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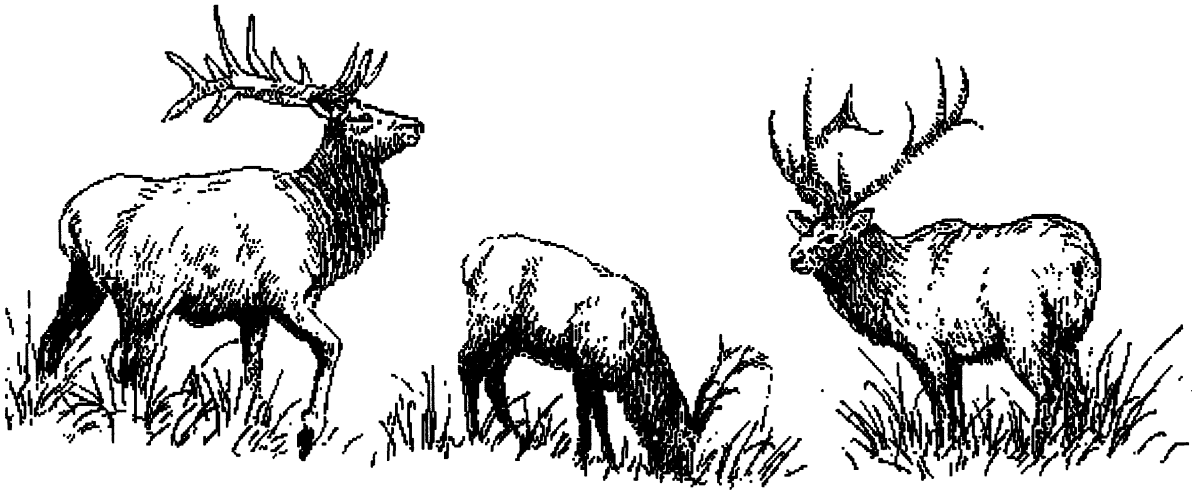

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Letter to the Editor

Endangered Species and Peripheral Populations: Cause for Conservation

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Introduction

Peterson (2001) suggests that conservation efforts aimed at peripheral populations of species dilute the effectiveness of the Endangered Species Act (ESA). Furthermore, he states that specific peripheral populations are often not viable, could be considered sink populations, or are often species of little conservation concern. He goes on to say that the biology of the species should be considered when deciding which species to put on the endangered species list. We strongly agree with the assertion that the biology of the species should be fully considered when assessing the conservation status of a species. Lack of such information is one of the biggest hurdles to a species' recovery (Schemske et al. 1994; Tear et al. 1995).

However, we differ from Peterson (2001) in the conservation value of peripheral populations. In contrast to Peterson's (2001) statement that peripheral populations have always been marginal, it is well documented that species' ranges change dramatically with global shifts in climate. Global warming could affect species that reach northern extremes along the U.S. southern border by shifting their ranges further north (Abbitt et al. 2000). Peripheral populations may survive in isolated refugia that later, with different environmental conditions, serve as a source population for an expanded range and subsequent adaptive radiation (Flannery 2001). What constitutes a peripheral population today could be the center of a species' range in the future. For example, the present California condor (*Gymnogyps californianus*) population is peripheral to its historical distribution, which ranged from California to New York (Snyder and Snyder 2000). We are unable to anticipate the future geographical distribution of species. We ignore the dynamic nature of the natural world if we assume that common species in one location (e.g., the gray wolf, *Canis lupus*, in Alaska) do not need protection elsewhere in their range where they may be rare (e.g., gray wolf in Idaho) (Botkin 1990). Even abundant and widespread species have gone extinct (e.g., the passenger pigeon, *Ectopistes migratorius*). Moreover, peripheral populations survive more frequently than do core populations when species undergo dramatic reductions in their range (>75%; Channell and Lomolino 2000).

Thus, we believe peripheral populations are vitally important to a species' past, present, and future existence. The ESA, by allowing for the listing of subspecies and distinct population segments, explicitly identifies the evolutionary potential of each species as our conservation goal in law. We contend that ultimately the management unit of interest for a species is its full range of variation, for only then can a species' evolutionary trajectory be possible.

Evolutionary potential of peripheral populations

The concept of "peripheral populations" can be interpreted on several scales. Value judgments made about the viability or importance of such populations are derived from personal perspectives. Peterson states, "conservation priorities based on biodiversity considerations are sensitive to a taxonomic viewpoint" with biological species found in central areas and phylogenetic or evolutionary species along the periphery of the distribution (Peterson and Navarro-Siguenza 1999). Many scientists prefer to take a top-down perspective on population structure where systematics at the "biological species" level is the critical unit of conservation. Other scientists tend to think from the bottom-up where population genetics drives the level of diversity and the scale of appreciation. Biological development and evolution, however, operate in the range of values found between these two extremes.

Because we know so little about so many populations and species, we should not preconceive "peripheral" conditions as a single state or characteristic (Schemske et al. 1994: Channell and Lomolino 2000). Doing so would violate the precautionary rule of Conservation Biology. This is articulated well by Aldo Leopold (1966): "To keep every cog and wheel is the first precaution of intelligent tinkering."

Declines in genetic variation due to demographic bottlenecks in small or declining populations (i.e. peripheral populations) are of great concern to conservation biologists. According to population genetic theory, a reduction in genetic variation following demographic bottlenecks and inbreeding can lead to lower individual fitness and lower population adaptability (Lande 1988; Lacy 1997). Genetic surveys of endangered populations, however, typically look at the level of genetic variation currently carried by a population rather than the magnitude or rate of change in genetic diversity over time. Both theoretical studies (e.g. founder-flush for Templeton 1980) and empirical evidence (Nielsen 1999) show that populations founded by a small number of individuals do not necessarily suffer from the expected reduction in genetic diversity marking peripheral populations as weak representatives of their overall species diversity. Genetic drift in such populations can be weaker than would normally be expected, particularly for low frequency alleles. Small populations with adequate reproductive habitat show low levels of intraspecific competition, and most individuals contribute to subsequent generations, leading to a period of rapid growth. Therefore, the probability of loss of a neutral lineage is low, and the probability of fixation for advantageous alleles is much higher than in populations that remain a constant size (Slatkin 1996). In other words, peripheral populations at the edge of a species' range can carry unique genetic structure and provide new evolutionary material when compared to populations at the center of the species' range (García-Ramos and Kirkpatrick 1997; Lammi et al. 1999). The evolutionary future of a species could ultimately rely on its peripheral populations (Sexton et al. 1992; Lesica and Allendorf 1995).

If a peripheral population has been demonstrated to have low genetic diversity, this state may be historic and not associated with recent population declines (Matocq and Villablanca 2001). Natural levels of genetic diversity found in endangered populations need to be analyzed on multiple scales to differentiate historic demographic patterns from contemporary colonization effects (Luikart et al. 1998). A demographic crash in a peripheral population can result in the loss of diversity, but many endangered populations have a history of small effective population size with low historic levels of diversity over long periods of time. That does not qualify them as throwaway populations. It is important not to accept the premise that all peripheral populations are alike or are equal in the level and type of diversity they reflect in relationship to populations at the center of the species' range.

Determining a peripheral population

The selection of reference populations for the determination of peripheral states can drastically alter the interpretation of natural levels of genetic diversity in endangered species (Matocq and Villablanca 2001). Populations at the edge of a species' range may have been colonized by evolutionary or demographic processes that have nothing to do with the current demographic distribution of the species. Populations that are

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derived from alternative refugia populations are a clear example. The anadromous steelhead of southern California (*Oncorhynchus mykiss*) represents such a case. Current demographic data support a pan-Pacific radiation for this species from Pleistocene Beringia refugia. Genetic analyses performed on contemporary, small populations of this species at the southern extent of their range (Nielsen et al. 1994, 1998) shows that these fish are not a peripheral population of no conservation value. Rather, these fish are unique to the evolutionary history of this species, probably derived from Gulf of California refugia (Nielsen 1999) instead of hatchery fish lost at sea. Based on multiple genetic studies, all southern California steelhead are now listed as an endangered Evolutionarily Significant Unit (ESU) under the ESA. Ignoring this "peripheral" population would mean the loss of a unique historic evolutionary lineage for this species, which could be important to the survival of steelhead in the face of global warming.

Habitat conservation

One inevitable result of writing off peripheral populations without efficient and critical assessment of their state is the loss of habitat protection in the areas where these populations are found. The ESA is designed "to provide a means whereby, the ecosystems upon which endangered species and threatened species depend may be conserved." Many species with restricted ranges are strong candidates for the next generation of listed species (Abbitt et al. 2000). Of these species, many are also peripheral populations that represent the northern extreme of a species' occurrence in the Americas that with global change could become the center of a species' distribution. Peterson's (2001) arguments speak strongly to the need for transboundary multinational conservation (Roca et al. 1996) in order to preserve the entire species range and address the biology of the species in our conservation efforts. If human activities, which often create peripheral populations through habitat loss, are to be sustainable, we need to ensure resilient ecological systems on which our multinational economies depend.

Metapopulations

Peterson (2001) applies population ecology to show peripheral populations are often not viable. However, peripheral populations could represent a single population within a metapopulation. The metapopulation concept assumes a discontinuous distribution over spatially disjunct "patches" of suitable habitat (McCullough 1996), which could include peripheral populations. The focus is on dynamics and processes that affect all the populations, not just a single population. Each population within the metapopulation possesses a different probability of extinction as well as a different probability of (re)colonization. However, all those probabilities combined may result in the persistence of the metapopulation. Interpopulation dynamics, amongst all core and peripheral populations, are what the metapopulation concept describes. Discounting peripheral populations could reduce the viability of the metapopulation.

