al. 1995, Jones and Taylor 1999). Restoration of native fish communities became the overall management goal for each of the lakes (Bushian 1990). The sea lamprey control program reduced lamprey abundance to a small percentage of former abundance, and allowed recovery of lake trout in Lake Superior (Smith et al. 1974). Invasions by exotic alewife (*Alosa pseudoharengus*) and rainbow smelt (*Osmerus mordax*) displaced the native forage fishes, including the assemblage of endemic coregonid species. Stocking of non-native salmonids established a biological control for alewife and smelt in the lower lakes, and created recreational fisheries worth billions of dollars in annual economic benefit. In Lake Superior, recovery of the native piscivores, lake trout and burbot (*Lota lota*), led to depletion of smelt stocks and had strong negative impacts on the recovering lake herring (*Coregonus artedii*) populations (Cox and Kitchell 2005).

However, Lake Superior lake trout have two distinct ecotypes (Harvey and Kitchell 2000, Harvey et al. 2003). The nearshore, or lean lake trout, was the target of historical fisheries, and was most vulnerable to sea lamprey attacks. Although fisheries were restricted, fishing mortality and the residual sea lamprey population continued to suppress recovery of this ecotype. The deepwater ecotype (called siscowets or “fats”) were less vulnerable to fishing and to sea lamprey; their populations expanded exponentially (Hansen et al. 1995). This form of lake trout is of little value to fisheries because adults develop extremely high levels of body fat—up to 70% by weight. As siscowet populations increased, their primary prey (smelt and lake herring) declined, causing a growing concern about excessive predation on the prey resource required for recovery of the nearshore, lean lake trout (Cox and Kitchell 2005). Most recent estimates indicate that siscowets outnumber lean lake trout by tenfold, and may be more abundant than at any other time in history of the lake (Ebener 2005). Indicative of this excess is the fact that siscowet growth rates have declined dramatically as their populations have increased.

Recovery of the siscowet is viewed from two perspectives. First, siscowet abundance represents a major success in the restoration of a native species (Bushian 1990). On the other hand, excessive siscowet abundance, and concomitant predation, compromises the recovery of the highly valued lean lake trout. Selective removal of siscowet was offered as a management option directed toward enhancing recovery of lean lake trout. Ecosystem models built to evaluate policy options (Kitchell et al. 2000) indicate that an aggressive siscowet removal policy would be costly because there is no market for the captured fish. More importantly, this model indicates that the first and most prominent ecological response would be an increase in burbot abundance that would continue the heavy predation on prey resources required to recover the lean lake trout. The irony in this case is that an aggressive fishery for both self-sustaining stocks of native fishes (siscowet and burbot) would be required to enhance recovery of the native lean lake trout and the native lake herring. Policies based around “letting nature take its course” would simply allow continued decline in the native lean lake trout and the lake herring.

Ecosystem Control Options

In each of the examples above, there is a substantial risk that “letting nature take its course,” or relying solely upon habitat protection and restoration measures, will lead to widespread extinction of some prey species of one of the abundant predators. Furthermore, management based solely on habitat protection and restoration is either not an option (Great Lakes trout, SOG salmon), would involve high extinction risk for valued species during a long habitat recovery period (boreal forest caribou), or might create even worse problems through exotic species responses (Grand Canyon humpback chub). In all cases, policies should be tested for system responses across a range of densities. There is extreme uncertainty about the efficacy of any policy aimed at more complex control of interactions leading to extinction risk for some species, so the policies that are tried should be treated as management experiments with careful treatment–control comparisons and monitoring. Only in the Grand Canyon case has there been a serious commitment to actually design such experimental policies, and even in that case there is not yet clear consensus among stakeholders (particularly environmental groups and water-power management representatives) to proceed further with the titration approach to compare exotic control vs. habitat restoration options.

There are basically two types of policy options for avoiding high extinction risk, both involving active intervention beyond simple protection from further disturbance. They are as follows:

1. *Symptomatic*: try to directly control predation risk and productivity of the prey species that are at risk from high predation rates.
2. *Systemic*: reach further out into the ecosystem to try and control those factors that have led to high abundance of predators in the first place.

It is not immediately clear what combination of these options would be best for the case examples, given the goal of preventing extinction of valued species.

Symptomatic or direct control measures, particularly predator culling, have the obvious advantage of producing immediate population responses in the species impacted by unnaturally high predator abundance, which makes them at least worth considering in cases where prey extinction appears imminent (e.g., Grand Canyon fishes, boreal forest caribou). But, as is typical of such “quick fixes,” there are at least three arguments against using them. First, they typically result in compensatory responses in the controlled (predator) population, leading to a requirement for sustained culling that can become very costly over time. Second, they may result in unexpected ecosystem responses, e.g., by exotic species that have been prevented from prospering by high predator abundance (Yodzis 2001). Third, they generally trigger strong opposition from conservation groups, who typically object to killing predators on both ethical and practical grounds. Where there is immediacy of extinction risk for some prey species, it is difficult to see how it is any less ethical to cull some predators than to stand by and allow the extinction to occur when it could have been prevented by direct control action.