Final thoughts

Two future paradigms seem to permeate scientific and popular perspectives: 1) nature as the ward of humanity with visions of unlimited growth, new technologies and important developments obtained from "wild" environments; 2) people as stewards of nature where it is in the global interest to keep as much diversity as possible at the genetic, species, and ecosystem levels regardless of their immediate social value (Fuentes-Quezada 1996; Harte 1996). As scientists, we do a poor job of communicating to the public how these philosophies are integrated into scientific research. Categorical hierarchies of scale and definition in biology are conceived and invoked by a basic human need to impose order and control. In our ignorance of the processes of evolution and the complexities of ecosystems, the dialogue on "saving all of the pieces" or defining what parts to save continues to haunt the conservation community into the foreseeable future. It is fortunate that societal values of nature are changing constantly and scientists are always and inevitably a product of their time.

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Correction: In the special issue on carnivore conservation (Vol. 18 no. 4), there was an error in Table 1, p. 135. The corrected figure is printed here. We apologize to the author for the mistake.

Table 1. A comparison of prey frequencies with scats separated by size and molecular analysis. One jaguar scat was disqualified from the dietary analysis for containing bait (from Farrell et al. 2000). Small predators = Fox and ocelot. Large predators = Puma and jaguar.

Frequency (%) of Prey Types	Scat size		mtDNA	
	Small predators <25mm	Large Predators ≥25mm	Small Predators	Large Predators
Small mammals	75	46	64	-
Medium mammals	12.5	12	3	50
Large mammals	12.5	9	-	50
Reptiles	-	9	9	-
Birds	-	12	12	-
Fish	-	3	3	-
Crabs	-	9	9	-
	n=3	n=16	n=12	n=7

Conservation Spotlight

Keeping Yellow-footed Rock Wallabies on the Rocks: Integrating In- and Ex-Situ Conservation in Australia and North America

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Abstract
*The most successful species recovery programs incorporate many components; the work being done with yellow-footed rock wallabies (*Petrogale xanthopus xanthopus*) involves three of the most important ones: collaboration, conservation, and community involvement. Active captive conservation work is occurring with both the North American and Australian populations. The American Zoo and Aquarium Association is collaborating with the Australian Regional Association of Zoological Parks Aquaria and Environment Australia to import new founder stock needed to genetically revitalize the North American population. In-situ conservation work has involved habitat reclamation and reintroduction projects. In an additional collaborative venture, some of the same methodology used in the reintroduction project is being applied to work with tree kangaroos in Papua New Guinea. The value of community involvement was shown to be essential in the success of these projects.*

Background
In the late 1840s, the yellow-footed rock wallaby (YFRW) (*Petrogale xanthopus xanthopus*) was first noted by European naturalist Frederick Strange in the Flinders Ranges of South Australia, near what is now Aroona Dam (Copley 1983). The YFRW was an important resource for the Australian Aborigines. The meat was eaten, pelts were used for clothing, and sinew was used for sewing or making nets. Although all tribe members could hunt them, only initiated men could butcher and distribute the meat. After tribal initiations ceased in the 1940s, it is doubtful that YFRWs continued to be used by the Aborigines (Sharp 1994).

Native only to Australia, YFRWs inhabit rocky outcroppings in semiarid and arid landscapes, using the deep caves and fissures as shelter from climate extremes and predators. It is believed their ancestors formed a continuous population from central South Australia into Queensland and on into the Great Dividing Range (Strahan 1995). The current population, although locally common in some areas of its range, is severely fragmented due to the initial over-hunting by Europeans, habitat destruction, predation by introduced foxes and cats, and resource competition from domestic sheep and goats. This fragmentation prohibits the natural dispersal of animals that helped maintain genetic diversity in their colonies.

Current population estimates range from a minimum of 5,000 (S. Lapidge personal communication) to a maximum of 10,000. However, this maximum count includes the closely-related Queensland subspecies, *Petrogale xanthopus celerius* (Sharp 1994) (#6 on Figure 1). The largest populations of *Petrogale x. xanthopus* are in the Flinders Ranges, South Australia (SA) with smaller colonies found in the Gawler Ranges, Olary Hills and Carriewerloo of SA (Figure 1). The two extant colonies in New South Wales (NSW) have less than 150 individuals (P. Christie personal communication).

The World Conservation Union (IUCN) (Baillie and Groombridge, 1996) lists the YFRW as Vulnerable; the U. S. Fish and Wildlife Service (USFWS), the only country to list nonnative species, lists it as Endangered; and the NSW population is listed as Endangered under the NSW Threatened Species Conservation Act of 1995. Recently, the Australasian Regional Association of Zoological Parks and Aquaria's (ARAZPA's) Australian Species Management Plan (ASMP) raised the species from a Category 3 (a medium level of regional management) to a Category 1 (a high level of regional management with the captive population managed as part of a wildlife agency species recovery program). At the same time, the American Zoo and Aquarium Association's Marsupial and

Information for Conservation Spotlight *is provided by the American Zoo and Aquarium Association.*

Monotreme Taxon Advisory Group (AZA M & M TAG) recommended in its Regional Collection Plan (RCP) that the YFRW become a Species Survival Plan (SSP) species (AZA M & M TAG 2000). These separate actions indicate the importance of captive YFRW populations both in its native land and in North America.

In addition to conservation efforts in the wild, one of the goals of YFRW captive management in Australia has been to export surplus captive animals to North America to help establish and maintain a genetically stable population. The current captive North American population has less than twenty animals, with only one male capable of reproduction. One of Environment Australia's (EA) requirements prior to export was that a North American studbook and a species management program be in place. The first edition of this studbook has been published by the author, and the species has been given SSP status, with Jeff Holland from the Los Angeles Zoo recently being approved by the AZA M & M TAG as the SSP coordinator.

At the March 2001 Species Summit meeting of the ARAZPA, EA and AZA, one of the priority species was the YFRW. Much time was spent on discussions of cooperative exports/imports and the Australian requirements for institution approval. Currently, the Los Angeles Zoo is coordinating with ARAZPA and EA to complete the first step toward a self-sustaining North American population - the import of new genetic stock. It is estimated that importation of two breeding pairs (four founders, or animals unrelated to the current population) at six-year intervals could result in 90% gene diversity in the North American population (Lynch 2001).

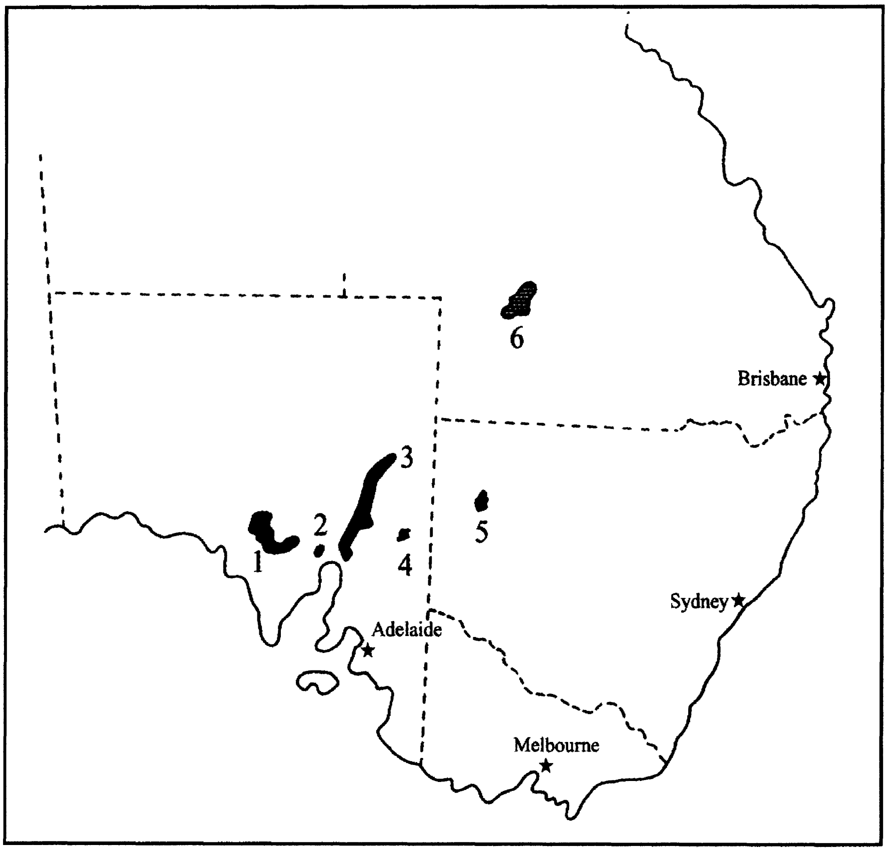

Figure 1: Distribution of the YFRW (adapted from Lim 1992). *Petrogale xanthopus xanthopus*: (1) Gawler Ranges; (2) Carriewerloo; (3) Flinders Ranges; (4) Olary Hills; (5) New South Wales. *Petrogale xanthopus celerius*: (6) Queensland.

Challenges of captive breeding

The same problems plague both the Australian and the North American captive breeding programs. The first is accurate determination of sires. Often several males are kept in captive colonies and, although the dominant male might indeed sire most of the offspring, it is not a certainty. Institutions that keep one male per female group often cannot determine sires when males are exchanged due to the reproductive adaptation of embryonic diapause. Since the cost of DNA analysis is prohibitive for many zoos, accurate record keeping has become a top priority for institutions wishing to house YFRWs. To enable genetic management, both the Australian and the North American studbook keepers have created analytic studbooks where hypothetical parents are created for the unknowns.

Second, the primary management challenge with YFRWs is surplus males. As male-male aggression is common, even if females are not present, the solution to create bachelor groups is generally unsuccessful. Therefore, pouch management, in the form of euthanasia of excess males, might become a husbandry requirement for a properly managed population. This is a controversial subject that may not be supported by all interested institutions.

Although one of the purposes of the Australian captive population is breeding for possible reintroductions, this is not the case with the North American captive population. Concerns over conspecific quarantine and possible introduction of disease make entry into Australia from captive North American collections highly unlikely. Thus, reintroduction is not a top priority for inclusion of the species in the TAG Regional Collection Plan. Instead, it is a flagship rock wallaby species, selected for its educational value in teaching habitat fragmentation, introduced species and adaptations, and for its collaborative *in-situ* conservation and *ex-situ* research possibilities.

In-situ conservation

Adrienne Miller, North American Studbook Keeper for the YFRW, participated in two *in-situ* projects as a volunteer field assistant. The first was a recovery program that focused on the impact of introduced species and involved the endangered population of New South Wales (Figure 1). Phase I of this project took place from 1980 to 1995 and involved the removal of over 42,000 goats from the Gap and Coturaundee Ranges to decrease the level of resource competition between the two species (Sharp 1999). Phase 2 began in 1995, testing the hypothesis that fox predation was the major factor negatively impacting YFRW population growth. The Coturaundee Range was baited with 1080 (sodium fluoroacetate) to eliminate the predatory fox while the Gap Range was not (Sharp 1998). Fecal pellet counts were used as a means to monitor the rock wallaby population at both sites. The results of this project strongly indicated a negative impact of foxes on the wallaby population. Both sites are now baited and the YFRW population appears to be growing on both (P. Christie personal communication).

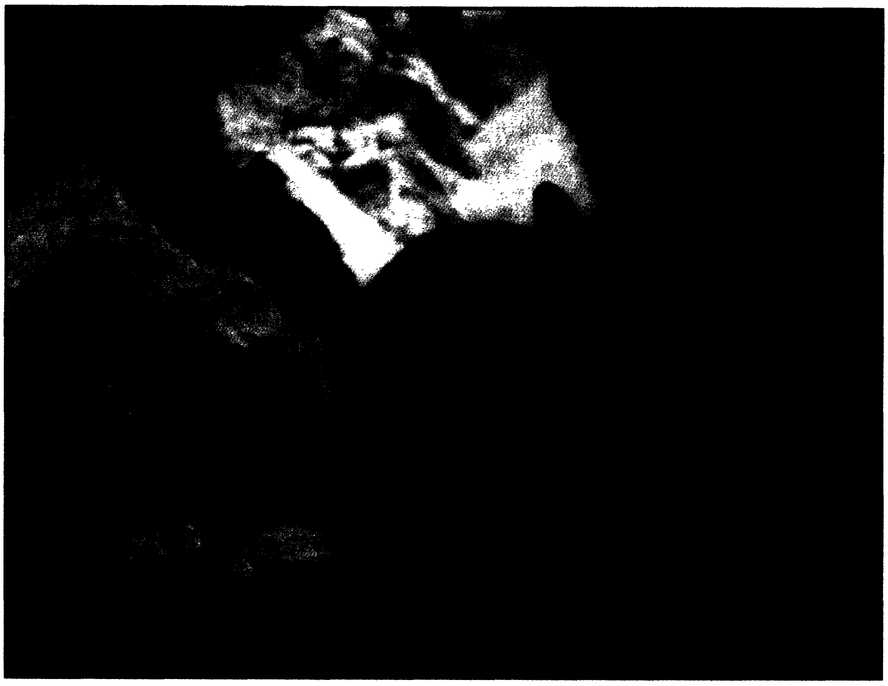

Figure 2. Juvenile yellow-footed rock wallaby in the Coturaundee Range. Photo by Russ Menard.

The second was a reintroduction project at Aroona Dam, Leigh Creek, in the Flinders Ranges of South Australia, the site where it is believed the first European sightings occurred, but where YFRWs have not been seen in over ten years. During the 1994 National Rock Wallaby Symposium, the Adelaide Zoo received unanimous support for a trial release of YFRW. The Aroona Dam site was selected because land use was stable as it had been dedicated as a sanctuary in 1995. Elimination of introduced animals (i.e. fox, cat, and goat) had already begun. A buffer zone of ten kilometers was created around the sanctuary with the assistance of local pastoralists.

Figure 3. Measuring growth on a yellow-footed rock wallaby at Aroona Dam. Photo by Adrienne Miller.

The release of 2.7 captive animals from Monarto Zoological Park occurred on September 16, 1996. Steven Lapidge (1997) began a dietary study on the adaptation of the captive animals to their wild diet. The results indicated a smooth change to eating a wider variety of natural foods, which is valuable for future marsupial reintroductions.

In January 1998, Steven Lapidge also began monitoring of the reintroduced colony. The goals were to (1) identify the most successful methods of reintroducing captive-bred rock wallabies; (2) determine how individuals and the colony as a whole adjust once released; and (3) examine the effect of environmental variables and sympatric species on the establishment, ecology, and physiology of the YFRW. Quarterly trapping trips assessed the general health of the reintroduced population and their reproductive status. There are now second-generation wild YFRWs thriving at Aroona Dam. This reintroduction can serve as a model for other rock wallaby reintroductions.

The success of this venture was based not only on the health and reproduction of the wallabies, but also on community support as well. Leigh Creek took the wallaby reintroduction on as its own. Students were involved with radio-tracking, compiling issues of *Rock Wallaby News*, producing a model of the sanctuary, and inventing the "Wallaby Hop" for a school dance. The landowners around the sanctuary baited for fox and feral cats, and area residents baited the wallaby traps throughout the year, resulting in significantly higher success rates during trapping trips.

Conclusions

Due to the success of the YFRW reintroduction, the same methodology is being applied to tree kangaroos in Papua New Guinea where Steven Lapidge is collaborating with Dr. Lisa Dabek, Director of the Tree Kangaroo Conservation Program operating through the AZA Tree Kangaroo SSP.

The future looks bright for the yellow-footed rock wallaby. The captive population is sustained by collaborations between Australian and North American species managers, and the wild population is sustained by feral animal control, possible future reintroductions, and other *in situ* conservation efforts. On the rocks? Only if they want to be.

Acknowledgments

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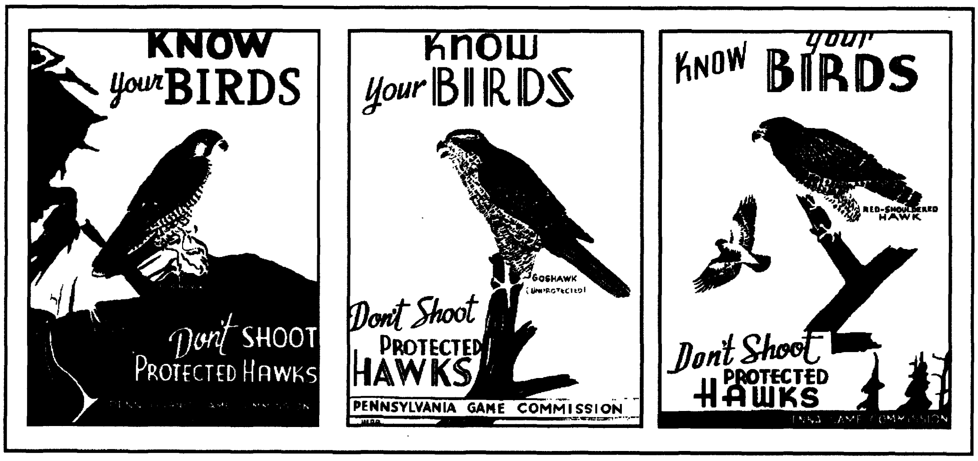

Figure 1. A series of three Works Progress Administration posters from the late 1930s commissioned by the Pennsylvania Game Commission in an attempt to help educate hunters regarding the identification of 'good', and therefore protected species of raptors (e.g., Red-shouldered Hawks and Peregrine Falcons), versus 'bad' hawks (e.g., Northern Goshawks). Note that the 'bad' goshawk is labeled "unprotected."

The Importance of Large Carnivores to Healthy Ecosystems

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Abstract
Land managers often are responsible for the maintenance of species diversity and resilience. This requires knowledge of ecosystem dynamics over decades and centuries. Resource-driven (bottom-up) *models have guided early thought on managing species and ecosystems. Under this paradigm, carnivores have little ecological value, and throughout the 20th Century carnivore management strategies (often extirpation) have reflected that concept. An alternative hypothesis, however, states that herbivores reduce the biomass of plants, but in turn, the biomass of herbivores is checked by the presence of carnivores. As such, carnivores have great ecological value. Their predation activities create impacts that ripple downward through the trophic levels of an ecosystem. Here we discuss some potential pathways through which carnivores contribute to ecosystem processes and species diversity. The subtleties of these interactions have strong implications for management strategies of carnivores. Without considering these indirect impacts, short-sighted management strategies to reduce carnivores might cause extensive and long-term changes in ecosystem structure and function.*

Introduction
Aldo Leopold (1966: 197) wrote that, "One of the penalties of an ecological education is that one lives alone in a world of wounds." The wounds come in many types. In cities it is easy to experience congestion, traffic, noise, and fouled air. People accept that urban lights obliterate stellar pleasures. But our non-urban land has also been wounded by crop agriculture, mineral extraction, fire suppression, logging, pollution, and overgrazing (Terborgh and Soulé 1999). Despite Leopold's (1966) half-century old advice on "intelligent tinkering" we have not kept "every cog and wheel." Today, the scythe of extinction cuts 1000 times faster than historical background rates, and its pace is increasing (Wilson 1992).