Direct enhancement of prey productivity is now common practice for Pacific salmons, and is being contemplated for humpback chub in the Grand Canyon case. The use of hatcheries to bypass periods of low juvenile survival has a long tradition, and might be useful as a stop-gap measure until longer-term solutions are found. But this is an expensive option, may not be sustainable in the long run because of problems (such as genetic selection for traits that are favored in hatcheries but not in the wild, or cause widespread epizootics), and may backfire badly by stimulating further abundance increases in predators in cases where the enhanced prey become a significant portion of the total predator food resource. Furthermore, the presence of hatchery rearing that visibly seems to save and produce fish can become an excuse for inaction (i.e., for delaying more costly or controversial management measures).

METHODS

We examine the effects of actively controlling seal populations in the SOG (Fig. 1a), and moose and wolf populations in the boreal forest (Fig. 1b). Through the use of empirically parameterized simulation models, we predicted species abundances under alternative management regimes.

Case 1: Seal Control Programs in the Strait of Georgia

We constructed an ecosystem mass-balance model of the SOG from 1950–2000 using parameters derived from Dalsgaard et al. (1998). The model was implemented using Ecopath with Ecosim, a software program for modeling complex trophic interactions. Ecosim simulates complex trophic interactions, and predicts the species abundances under alternative behavioral assumptions, environmental conditions, and harvest policies. It is widely used to model marine ecosystems and fisheries policies. Using this model, we compared a seal culling policy with a status quo policy to examine the potential of this control option to reduce extinction risk for coho and chinook salmon.

The trophic mass-balance model used in Ecosim uses a set of simultaneous linear equations that assumes the production of species *i* is equal to the consumption of group *i* by all predators *j*, plus export and non-predation losses (including fisheries landings) of group *i*, over a specified time period (Pauly et al. 2000). Two general classes of time series data can be used as input for an Ecosim scenario: forcing data and observation data. Forcing data can include abundance, fishing mortality, or relative fishing efforts, and are used in calculating dynamic changes in the model (e.g., fishing effort time series used to calculate fishing mortality rates over time). Observation data come in two general forms, relative and absolute information, where relative information is assumed to be proportional to model predictions. There are four different observational time series data types: abundance (biomass), total mortality, absolute catch, and mean body weight. Abundance may be treated as absolute or relative, and relative abundance indices are assumed to be proportional to the true abundance and are scaled (using the conditional maximum likelihood estimate of catchability) to calculate a residual sum of squares. Abundance indices and total mortality data are treated as relative indices. Absolute abundance and catch time series information are scaled to the Ecopath units (i.e., t km^{-2}).

Historical abundances trends and catch data were used to estimate vulnerability parameters and relative trends in primary production. The Ecosim model uses a non-linear search routine to minimize the residual sum of squares. Estimating relative trends in primary production is equivalent to

Table 2. Input parameters for 1950 SOG Ecopath model: B = biomass (t/km^2), P/B = production biomass ratio (year¡1), Q/B = consumption biomass ratio (year¡1), EE= fraction of P/B explained by fisheries and trophic interactions, BA = biomass accumulation (t km-2 year-1), and Y = landings from fisheries (t km-2 year-1). Bold values represent estimate parameters, and -BA = Y for fisheries that start after 1950.

Group Name	B	P/B	Q/B	EE	BA	Y
Transient Orcas	0.003	0.02	7.4	0	0	0
Dolphins (Res. Orca)	0.05	0.02	7.3	0.844	0	0
Seals & Sealions	0.4	0.16	8.1	0.96	0	0.04
Halibut	0.004	0.44	1.7	0.776	0	0.001
Lingcod	5.591	0.39	1.2	0.169	0	0.273
Dogfish Shark	6.5	0.1	2.5	0.033	0	0
A. Hake	7.737	0.5	5	0.863	-0.3	0.3
J. Hake	2.321	2.48	9	0.596	0	0
A. Res. Coho	0.198	1.3	3.24	0.968	0	0.12
J. Res. Coho	0.838	2.4	7.3	0.475	0	0
A. Res. Chinook	0.33	1.4	5.475	0.959	0	0.296
J. Res. Chinook	1.231	2.4	7.3	0.651	0	0
Demersal Fishes	12.6	0.52	2.5	0.995	0	0
Sea Birds	0.02	0.1	91.7	0.949	0	0
Small Pelagics	2.86	2	18	0.95	0	0
Eulachon	2.114	2	18	0.95	0	0
A. Herring	16	0.67	6.3	0.917	0	7.22
J. Herring	3.58	1.172	11.06	0.725	0	0
Jellyfish	15	3	12	0.211	0	0
Predatory Invertebrates	9.1	1.65	8.8	0.55	0	0
Shellfish	220.5	0.5	5.6	0.776	0	0
Grazing Invertebrates	400	3.5	23	0.55	0	0
C. Zoolplankton	12.948	12	40	0.95	-0.5	0.5
H. Zoolplankton	24.688	25	183.3	0.95	0	0
Kelp/Sea Grass	20.3	4.43	-	0.158	0	0