That scythe has dire implications. Finely tuned interactions among species, physical environments, and ecological processes form the webs of life on our planet. Each web is not static, but continuously varies within certain bounds, and the species and systems have adapted over time to the range of variability in their particular region (Noss 1999). When "cogs or wheels" are lost, a system can fluctuate outside of the bounds to which it has adapted. Depending on which parts are lost, and the rate of loss, the pressure on a given system can exceed its ability to respond. Once such a vortex is entered, runaway positive feedback can make escape difficult, as altered structure and function can cause secondary waves of extinction that further heighten the instability.

We would like to discuss a specific category of such an event – the loss of carnivores and how that simplifies ecosystems over the long-term. Carnivores are not the only group whose decline has significantly impaired ecosystem processes. Pollinators, seed-dispersers, and even many small, often largely "invisible" organisms contribute enormously to the structure and function of biological communities (Buchmann and Nabhan 1996). We leave the task of reviewing the "sideways" effects of these organisms to others. Here we emphasize carnivores and their *top-down* effects.

How carnivores impact ecosystem health

When people discuss ecological interactions that determine abundance, distribution, and diversity across trophic levels, they often talk about *top-down* or *bottom-up* control. In the ecological sense, control means a qualitative or quantitative effect on ecosystem structure, function, and diversity (Menge 1992).

Simplified, if *bottom-up* control dominates, the system is regulated by energy moving upward from lower to higher trophic levels. Thus, increases in the biomass of consumers and their resources will parallel increases in productivity. Species richness and diversity are maintained by defenses of both plants and herbivores, or because competition forces species to specialize and use discreet niches (Pianka 1974; Hunter and Price 1992; Polis and Strong 1996). Because carnivores sit atop the food chain, *bottom-up* theories provide them with little ecological utility (Estes et al. 2001). They would receive more than they would contribute. Implicitly, this can justify politically-based management strategies that hold carnivore numbers artificially low or eliminate them altogether.

Alternatively, in a system with *top-down* regulation, herbivores can reduce the biomass of plants, but in turn, herbivore biomass is held in check by carnivores (Hairston et al. 1960; Fretwell 1977, 1987; Oksanen et al. 1981; Oksanen and Oksanen 2000). This idea implies strong interactions among three general trophic levels: plants, herbivores, and carnivores.

At very low levels of productivity, there is only one trophic level, plants (see Oksanen and Oksanen 2000). The only factors limiting plant biomass are available resources and competition with other plants for those resources. As productivity increases so does plant biomass, until there is enough productivity to support a second trophic level, the herbivorous consumers. With two trophic levels, herbivore biomass increases with increasing productivity, but their grazing activity limits plant biomass until productivity increases enough to support a third trophic level, the carnivores. Carnivores, in their role as keystone species, now limit the number of herbivores, and that reduces the amount of pressure that herbivores place on plants. The plants and carnivores now flourish (first and third trophic levels), whereas the herbivores (second trophic level) are held in check by carnivores.

In short, with odd numbers of trophic levels, plants flourish, but even numbers of trophic levels limit plant growth. In contrast to *bottom-up* theory, when there is *top-down* regulation neither plant nor herbivore biomass increases linearly with increases in productivity. Instead, there is a stepwise accrual as the food chain lengthens (see Oksanen and Oksanen 2000).

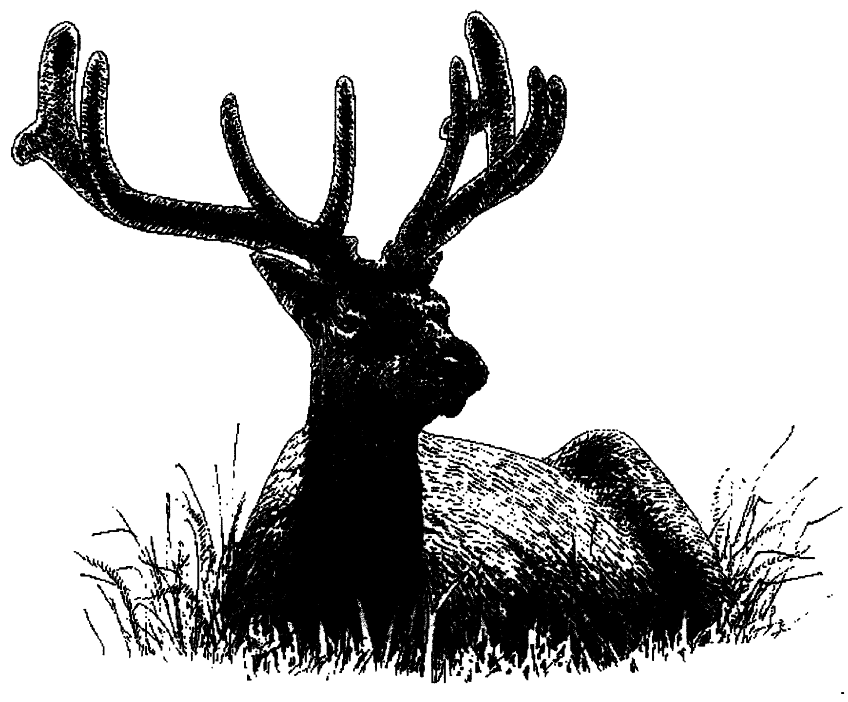
Under *top-down* regulation, diversity can be maintained through the actions of keystone species (Paine 1966; Estes et al. 2001). Although a numerically dominant species may also serve that function, sometimes a species with low biomass can have an ecological effect that is disproportionate to its abundance. If a carnivore species checks a prey species that is competitively superior, or changes prey behavior in some way, then the carnivores are erecting ecological boundaries that protect weaker competitors from competitive exclusion (Paine 1966; Terborgh et al. 1999; Estes et al. 2001). Under this paradigm, carnivores play an important role in regulating interactions, and predation can cause indirect impacts that ripple downward through a system affecting flora and fauna that seem ecologically distant from the carnivore (Terborgh 1988).

Of course, reducing trophic interactions to a dichotomous rubric of either *top-down* or *bottom-up* is counterproductive. It is clear that forces flow in both directions simultaneously and interact while doing so (Menge and Sutherland 1976; Fretwell 1987; Hunter and Price 1992; Menge 1992; Power 1992; Estes et al. 2001). For example, while the number of trophic levels in a *top-down* cascade impacts plant biomass, the productivity from the *bottom-up* also affects the number of trophic levels (Fretwell 1987; Power 1992).

Scientists quickly recognized the qualitative and quantitative role a resource like food has for consumers. Until recently, however, knowledge about the impact of carnivores on a system remained more enigmatic. Large carnivores are difficult to research because of the necessary scale (temporal and geographical) and expense (Estes 1996). In many areas, they have already been eliminated or severely reduced in number (Weber and Rabinowitz 1996; Terborgh et al. 1999). Finally, social and political factors have militated against research on the role of carnivores in ecological systems.

Impacts of carnivores on prey & plants
Carnivores control prey by direct and indirect methods. Through predatory activities, carnivores directly reduce numbers of prey (Terborgh 1988; Terborgh et al. 1997; Estes et al. 1998; Schoener and Spiller 1999). Indirectly, carnivores cause prey to alter their behavior so that they become less vulnerable (Kotler et al. 1993; Brown et al. 1994; FitzGibbon and Lazarus 1995; Palomares and Delibes 1997; Schmitz 1998; Brown 1999; Berger et al. 2001). They choose different habitats, different food sources, different group sizes, different time of activity, or they reduce the amount of time spent feeding.

By reducing the numerical abundance of a competitively dominant prey species (or by changing its behavior), carnivores erect and enforce ecological boundaries that allow weaker competitors to persist (Estes et al. 2001). If a predator selects from a wide-range of prey species, the presence of the predator may cause all prey species to reduce their respective niches and thus reduce competition among those species. Removing the predator will dissolve the ecological boundaries that check competition. As a result, prey species may compete for limited resources and superior competitors may displace weaker competitors leading to less diversity through competitive exclusion (see Paine 1966; Terborgh et al. 1997; Henke and Bryant 1999). The impact of carnivores thus extends past the objects of their predation. Because herbivores eat seeds and plants, predation on that group influences the structure of the plant community (Terborgh 1988; Terborgh et al. 1997; Estes et al. 1998). The plant community, in turn, influences distribution, abundance, and competitive interaction within groups of birds, mammals, and insects.



American Elk by Robert Savannah, USFWS.

At the beginning of this section, we briefly introduced the idea that plants suffer or thrive when there are even or odd numbers of trophic levels (Hairston et al. 1960; Fretwell 1977, 1987; Oksanen et al. 1981; Oksanen and Oksanen 2000). Direct evidence for this idea came when sea otters (*Enhydra lutris*) were overexploited in the north Pacific (see Estes 1996; Estes et al. 1978, 1989, 1998; Estes and Duggins 1995). This system evolved with three trophic levels (carnivorous sea otters, herbivorous macroinvertebrates, and kelp forest). Following sea otter decline because of the fur trade, marine invertebrate herbivores increased in number and devastated the kelp forest (creating a system with two trophic levels). This produced a cascade of indirect effects that reduced diversity in a host of fish, shorebirds, invertebrates, and raptors (see Estes 1996; Estes et al. 1978, 1989, 1998; Estes and Duggins 1995).

Gradual recovery of the sea otter in recent years restored the third trophic level. Invertebrate grazers then declined, and the kelp forests and associated fauna recovered (Estes et al. 1978, 1989, 1998). When killer whales (*Orcinus orca*) entered the area, they imposed a fourth trophic level (Estes et al. 1998). The killer whales reduced numbers of sea otters, allowing the invertebrate grazers to increase in number, and that reduced the biomass of the kelp forest. Estes (personal communication) emphasized the importance of long-term studies; he stated that analyzing any five-year block of time from their 30 years of data would lead to different conclusions.

Similarly, Krebs et al. (2001) synthesized 40 years of studies on the snowshoe hare (*Lepus americanus*) cycle. This 10-year oscillation has been highlighted as a predator-prey cycle between lynx (*Lynx canadensis*) and hare in ecology textbooks. Krebs et al. (1995, 2001), however, revealed that we can only understand the process by analyzing all three trophic levels. To quote Krebs et al. (2001: 34), "The hare cycle is caused by an interaction between predation and food supplies, and its biological impacts ripple across many species of predators and prey in the boreal forest." When examining these interactions, Krebs et al. (2001) stated that the dominant factor regulating the hare cycle was predation; the dynamics of the cycle were not changed by adding nutrients, and the immediate cause of death in 95% of the hares was predation. Furthermore, lynx were not the only predator for hares. Snowshoe hares, adult and juvenile, were killed by lynx, coyotes (*Canis latrans*), goshawks (*Accipiter gentilis*), great-horned owls (*Bubo virginianus*), small raptors, and small mammals, particularly red squirrels (*Tamiasciurus hudsonicus*) and ground squirrels (Krebs et al. 2001). When lynx were removed from the suite of predators, the hare cycle continued unchanged because of compensation (Stenseth et al. 1998). Both the sea otter study and snowshoe hare work demonstrated the importance of long-term studies, and accented the need to investigate predator-prey interactions over more than just two trophic levels, let alone only examining the interactions between one species of predator and one species of prey.

Long-term monitoring data from the boreal forest of Isle Royale indicate that predation by wolves (*Canis lupus*) affects the number and behavior of moose (*Alces alces*) (McLaren and Peterson 1994). This, in turn, affects the balsam fir forest (and other woody plants) by regulating seedling establishment, sapling recruitment, sapling growth rates, litter production in the forest, and soil nutrient dynamics (Pastor et al. 1988; Post et al. 1999 and references within).

In the Neotropics, Terborgh et al. (1997) has taken advantage of a hydroelectric project that recently formed Lago Guri in Venezuela. The lake is 120 kilometers long and up to 70 kilometers wide with islands scattered throughout, and the experiment has both a temporal and spatial control. After seven years of isolation, nearly 75% of the vertebrate species have disappeared from the islands too small to hold jaguars (*Panthera onca*) and pumas (*Puma concolor*) (Terborgh et al. 1997). The few species that remain are hyperabundant with gross effects on the plant community, and there is little regeneration of the canopy trees (Terborgh et al. 1997). This study continues.

As a final example, researchers working on grasslands in Texas found that nine months after coyote removal, rodent species richness and diversity declined compared to areas with coyotes (Henke and Bryant 1999). Twelve months after coyote removal, the Ord's kangaroo rat (*Dipodomys ordii*) was the only rodent species captured on the treated grassland (Henke and Bryant 1999). The removal of coyotes allowed the Ord's kangeroo rat, a superior competitor, to increase in number and displace other species.

Impacts of predators on mesopredators
Large carnivores also directly and indirectly impact smaller predators, and therefore the community structure of small prey (Soulé et al. 1988; Bolger et al. 1991; Vickery et al. 1992; Palomares et al. 1995; Sovada et al. 1995; Crooks and Soulé 1999; Henke and Bryant 1999; Schoener and Spiller 1999). Small prey distribution and abundance affects ecological factors like seed dispersal, disease epizootics, soil porosity, soil chemistry, plant biomass, and plant nutrient content (Whicker and Detling 1988; Hoogland 1995; Keesing 2000).

In California, Soulé et al. (1988) and Crooks and Soulé (1999) documented more species of scrub-dependent birds in canyons with coyotes than in canyons without coyotes. The absence of coyotes allowed behavioral release of opossums (*Didelphis virginianus*), foxes (*Vulpes* spp.), and house cats. These species preyed heavily on song birds and native rodents. The effects of mesopredator release have also been observed in grasslands (Vickery et al. 1992; Henke and Bryant 1999), wetlands (Sovada et al. 1995), and Mediterranean forest (Palomares et al. 1995).

Macroecological evidence for top-down forces

The previous section outlines some mechanisms through which carnivores can regulate ecosystems. But, how widespread are these impacts? There is a growing body of macroecological evidence to support the impact of carnivores on ecosystems. For example, Oksanen and Oksanen (2000) compare plant biomass and primary productivity in Arctic/Antarctic areas with and without herbivores. In areas with herbivores, the regression slope between plant biomass and increasing productivity is flat, whereas in areas without herbivores the regression slope between plant biomass and increasing productivity is positive and steep (Oksanen and Oksanen 2000). This mirrors their prediction from a perspective of *top-down* regulation (herbivores exert a controlling effect on plants).

Outside the Arctic/Antarctic, most macroecological evidence for impact of carnivores on ecosystems must be viewed with caution because humans have already altered such a large percentage of temperate and tropical systems. This complicates our ability to tease out effects of carnivores from those of humans. Nevertheless, we believe it is important to conduct such analyses, and the evidence that does exist suggests that carnivores are important.

For example, Crête and Manseau (1996) and Crête (1999) compared the biomass of ungulates to primary productivity along latitudinal gradients. For the same latitude, ungulate biomass was five to seven times higher in areas where wolves were absent compared to where wolves were present. In areas of former wolf range, but where currently no wolves exist, a regression of ungulate biomass to primary productivity produced a positive slope (Crête 1999).

Four recent reviews also support the importance of carnivores to systems. Considering the qualitative and quantitative evidence as a whole, Terborgh et al. (1999) concluded that top-down control was stronger and more common than previously thought. In addition, Schmitz et al. (2000) conducted a quantitative meta-analysis of trophic cascades in terrestrial systems. Their definitions limited data to invertebrates and small vertebrates, but they detected trophic cascades in 45 of the 60 tests (Schmitz et al. 2000). In other words, in 75% of the studies, predator removal had a significant direct impact on herbivore numbers (positive), and that had a significant impact on plant damage (positive), plant biomass (negative), and plant-reproductive output (negative). They concluded that trophic cascades were present under different conditions, with different types of predators, and occurred more frequently than currently believed (Schmitz et al. 2000).

Another quantitative meta-analysis examined terrestrial trophic cascades in arthropod-dominated food webs (Halaj and Wise 2001). The investigators reported that 77% of the 299 experiments showed a positive response of herbivores when predators were removed (Halaj and Wise 2001). Whereas Schmitz et al. (2001) suggested that the strength and pattern of terrestrial cascades were equal to aquatic cascades, Halaj and Wise (2001) suggested that terrestrial trophic cascades were weaker than aquatic cascades.

Finally, Estes et al. (2001) reviewed the impacts of predation from a variety of different ecosystems, including rocky shores, kelp forests, lakes, rivers/streams, oceanic systems, boreal/temperate forests, coastal scrub, tropical forests, and exotic predators on islands. They concluded that the process of predation has dramatic impacts at organizational levels ranging from individual behavior to system dynamics, and on time scales that range from ecological to evolutionary (Estes et al. 2001).

Drastic changes in ecosystems have been linked to carnivore extirpation or control. For example, managers have reduced carnivore numbers to keep ungulates at artificially high levels for recreational hunting. Yet, overabundance of white-tailed deer (*Odocoileus virginianus*) has been shown to reduce numbers of native rodent species, cause declines in understory nesting birds, obliterate understory vegetation in some forests, and even eliminate regeneration of the oak (*Quercus* spp.) canopy (Alverson 1988, 1994; McShea and Rappole 1992; McShea et al. 1997). Similarly, hyperabundance of moose in areas of the Greater Yellowstone Ecosystem without wolves and grizzly bears (*Ursus arctos*) has reduced neotropical migrant bird populations (Berger et al. 2001). Ripple and Larson (2000) have reported that aspen (*Populus tremuloides*) overstory recruitment ceased when wolves disappeared from Yellowstone National Park. Wolves are a significant predator of elk (*Cervus elaphus*), and wolves may positively influence aspen overstory through a trophic cascade caused by reducing elk numbers, modifying elk movement, and changing elk browsing patterns on aspen (Ripple and Larson 2000).

If we continue to manage carnivores without considering the indirect effects on habitat quality and species diversity, we will undoubtedly continue to alter the structure and function of an area in ways that we may later regret. We contend that it is not a question of whether or not carnivores play an important role. It is a question of how they play their role in trophic interactions.