Phytoplankton	65.206	200	-	0.6	0	0
Detritus	1	-	-	0.711	0	0

estimating process errors in a mixed error model (Walters and Martell 2004). Estimates of vulnerability exchange rates are most sensitive to Ecopath biomass input parameters, consumption rates (Q/B), and the diet matrix, as this information is used to define the functional responses in the Ecosim model (see Walters and Martell (2004) for more details). These exchange parameters, combined with simulated adjustments in foraging time with changes in competitor density, create predation functional response patterns ranging from type I to types II–III. Type I responses are predicted when vulnerability exchange rates are low (prey behavior controls availability to predators); type II responses are predicted when exchange rates are high; and type III responses are generated for prey types that are likely to reduce activity or feeding time in response to predation risk when abundances of those prey types are low. Fitting procedures generally indicated quite low vulnerability exchange rates (i.e., strong limitation of predation rates by changes in prey behavior at lower prey densities). For some species, composition information was taken from Dalsgaard et al. (1998) whereas for others, it was taken from results derived from the literature provided in Pauly et al. (1998). In cases where species leave the SOG ecosystem on a seasonal basis, a fraction of the diet was imported. For example, recent evaluation of herring tagging studies has demonstrated that a large fraction of the SOG herring population undergoes annual migrations (Hay et al. 2001). For this reason, 39.7% of adult herring diet was imported. We used the same parameters that produced the best statistical fit to historical population trends (see Table 2) to predict abundances in future years (i.e, 1998 and beyond). We chose a fixed fishing rate of 0.3 from 1950 to 1970 for the harbor seal bounty program, and set the policy options in Ecosim’s software interface. We then simulated the outcomes of controlling seal populations for 10 years vs. not controlling seals. The abundance predictions were then used as a basis for evaluating the benefit of culling.

Case 2: Wolf Control Programs in the Boreal Forest

As with the seal model, we parameterized our model using empirical results from the literature. Messier (1994) calculated the maximum killing rate and half saturation coefficient using 100-day killing rates from 17 moose subpopulations. This gives an effective rate of search of 27 km^2 effectively searched per wolf per year. Given a moose attack success rate of 5% (Peterson 1977), we calculate an overall search rate of 533 km^2 per year. We used 1 day as the handling time (Hayes and Harestad 2000a) of caribou, and scaled these relative to body weight for moose (2.5 caribou units). We used type II (hyperbolic) functional responses to model wolf predation on caribou and moose adults as well as calves. The type II response is the accepted form for the functional responses of both caribou (Dale et al. 1994) and moose (Messier 1994, Hayes and Harestad 2000a). Given that caribou herds have been declining and are being extirpated from regions where they share common predators with other ungulate species, a type III functional response seems overly optimistic despite the appeal that switching could naturally lead to alternative stable states. We used the attack success probabilities from Haber (1977) to scale the overall search rate to respective effective rates of search for each prey class. These were 0.45, 0.65, 0.05, and 0.25 for caribou adults, caribou calves (in this case &#60 6 months old), moose adults, and moose calves, respectively. We also scaled the effective rates of search on caribou further to account for seasonal overlaps with predators and relative probabilities of encounter due to spatial and temporal separation from predator territories. Net birth rates were 0.18 and 0.43 for caribou and moose, respectively. These account for all causes of calf mortality before contact with wolves, including effects of other predators. Although this model has not been rigorously tested, it captures some important points about this system: 1) caribou are more vulnerable to predation than moose, and 2) caribou are less productive than moose. These simple facts dominate the behavior of this system.

Fig. 3. Components of the Strait of Georgia ecosystem model in response to a 10-year seal cull (represented by the shaded region). An increase in abundance of transient orcas eventually reduces harbor seal abundance, and coho and chinook salmon abundance stabilizes at levels below historical average (top panel). Under a 90% reduction in harbor seals, transient orcas do not respond numerically, allowing harbor seal abundance to increase after the cull. Chinook and coho populations increase during the cull. However, the reduction in predation mortality is short lived, and abundance declines after the seal cull.

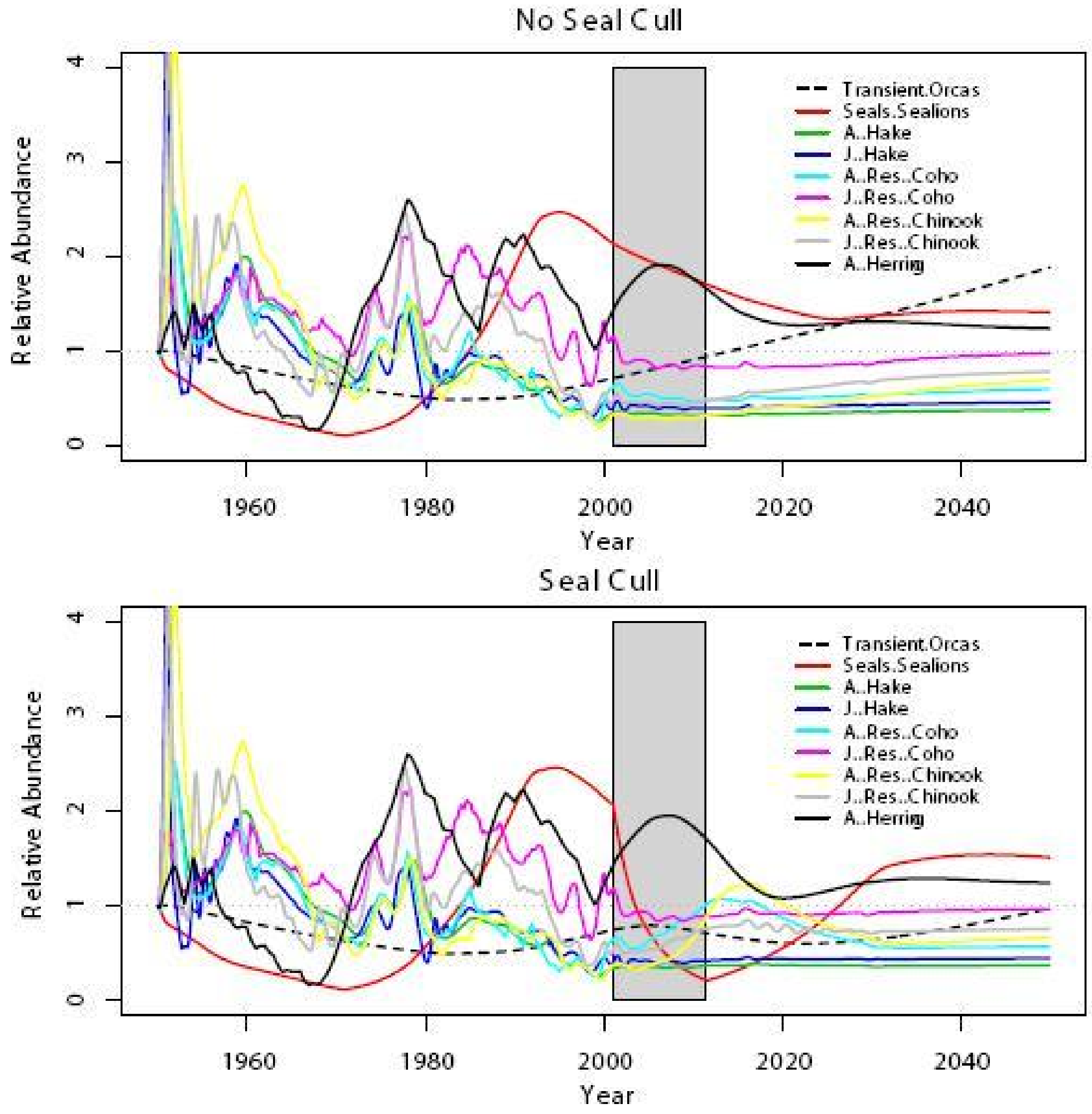


Fig. 4. Predicted caribou densities (animals km^2) under alternative management options. WC = Wolf control; MH = Moose harvest; Pulse WC = 10-year timed wolf control.