Relative strength of interactions under different conditions

We stress that the subtleties of interactions can vary significantly under different environmental conditions. Abiotic factors, such as type, frequency, and scale of natural disturbance (see Connell 1978) can influence the relative importance of *top-down* or *bottom-up* forces. Disturbance over large geographic scales shortens food chains (at least temporarily) and thus changes interaction dynamics among trophic levels (Menge and Sutherland 1976).

Climatic patterns, such as *El Niño* or *La Niña* affect the ability of keystone predators to regulate prey in aquatic (Sanford 1999) and terrestrial systems (Ballard and Van Ballenberghe 1997; Post et al. 1999). In years that the North Atlantic Oscillation produces deep snow-cover, moose (*Alces alces*) are more vulnerable to wolf predation (Ballard and Van Ballenberghe 1997; Post et al. 1999). Thus, the fir forest of Isle Royale is released from heavy browsing, more seedlings are established, more saplings survive, and litter production and nutrient dynamics are affected (Pastor et al. 1988; Post et al. 1999). Similarly, seasonality can alter rates of compensatory mortality and natality, and thus change population density of prey (Boyce et al. 1999).

Behaviors like migration allow animals to make use of food over a larger area (Fryxell et al. 1988). If terrestrial predators are unable to follow migrating ungulates over a long distance movement, then they will have less relative impact on population numbers of the migrants (Fryxell et al. 1988; Fryxell 1995). Migratory wildebeests (*Connochaetes taurinus*) fit the hypothesis of predation-sensitive foraging, where both food supplies and predation interact to regulate populations (Sinclair and Arcese 1995). Like the earlier example of snowshoe hares, predation is the final agent of mortality. Unlike the case of the hares, however, food supply plays a driving role in mortality of wildebeests by predation. As food supply decreases, wildebeests increase their risk to find food (Sinclair and Arcese 1995).

We have already discussed the link between level of productivity and number of trophic levels. Behavior of predator and prey, however, also changes as habitats progress along a cline from open (e.g., steppe grassland) to closed (e.g., tropical forests or kelp beds). The physical habitat in which an animal lives imposes adaptive pressures that mold behaviors and population structures, which in turn affect the role of predation.

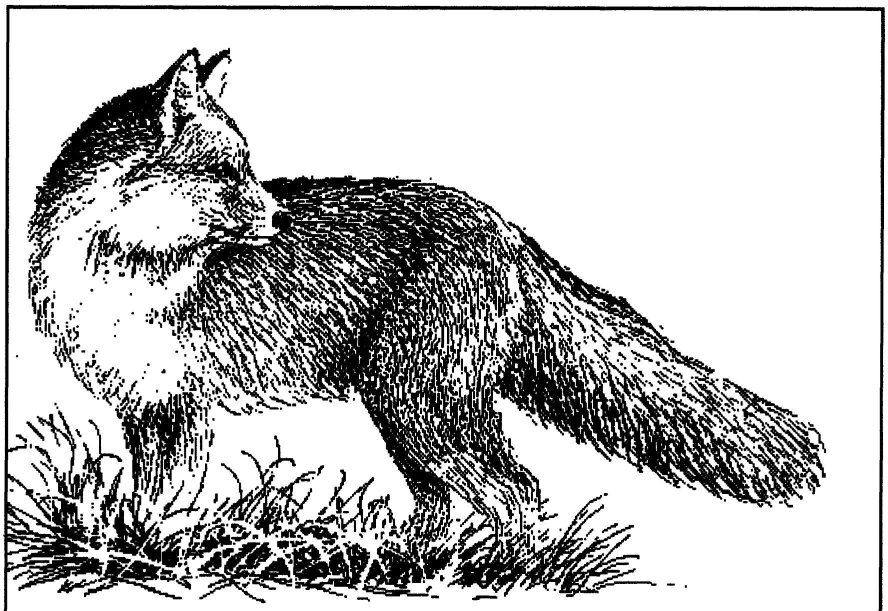
In open habitats, prey species can detect predators at a distance and flee or enter burrows. Sociality enhances avoidance capabilities, as does large body size. Such traits may reduce the number of prey species that are available to a given predator. In response, grassland predators may become more specialized on one or a few prey species to increase the probability of capture (MacArthur and Pianka 1966; Hornocker 1970; Schaller 1972; Emmons 1987). When the number of prey species available to a predator is reduced, the interactive links between prey species and the predator should be fewer and stronger (McCann et al. 1998). Such a system should undergo stronger oscillations, and therefore be less stable, than a system characterized by many links (McCann et al. 1998; for examples see Erlinge et al. 1991; Hanski et al. 1991; McKelvey et al. 1999).

Specialist predators play a *top-down* role as part of the entire suite of predator species. Models of *top-down* interactions between specialized carnivores and prey function because of self-limitation factors in the prey (Turchin et al. 2000). For example, both predator and prey start at low numbers. Prey numbers build to the point where further growth is inhibited by social interactions, and prey numbers then stabilize at a peak density. Thus they now supply a positive energy balance to carnivores, which increase rapidly in number. When carnivore numbers rise quickly, heavy predation causes prey to decline, or hastens a decline caused by other factors. Thus, specialized carnivores, as part of a suite, exert control on a system, and that control is strongest when the given prey cycle is past its peak or in decline.

Structurally complex systems, such as tropical forests, can be populated by prey species that do not generally migrate over long distances, have the large size, or have highly socialized anti-predator behaviors. Predators typically hunt by ambush and might have access to more species of prey than predators hunting by pursuit in structurally open systems. They tend to take available prey in relation to abundance and vulnerability (Emmons 1987; Terborgh 1988). If relative abundance of prey species changes, then the predators can switch to another prey that is commonly encountered and meets energetic demands (MacArthur and Pianka 1966).

Through opportunistic predation, carnivores can maintain prey assemblages, which in turn maintains the structure of the plant community (Terborgh 1988; Estes 1996; Terborgh et al. 1997, 1999). When a top carnivore is opportunistic, the links between that carnivore and the diverse prey community should be numerous. Because such predators switch among prey species, fluctuations in numbers of a given prey species have less effect on the predator (and system) than fluctuations in systems with fewer and stronger links (McCann et al. 1998; see also Erlinge et al. 1984, 1988, 1991; Hanski et al. 1991).

Because the diet of an opportunistic predator is broad, it can be expected to exert broader top-down community effects than a species of specialist predator. For carnivores to have top-down influence, they must maintain a certain population density, yet the rate of increase generally is lower for predators than for prey. An opportunistic carnivore can maintain its population numbers at an influential level, however, by switching among alternative prey as the relative numbers of the prey species change (Erlinge et al. 1984). Thus an opportunistic predator can exert constant top-down influence throughout the population cycle of prey, whereas a specialist predator exerts its strongest influence on prey numbers when the prey are in the declining phase of their cycle. Thus, unlike the strongly



Fox by Robert Savannah, USFWS.

fluctuating time-series signatures of specialized predators and prey, we expect the time-series signature of opportunistic predators and their suite of prey to be more stable.

Carnivores and management

Scientific data increasingly indicate that carnivores play an important role in ecological health. Yet, carnivore control has been the center of our management solutions, and it even has been institutionalized by several government agencies. When control is used, there typically is little consideration of the circumstances, season, behavior, or other conditions that affect a carnivore's role in its system.

Short-term control and hunting restrictions sometimes are necessary when a system is highly perturbed. As with heavy human harvest, predators can influence prey numbers, particularly when prey densities are low (Boyce et al. 1999). But such tactics only address a symptom. We need to ask deeper questions about why our systems are perturbed. What indirect effects could ripple through a system if carnivores are reduced below the bounds of their natural variation? What will happen to vegetation and non-game species diversity if we try to hold ungulate numbers at unnaturally constant and high numbers for recreational hunting? Can we manage populations of predators and prey in ways that more closely resemble natural patterns? We emphasize that predators impact prey populations in more than a demographic fashion. They change movement and activity patterns, and these behavioral effects can have ecological significance.

These are not new questions (see Leopold 1966). Yet, as long as we fail to think in terms of an ecosystem, we will continue to lose diversity despite good intentions, higher budgets, and increasing human effort. In short, management policies based on reducing carnivore numbers have caused, and will continue to cause, severe harm to many other organisms (see examples in Section 2).

For these reasons, we contend that science is increasingly relevant to decision-making. But typically, when faced with political and economic resistance, conservation strategies for large carnivores have been compromised by trying to move incrementally—perhaps trying to protect small numbers of a top carnivore in a few locations. While this might prevent taxonomic extinction (at least in the short-term) it does little to mend ecosystems. In short, past policies, driven by paradigms that view carnivores as pests to agriculture, sport hunting, and development, continue to play a stronger role than new scientific information. As a result, ecosystems continue to decline. While incremental approaches may work with species that still have some biological resilience, too many large carnivore species have declined drastically (see Weber and Rabinowitz 1996) and are too close to extinction for such tactics.

Leopold (1966) once said that if we are content relegating grizzlies to Alaska it would be like relegating happiness to heaven. The problem is, we might never get to either place. The politics of carnivore management will continue to take precedent over biology as long as we let it. Unless we put biological sideboards on carnivore management, we will continue relegating happiness to heaven. And we won't get there.