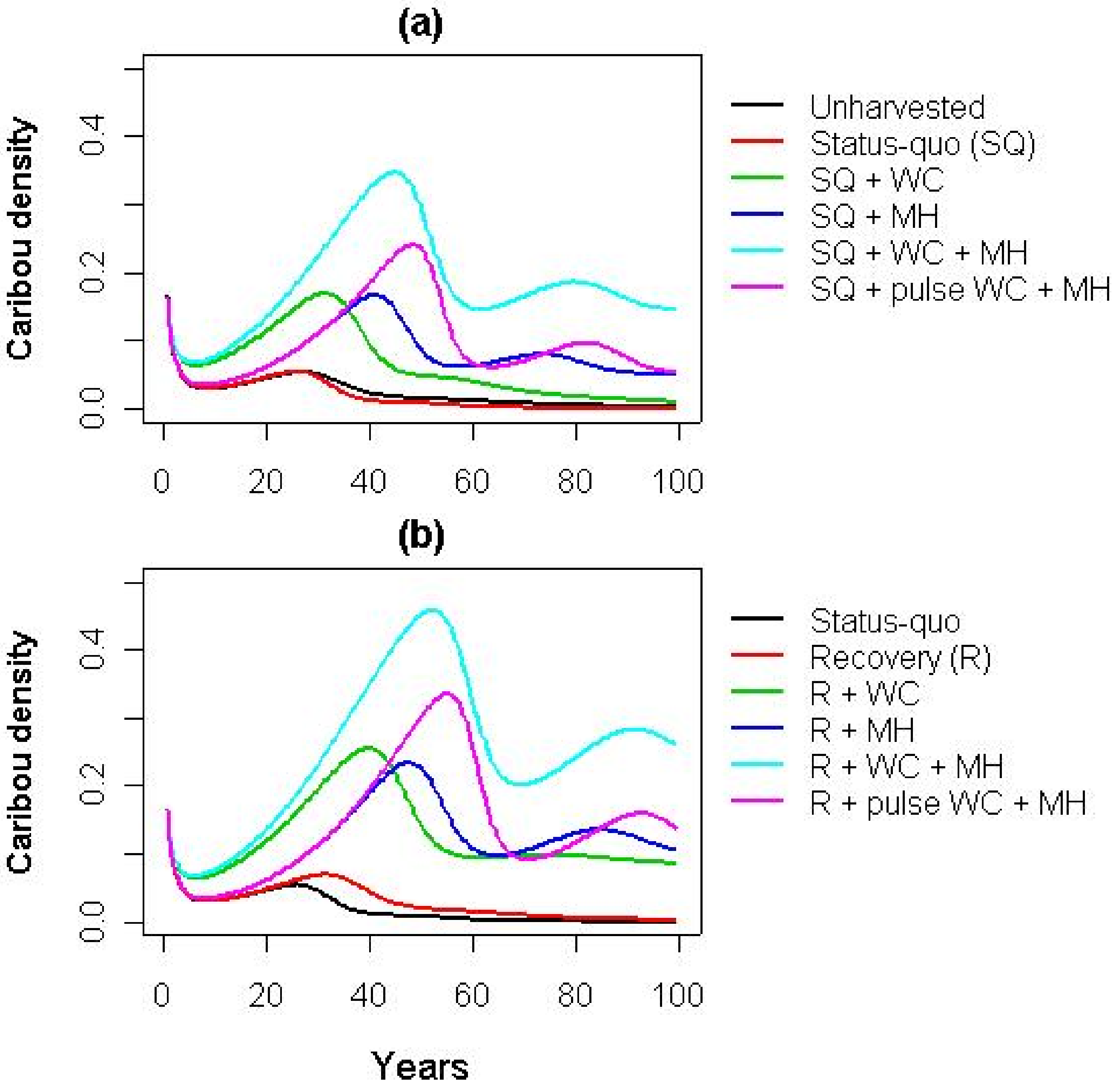
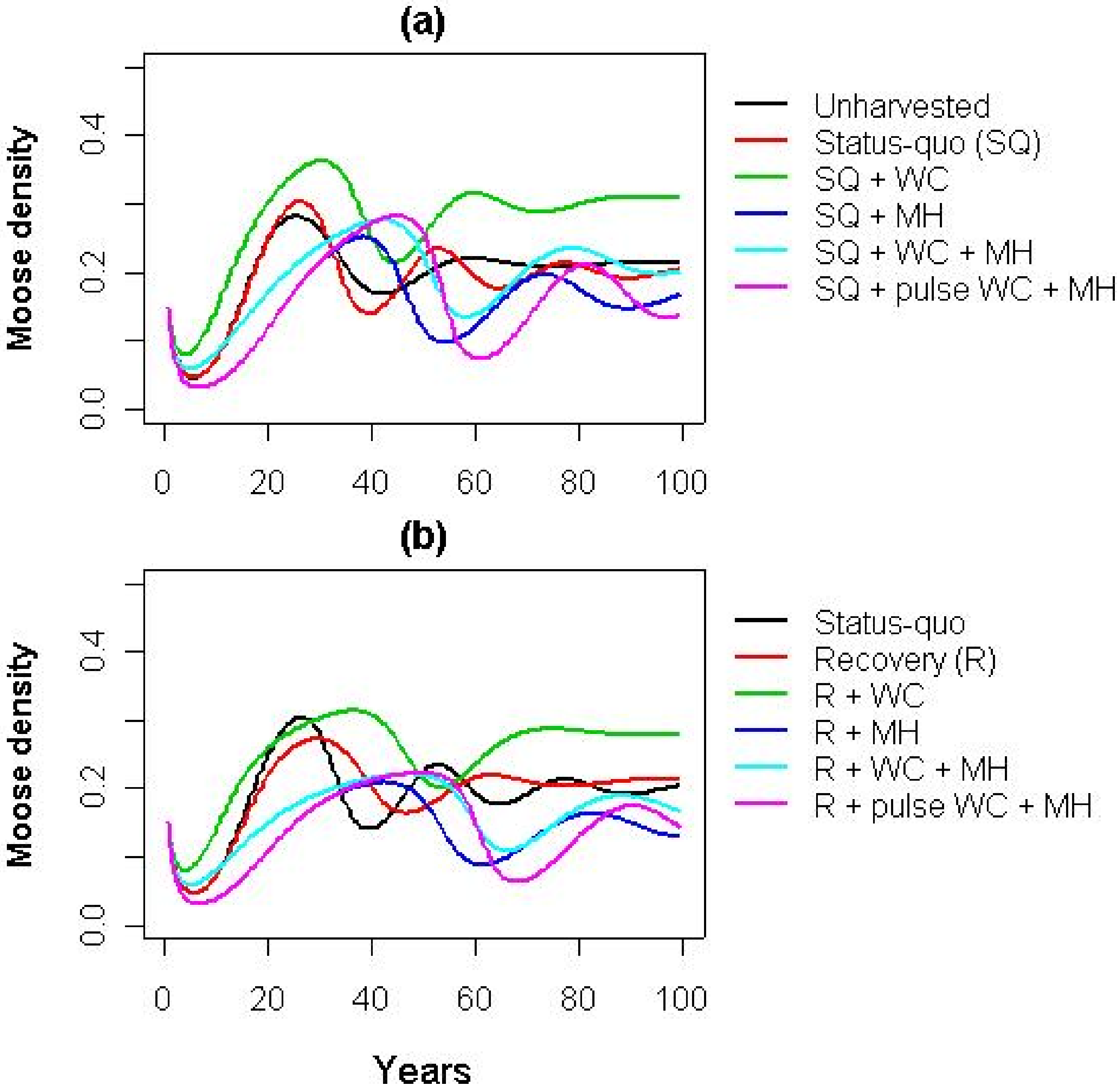


Fig. 5. Predicted moose densities (animals km^2) under alternative management options. Recovery refers to a 15% reduction in forest harvest. WC = Wolf control; MH = Moose harvest; Pulse WC = 10-year timed wolf control.



We first contrast the behavior of the system unharvested (no logging) vs. status quo (100-year harvest rotation), applying four scenarios of species abundance control in each context. We then contrast the same scenarios, but in the context of status quo vs. a forest recovery plan aimed at providing increased long-term supply of old-growth habitat and additional spatial refuge for caribou. The scenarios are as follows:

1. Wolf control policy (WC)
2. Moose harvest policy (MH)
3. Combination policy of wolf control with alternate prey control (WC + MH)
4. Short-term policy (10 years) of wolf control (pulse WC)

The wolf control policy involved raising the instantaneous mortality rate of wolves from 0.50 (natural) to 0.70. Moose harvest removed an additional 10% of adult moose from the population. The forest harvest policies were varied from a status quo rotation of 100 years to a 125-year rotation, where oldest stands were always harvested first.

RESULTS

Case 1: Seal Control Programs in the Strait of Georgia

The outcome of controlling harbor seals is shown in Fig. 3. When harbor seal abundance in the SOG was reduced by 90% over a period of 10 years, Ecosim predicted that adult populations of coho and chinook salmon would increase with continued recreational and commercial fishing, although only transiently during the cull. The extent of the increase would be determined by the assumed values of chinook and coho in harbor seal diets. This result assumes that harbor seals are significant predators on both juvenile and adult salmon, and that Pacific hake (another major juvenile salmon predator) abundance does not increase. In 2000, harbor seal predation and fisheries accounted for roughly 57% of the hake mortality. After the cull, lingcod (not shown in Fig. 3) increased in response to the reduced seal predation. This numerical response maintains the relatively high predation mortality rate on Pacific hake, allowing juvenile salmonids to escape possible increases in hake predation mortality. However, if the hake fishery does not persist or lingcod fail to respond numerically to reduced seal predation, then potential increases in hake abundance could severely increase juvenile salmonid mortality rates. The model did not predict this, but it still remains a possibility. Adjustments to the diet matrix after monitoring salmonid predation rates may cause the model to predict these increases in hake predation on juvenile salmon. Management policies could be designed to be sensitive to information gained by monitoring for this.

In this case, treating the symptom (increased harbor seal predation) may increase juvenile and adult salmon survival rates, but it may also lead to unintended consequences. It is just as likely that Pacific hake stocks could increase dramatically in response to reduced harbor seal predation. Pacific hake are also consumers of herring and other commercially important species in the SOG, and indirect competition for resources may also limit the ability of salmon populations to increase. The symptomatic control option (reducing harbor seal abundance) only has short-term effects. After the cull, the harbor seal abundance increases over the next 20 years, and causes a delay in the increase of transient orca (*Orcinus orca*) abundances (a harbor seal predator). Salmon abundance declines in response to continuous fishing and increasing predation mortality rates.

Case 2: Wolf Control Programs in the Boreal Forest

Figure 4(a) shows the effect of a status quo harvest scenario on caribou density. We can see that, in the long term, it is more effective to control moose densities than to continuously control wolves. Figure 4(b) shows the effect of reducing the impact of forest harvest. In this case, the forestry annual allowable cut was reduced by 20%, and we modeled a forest harvest design that provides additional old-growth refuge for caribou, thereby lowering the encounter rate with wolves. The net effect, regardless of wolf culling or moose harvest, is an increase in caribou abundance. In Fig. 4(a) and 4(b) we can see that moose harvest has a more noticeable effect than wolf culling, but that a 10-year pulse of wolf harvesting early in a decline in caribou can hasten recovery. When combined with a moose reduction, caribou populations benefit nearly as much from a well-timed pulse of wolf culling as from a sustained cull.

Figure 5 shows the response on moose populations. In contrast to caribou, moose respond more to the changes in forest harvest practices than to wolf culling. Moose are much more resilient to being harvested when the forest is also being harvested. It is not surprising then that caribou populations suffer the opposite fate under those conditions, if we consider that wolves are responding numerically to moose abundance. Ultimately, wolf culling has little effect at the rate used. The most obvious benefit to moose populations is an increase in the rate of forest harvest and the biggest negative effect is moose harvest.

The most important predicted result is that, when moose are harvested and wolves are culled, caribou recover and moose remain more or less at the same densities as when no action is taken.

DISCUSSION

A key reason for bringing forward the examples above is to emphasize that simple ecosystems principles derived from assumptions about natural ecosystem development and performance (“natural is better” and “let nature take its course”) cannot be safely or wisely used to screen operational management choices. In particular, such principles cannot be used to reject, out of hand, such symptomatic policies as direct predator culling, in favor of systemic choices such as protected area policies. This point has long been obvious to ecologists in relation to ecosystems that have been severely altered by exotic invasions, but it has not been admitted in cases where an unnatural abundance of natural predators has arisen through some combination of historical “accidents” (e.g., increased seal abundance as a result of reduced predation on seals by First Nations peoples) or myopic management prescriptions (e.g., increased boreal forest disturbance leading to increased moose and wolf abundances).

We admit that recent human history contains abundant examples of good intentioned and seemingly appropriate policy actions that have gone disastrously awry. A particularly tragic example can be found in the attempts to improve drinking water supplies in Bangladesh that ultimately led to widespread arsenic poisoning (Nickson et al. 1998). We cannot pretend that aggressive policies are without risk, nor that we can reduce all uncertainties by developing more detailed models. Rather, we are advocating that these aggressive management controls at least be considered in formal risk analyses, wherein the potential for unintended consequences can be weighed against the more certain consequences (e.g., extinction) of passive controls.