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FOCUS ON NATURE™ *by Rochelle Mason*

The DWARF NAUPAKA (*Scaevola coriacea*) is a ground-dwelling, coastal shrub with sparsely alternating, 1-2 inch long, green, succulent leaves on low-lying stems. Each creamy-white, monoclinous flower (having both stamens and pistils) measures 3/8-3/4 inch in length and produces a small, purplish-black ovoid berry. Flower and fruit formation can occur year round with adequate rainfall. Like most plants, the dwarf naupaka is an autotroph, making its own food by photosynthesis. This native species grows very near the ocean on non-shifting, compacted sand helping to stabilize the shoreline. Formerly on all main Hawaiian Islands (except Kaho'olawe) but probably never very common, the only significant population now occurs in Waiehu, Maui. Intolerant of habitat disturbance or degradation, this endangered plant can be helped by a donation of your time or money to a nature conservation organization.

Marine Matters

International Efforts to Protect Marine Biodiversity Through Marine Wilderness Preservation in the Northwest Atlantic (New England)

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Abstract

Currently, marine diversity on the continental shelf in the Gulf of Maine has minimal protection from commercial activities. Last year, numerous environmental organizations, scientists, and other concerned citizens proposed a 20 by 178 nautical-mile marine protected area in the Gulf of Maine and Georges Bank ("Gulf of Maine") along the United States-Canadian international boundary (the "Hague line") to protect marine diversity. The marine protected area, the Gulf of Maine International Ocean Wilderness ("International Ocean Wilderness"), would straddle the Hague line – ten miles on each side – as it passes through the Gulf of Maine. The International Ocean Wilderness would include large portions of the five major habitat types that are representative of the Gulf of Maine and protect these areas from extractive fishing and non-fishing industrial activities. If designated, the International Ocean Wilderness would comprise only 6.2% of the total area in the Gulf of Maine, leaving most of it open to existing industrial activities. The International Ocean Wilderness would serve four principal functions: (1) preserving marine diversity; (2) preserving large areas of the five major habitat types; (3) protecting cultural and historical artifacts; and (4) providing control areas for future benthic ecological study. The International Ocean Wilderness would also provide the following incidental benefits: (1) enhancing important benthic fisheries, notably the scallop fishery, by leaving a subpopulation to grow to advanced adult ages at which egg production is much greater than by adults at average time of harvest in the present fishery; (2) protecting sensitive essential fish habitats from the effects of bottom-tending mobile gears; (3) providing a precautionary buffer from the effects of overfishing; and (4) providing a buffer zone along the Hague line to facilitate enforcement of this international boundary.

Introduction

In 2000, numerous regional and national environmental organizations, scientists, and other concerned citizens petitioned the Clinton Administration in the United States and the Canadian Prime Minister to designate an international, cross-shelf ocean wilderness area in the Gulf of Maine to protect marine diversity. The proposed ocean wilderness area, the Gulf of Maine International Ocean Wilderness Area (GOMIOW), would start approximately 20 nautical miles from the northeasternmost point on the Maine coast and extend 178 nautical miles along the political boundary separating the US and Canadian Exclusive Economic Zones ("the Hague Line"), across the Gulf of Maine and Georges Bank, and out to the continental abyssal plain to depths greater than 4,000 meters. As a cross-shelf marine wilderness area, the GOMIOW would encompass representative portions of the five major habitat types found in the Gulf of Maine, including: (1) shallow-water glacial ridges; (2) deep-water basins within the Gulf of Maine; (3) shallow-water gravel and sand habitats on Georges Bank; (4) deep-sea canyons off Georges Bank; and (5) the continental abyssal plain.

The proponents claimed that the GOMIOW would serve three principal functions: (1) preserving marine diversity; (2) preserving large areas of the five major habitat types in the Gulf of Maine; and (3) providing control areas for future benthic ecological study. The GOMIOW would also provide the following incidental benefits: (1) enhancing important benthic fisheries, notably the scallop fishery, by leaving a subpopulation to grow to advanced adult ages that produce more eggs than adults in the present fishery; (2) protecting sensitive essential fish habitats (EFH) from the effects of bottom-tending mobile gears; (3) acting as a precautionary buffer against the effects of fishing and other commercial activities; and (4) providing a buffer zone along the Hague line to facilitate enforcement of this international boundary.

There are many examples of international transboundary protected areas on land (Zbicz and Green 1997), including five between the US and Canada, but in the marine environment, this conservation approach rarely has been tried. The few cases that exist are all coastal. If designated, the GOMIOW would be the first international ocean wilderness of its kind. It would encompass approximately 2,700 square nautical miles, or roughly 6% of the US Exclusive Economic Zone (EEZ) in the Gulf of Maine. An area of similar size and relative proportion would be protected in the Canadian waters of the Gulf of Maine.

The need for the GOMIOW

With the exception of several small areas, such as the Dry Tortugas Ecosystem Reserve in Florida and state protected areas off the coast of California, no permanent reserves protect marine biodiversity in deep-water continental shelf systems in the US from fishing or other commercial practices that damage marine habitats (Brailovskaya 1998). At present, less than 1% of US territorial waters and less than 1% of the world's oceans are protected in reserves (NCEAS 2001).

In the Gulf of Maine, there are few areas that are adequately protected for the purpose of conserving marine biodiversity. Even the National Marine Sanctuary (NMS) at Stellwagen Bank does not have sufficient restrictions on degradative activities. On the Canadian side of the Hague Line, there are as yet no permanent marine sanctuaries of any kind. The risk of significant loss of marine biodiversity is great because most of the Gulf of Maine is exposed to intense commercial uses, including commercial fishing and extraction of other natural resources. By and large, of all commercial and recreational uses, fishing, especially with bottom-tending mobile gears, poses the greatest threat. A description of the major fisheries in the Gulf of Maine is provided below, along with a discussion of the weaknesses of present-day fisheries management in protecting marine biodiversity and ecosystem functions.

Major fisheries in New England

Commercial and recreational fishing occurs throughout the New England continental shelf and slope areas. Scientists have recognized fishing as the most widespread form of human-caused disturbance on the North American continental shelf (Messieh et al. 1991; Auster et al. 1996; Auster and Langton 1999; Friedlander et al. 1999; Watling and Norse 1999; McConnaughey et al. in press). The three major commercial fisheries in the Gulf of Maine are the (1) Northeast Multispecies ("Groundfish") Fishery; (2) Atlantic Sea Scallop Fishery; and (3) Atlantic Lobster Fishery. Many of these fisheries are severely depleted and are now slowly recovering. Depletion of traditional groundfish species has forced fishermen into virgin fishing grounds, which exacerbates the ecological impacts of the industry. New fisheries have been created that target former "trash" species, like spiny dogfish (*Squalus acanthius*) and monkfish (*Lophius americanus*). Now these fish species are depleted as well and are under rebuilding plans.

Of these fisheries, the groundfish and scallop fisheries affect the greatest spatial area in the Gulf of Maine since bottom-tending mobile gear is used, including bottom trawls and scallop dredges. Approximately 90% of all groundfish landed from the Gulf of Maine is caught by bottom trawls (large nets and associated gear that are dragged along the seafloor to catch fish). Recent analyses to determine the extent of fishing practices in the Gulf of Maine have found that, on average, the entire US Gulf of Maine territory was trawled once annually between 1976 and 1991, while Georges Bank was trawled three to four times annually (Auster et al. 1996).

The scallop fishery extends from New England to the Mid-Atlantic in waters 40 to 100 meters in depth. Over 95% of scallops are landed using large, metal scallop dredges that are 15 feet wide and weigh over two tons. Most scallop fishermen use two 15-foot dredges. High-resolution vessel-monitoring data of fishing effort showed that in 1999 the scallop fishery affected, to varying degrees, over 12,000 square nautical miles – equivalent to the combined area of Connecticut, Rhode Island, and the state of Massachusetts (Rago and McSherry 2000). At the same time, New England's largest fishery, the Atlantic Lobster fishery, uses fixed gear (lobster pots) rather than bottom-tending mobile gear and affects only an estimated 219 to 657 square kilometers as of 1996 (Auster and Langton 1999).

Overall, commercial fisheries target species throughout their geographic range, and the wide array of harvesting techniques allow fishing to occur over the widest range of habitat types (Auster and Langton 1999).

Environmental effects of New England fisheries

Loss of marine biodiversity

Fishing reduces marine biodiversity in two major ways: (1) directly, by removing target and non-target marine species from the ecosystem; and (2) indirectly, through habitat disruption, homogenization, and reduction of habitat complexity.

Both scallop dredges and bottom trawls are non-selective and collect significant bycatch of other marine life. Discards in the US Gulf of Maine groundfish fisheries were 26 to 44% of total catch (by weight) in 1991 (Murawski 1993). Recent studies in the Northwest Atlantic have found that hundreds of species are caught incidentally in the scallop fishery (Fuller et al. 1998; Magee et al. 1999, 2000) and the groundfish fishery. Bycatch in both fisheries is a significant problem and likely is underestimated due to underreporting of discards at sea. There presently is no rigorous recording of vertebrate and invertebrate bycatch species, nor any attempt to estimate non-target species mortality.

Bycatch of non-target species that are long-lived and exceptionally sensitive to increased levels of mortality, such as barndoor skate (*Raja laevis*) and deep-water corals (Cnidaria), commonly occurs and could negatively impact their populations (e.g. Breeze et al. 1997; Casey and Myers 1998; Musick 1999). For organisms that easily pass through meshes in fishing gear, or are easily macerated during the process of fishing (such as sponges), analysis of bycatch does not indicate the degree of impact (Freese et al. 1999).