It could be argued in such cases as the boreal forest and the SOG that symptomatic control of predator abundances is simply a way to hasten recovery to a more healthy and balanced ecosystem state, while reducing risk of “permanent” biodiversity loss (extinction of some prey species) during the ecosystem recovery process. In these cases, the specter of extinction risk lends credibility to arguments for controls that will likely have immediate effects, and there is at least some expectation that such controls will not have to be used on a sustained and hence very costly basis as a routine part of sustainable management. This was illustrated in Fig. 4(a), where a short pulse of wolf control hastened recovery of caribou by more than 10 years, although the effect was transient.

Challenging decision problems about symptomatic controls arise in cases such as the Grand Canyon and Great Lakes, where there is no prospect of the ecosystem eventually returning to a diverse and productive state without continuing control of exotics (e.g., rainbow trout and warm water piscivores in Grand Canyon) or natural predators (siscowet trout in Great Lakes). In these cases, it is not a question of ethical principles regarding extinctions that is at stake, but rather the quantitative balance of costs and benefits associated with managing for alternative abundance regimes (e.g., costs of culling more siscowets in order to produce more of the valuable lean type lake trout). Economically and socially, government management agencies cannot simply argue that investment in symptomatic control should be maximized at whatever cost (for Grand Canyon exotics) or that control should be avoided at all costs (opportunity cost of foregone production of lean lake trout in the Great Lakes).

We admit that there is a great deal of uncertainty regarding sources of mortality to target species. In each case example, we recognize that active species controls may either not result in a commensurate increase in survival of target species or may lead to a compensatory mortality response from a competing mortality agent. Regardless, we feel that there is a credible argument to be made that risks of extinction of target species are likely to be reduced by active species controls.

An important message from the SOG simulation exercise is that it appears that a temporary reduction in harbor seal abundance is not a permanent solution (i.e., the system does not flip to a low seal abundance state (Fig. 3)). Harbor seal abundance returns to a high abundance state roughly 20 years later, and salmonid populations return to a lower state. If ocean conditions change favorably over this time period, the magnitude of the salmonid increase is proportional to the relative increase in primary production, however, harbor seal abundance and other salmonid predators also increase in abundance. If such an immediate action as a harbor seal cull is required to protect endangered coho and chinook salmon stocks, then a systematic approach should be considered, where fisheries are used to control the abundances of other potential predators to alleviate potential threats to a rebuilding program. Presently, ecosystem responses to predator control programs remain uncertain because there is no practical way to directly measure predation rates on juvenile salmon in the field. At best, we can hypothesize about the potential benefits of reducing predation on salmon populations for the benefit of salmon fisheries. The bigger question concerns the level of risk that we may be willing to take to carry out such an experiment. It may be just as likely that the high abundance of harbor seals has suppressed Pacific hake populations, preventing further increases in juvenile salmon mortality rates.

Predicting how to reverse a decline elicits questions regarding uncertainty and the length of time it would take for a recovery to occur. In predator–prey systems, it is widely considered that the key parameter is the effective rate of search of the predator, which represents the cumulative effects of the predator search rate, the encounter probability, and the probability of successfully killing the prey. Small changes in this parameter dramatically change long-term predictions. Intrinsic rates of growth and natural mortality rates of adults are more certain. Ungulate studies have traditionally been designed to study these rates, but with little thought regarding trophic interactions with predators. The inherent risk to policy design lies in the fact that uncertainty in the effective rate of search, compounded by numerical responses in predators, causes a wide range of variability in predicted net predation rates. Nonetheless, a policy designed to reduce the number of predators can only reduce the amount of predation in the short term. Our simulation results demonstrate the immediate value of predator reduction, but also indicate the transient nature of this benefit. This suggests that a combination short-term cull with a long-term recovery may be in order.

There is ample evidence that a reduction in wolves brings about an increase in ungulates. This arises from increases in both adult and juvenile survival (Gasaway et al. 1992, Bergerud and Elliot 1998, Hayes and Harestad 2000a). An obvious hypothesis for recent declines and rapidly growing extinction risks of woodland caribou herds is that wolves are now unnaturally abundant, because of increased productivity (and protection from harvesting in some areas) of their dominant prey species: moose. Even if the forest disturbance regimes were radically altered through changed harvest management and fire control, the legacy of increased moose productivity associated with successional vegetation communities will quite likely persist long enough that at least some rare woodland caribou herds will be driven to extinction. It can also be argued that, as caribou populations exist at densities far below theoretical carrying capacities, animals are not competing for food at present densities and would not benefit immediately from improved habitat on those grounds anyway. Caribou would benefit from protection not by any immediate increase in survival rates. Rather, the benefit would come mainly when moose populations decline, causing wolf populations to also decline.

It is worth noting that caribou and moose respond very differently to manipulations of the boreal forest system. The reasons for this are: caribou are more vulnerable to predation, they feed in old habitats that are slow to regenerate, and they are less fecund than moose. No form of habitat management can bring about a rapid reversal in any of these factors. The mechanism that partially compensates for the vulnerability to predation is refuge (or spatial separation). It may be possible to design management policies that create refugia, but the benefits will once again not likely be felt for some time. It appears that the most effective way to bring about a reversal in caribou population decline in a system where moose are the main cause of a wolf population increase is to directly control wolf and moose populations.

The four cases studies share one common characteristic. A change occurred that caused the net rate of growth of a species to decline because competitors and(or) predators enjoyed a population rate of increase. The choices presented to management agencies are simple: 1) bring about a change to the system, or 2) attack the symptom. It is clear that there are cases where symptoms have been brought about by alterations to the system, and that there may be insufficient time for recovery of a declining species. This occurs largely because the balance between the growth of one species, its consumptive needs, and the numerical responses of competitors and predators, can occur beyond the reproductive capacity of more vulnerable species. Management agencies cannot expect to accurately predict the futures of such systems where key information is currently lacking. Adaptive management experiments can help to reduce this uncertainty. Where experiments directly control predators and competitors of valued species, a measure of recovery will perhaps also take place. Careful monitoring of abundances should warn managers whether experiments are having the desired effect.

The use of systemic controls that attack causes of dynamic imbalance has obvious appeal to ecologists, particularly in cases like the Grand Canyon where controls involving restoration of more natural habitat conditions (warmer water, seasonal flow fluctuation) may (if exotic species do not interfere) allow natural dynamic processes to result in healthier ecosystem states in terms of species abundances. However, systemic controls can be thought of more broadly than controls on habitat disturbance factors. For example, in the boreal forest there is a “natural” dynamic interaction between big-game hunters and moose, such that relaxing regulations on moose harvesting may result in considerable reductions in moose abundance and net production available to support wolves. Progressively more restrictive ungulate harvesting regulations in jurisdictions like British Columbia may have unwittingly contributed to extinction risk for caribou, by considerably increasing moose abundance. A policy of increasing moose harvest rates may actually be a restoration of a natural order. In the Great Lakes case, there is an obvious need for ecosystem-scale policy analysis for stocking and harvesting of all species, to seek abundance and yield combinations that will permit recovery of biodiversity within the lake trout species.

Such cases cry out for complex, multi-species control policies, and it is pointless to argue that we do not have enough understanding of ecosystem dynamics to design such policies. Multiple species controls involving both harvest regulation and stocking, and various controls on deleterious inputs and habitat changes, will continue to be implemented whether or not they are well coordinated. In the absence of an ecosystem perspective and predictions about trophic interactions, such controls will simply continue to be evaluated using myopic and dangerous criteria: hatchery programs will be judged only by how many fish and how much fishing activity they produce, native fish restoration programs will be judged only by how abundant the target species become in the short term, etc. It is lack of coordination and prioritization that will make such fragmentary policies fail, not that they have complex consequences in the first place.

The key to successful policy implementation for cases where sustained symptomatic control of some predator abundances appears unavoidable may lie in understanding and creating incentives (Hilborn 2004) for particular stakeholder groups to undertake the “costs” of control. In the boreal forest case, it should not be at all difficult to create improved incentives for moose hunting, through tactics such as liberalized hunting regulations and access improvement. In the Great Lakes case, it will probably be possible to create incentives for commercial siscowet harvesting, through tactics ranging from cost and tax subsidies to assistance in developing marketing options (after all, fisheries management agencies have a great track record at helping stimulate development of overcapacity in many fisheries). In the Grand Canyon, it may be possible eventually to offset at least part of the cost of continued mechanical removal by developing markets for the fish that are harvested. In the SOG, it may be possible to use existing commercial fisheries to monitor hake consumption rates of juvenile salmon to determine whether increased hake harvests are required to reduce salmon predation rates.

CONCLUSIONS

Our final comments about incentives for implementation of symptomatic controls imply that the process of successful ecosystem policy design must be a fundamentally interdisciplinary one, involving careful analysis of both ecological interactions and the economic behaviors of ecosystem users and stakeholders. Given available methods for involving broad expertise in problem analysis and “brainstorming” of policy options, such as the AEAM workshop process (Holling 1978, Walters 1986), there is little reason for failing to use such methods to seek more complex and viable policy options than simply ecosystem protection, particularly when protection has obvious inherent risks in itself.

Passive approaches to ecosystem management are ideally suited for situations where imbalances, as demonstrated in the case studies herein, have not yet come to be. Should we have the ability to turn back time, we would certainly advocate such preventative measures to prevent the current status quo from happening. Given that this is impossible, we look to historical evidence, such as our case studies, to demonstrate the dominant effects of some trophic interactions. The simulated outcomes of the SOG salmon/seal populations and of the boreal forest wolf/ungulate system are two examples of how to identify potential control options that can be tested in an adaptive management design. Once the effects of uncertainty have been more thoroughly analyzed, the risks associated with symptomatic control can be better understood. In the interim, using models to identify symptomatic control policies presents an option that may allow immediate benefits to valued prey species in a way that passive policies do not.

It is noteworthy that only in the Grand Canyon case, where active intervention is both relatively inexpensive and involves an exotic species, has it been possible to obtain broad support for an adaptive, experimental management program. The other cases represent adaptive management “failures” as described by Walters (1997), where modeling and debate has failed to trigger any decisive plan of action. In those cases, there has been more debate about the models, the data used in developing the models, and ethical discussions than decisive action about designing experiments that correct the symptoms and deal with the uncertainty of unintended side effects. There is also misplaced hope that better data and models will eventually resolve the uncertainties, even if no decisive experiments are conducted. There is no broad recognition that inaction is itself an experimental policy choice, with a reasonable probability of failure.

Responses to this article can be read online at:
http://www.ecologyandsociety.org/vol10/iss2/art1/responses/

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