Over the period 1970 to 1993, the frequency of occurrence of 26 finfish species decreased on the Scotian Shelf, including the Bay of Fundy. The steepest declines were observed in smooth skate (*Raja senta*), thorny skate (*Raja radiata*), monkfish (*Lophius americanus*), cusk (*Brosme brosme*), haddock (*Melanogrammus aeglefinus*), and wolffish (*Anarhichas lupus*) (Strong and Hanke 1995). Scientists have identified similar declines in Stellwagen Bank National Marine Sanctuary (Auster in press).

Loss of pristine habitats

The Gulf of Maine contains uncounted numbers of benthic species, many of which are sensitive to bottom-tending mobile gear. Benthic invertebrates are the basis of marine food webs and healthy marine ecosystems. Sedentary structure-forming fauna such as corals, sponges, and tube worms form habitat and shelter for other species, including juvenile commercial fishes and shellfish species, and are particularly vulnerable to the effects of fishing gear. Current fishing practices catch and kill most benthic invertebrates and can lead to severe declines in population sizes and ranges of long-lived invertebrates like corals and sponges.

Fishing activities impact habitat integrity, community composition, and ecosystem processes (Auster and Langton 1999). Bottom-tending mobile gear reduces habitat complexity by (1) removing emergent epifauna; (2) smoothing sedimentary bedforms; and (3) removing taxa that produce structure (Auster et al. 1996). Studies of the effects of bottom-tending mobile gear have found that, in virtually every case, such gear alters the structure of the bottom physically and biologically and reduces species abun-

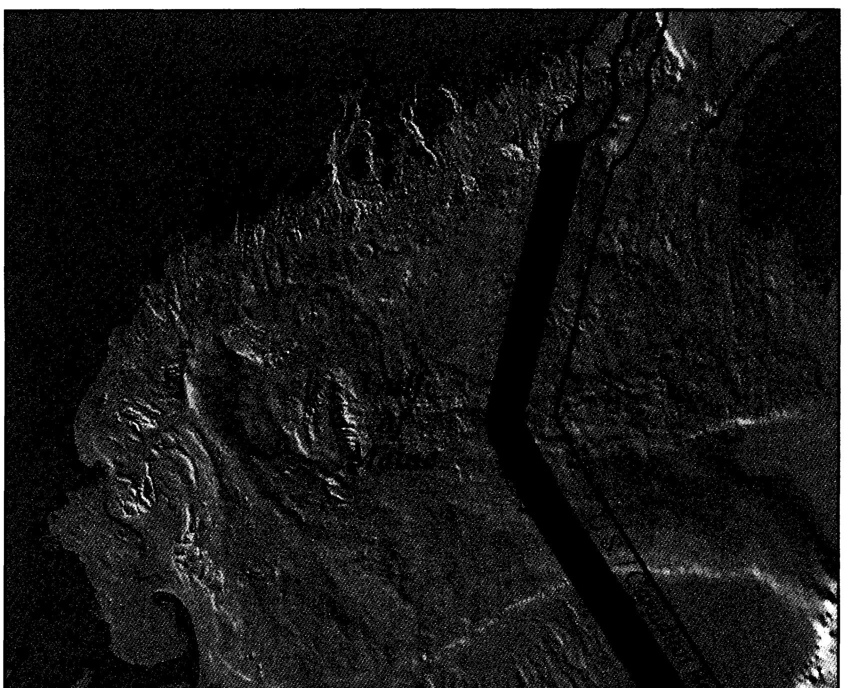

Figure 1. Proposed GOMIOW marine reserve in the Gulf of Maine along the US and Canadian boundary. Map source: National Undersea Research Center, University of Connecticut.

dance and diversity (for reviews, see Auster and Langton 1999; ICES 2000).

There are over 90 studies documenting the effects of scallop gear, which has a particularly heavy impact. A standard New Bedford scallop dredge can remove and suspend into the water column approximately four to five centimeters of the surface sediment layer. These surface sediments contain more than half of all the benthic invertebrates and most of the easily digestible organic matter that these invertebrates use for food. Scallop dredges capture significant amounts of bycatch and disrupt spawning aggregations of groundfish and other marine life. As the structure of the bottom increases in complexity, especially in muddy sand or gravelly areas, the loss of biomass and species numbers caused by scallop dredging increases dramatically. In most areas where scallop gear is used, the biodiversity of the area is inevitably reduced (Veale et al. 2000).

Scientists have also documented the need for complex habitats to support commercial groundfish populations. Several studies show that juvenile demersal fish die at a higher rate in less complex habtiats (Lindholm et al. 1999). Experimental research has demonstrated that structural shelter that provides refuges for prey is often a limiting factor for growth of the population (Hixon 1991). Lindholm and coworkers (1999) described how predation on juvenile cod was reduced significantly in areas where habitat structure was experimentally enhanced. These observations argue for the importance of protecting complex habitats on the sea floor from destructive fishing practices (see Watling and Norse 1999).

In the past twenty years, technological advances in fishing technology have allowed trawls to access previously inaccessible areas, including waters to depths of 2,000 meters. As gear technology continues to advance, there are few areas that remain inaccessible. By consequence, only areas that legally are closed to destructive fishing practices will experience reduced human impact in the Gulf of Maine and shelf area.

Inadequacies of present-day fisheries management

Lack of adequate habitat protections
Habitat damage due to commercial fishing has been exacerbated by inadequate management for conservation of marine habitat and marine biodiversity. For the past 25 years, fishery managers have virtually ignored the need for habitat protection, in part due to their focus on controlling fishing effort to prevent overfishing. Regulatory tools largely are aimed at the behavior of fishers through management of allowable catch and through effort limitation (Auster and Shackell 2000). The past failure of fishery managers to regulate fishing gear has led to uncontrolled use of technological advances that increase the ability of fishers to access deeper and more complex habitat types. One example of such a technological advance is the creation of "rockhopper" gear, which are large (12 inches to 48 inches) fixed rubber discs placed in front of a bottom trawl, allowing access to very rough bottoms. These structurally complex sites, now accessible to mobile fishing gear, no longer serve as natural refuges for fish and invertebrates. The "old growth" condition of the sites makes them particularly sensitive to disturbance. Both fishermen and marine scientists have recognized that there are few areas left which cannot be accessed by trawl gear (Fuller and Cameron 1998).

In October 1996, the US Congress passed the Sustainable Fisheries Act, which amended the Magnuson Fisheries Conservation and Management Act and required fishery managers to identify and protect "essential fish habitat." Despite estimates of the type, direction, and level of disturbance that fishing activities can have on continental shelf systems, fishery managers in New England and nationwide took few steps to implement habitat conservation measures. The basic rationale for lack of action was that without proof of impacts by particular gears and a greater understanding of the linkages between particular habitats and exploited species, there was not enough information to be precautionary (Auster 2001).

Overall, current habitat management is the antithesis of precautionary management.

Lack of ecosystem-based management
Fishery management presently overlooks ecosystem relationships and the protection of marine foodwebs. It also fails to provide protection to benthic invertebrates. Management instead focuses on maximizing fish extraction from the ecosystem, using a single-species approach. Such an approach ignores trophic interactions and attempts to conserve ecosystems through management of its parts. This approach is further limited to conserving only commercially-important fish species. There are presently no adequate plans to monitor or conserve non-target marine life or the benthic invertebrates commonly caught as bycatch in fisheries.

In 1999, the National Marine Fisheries Service-sponsored Ecosystem Principles Advisory Panel recommended an ecosystem-based management approach for fisheries (NMFS 1999) but found that existing Fishery Management Plans are not sufficient to implement such an approach. "No-take" zones and marine protected areas (MPAs) are an important component of an ecosystem-based strategy (Witherell et al. 2000).

The Stellwagen Bank NMS in the

Gulf of Maine does little to protect commercial fish stocks or fish habitat from the effects of commercial fishing practices. Presently, the use of all fishing gear, including bottom-tending mobile gear, is allowed in Stellwagen Bank NMS. Recent studies have shown significant changes in marine biodiversity over the past 25 years, mainly due to commercial fishing (Auster in press).

Lack of protection for species at risk
Recently, several species have been identified as being at risk of extinction, mainly due to incidental bycatch in fishing gears (Musick et al. 2000). For example, the barndoor skate has declined 90 to 99% over the last 50 years due to incidental capture in trawls and dredges (Casey and Myers 1998). Atlantic halibut (*Hippoglossus hippoglossus*) is eligible for listing under the Endangered Species Act and continues to be caught as bycatch. Most of this bycatch is unreported and unassessed. Atlantic halibut commonly are caught before they are able to reproduce, further depleting the population. Overall, fishery management does not have a systematic approach for protecting species that are prone to extinction. Due to discretion, there is no automatic protection for species that might be prone to extinction (Murawski et al. 2000).

Benefits of GOMIOW

A fundamental problem in marine conservation is our lack of knowledge regarding the number and location of important and sensitive areas that require protection. This information is essential for creating a regional system of marine refuges that adequately protects the biodiversity of any region. It is difficult to select habitats for protection and to determine their size given the paucity of knowledge about the relative importance of habitat features found in any region, such as the continental shelf. A precautionary approach is necessary to protect habitats while scientists gather information about fundamental habitat parameters across spatial and temporal scales. Auster and Shackell (2000) have shown that the most effective conservation strategy for protecting biodiversity is to categorize habitats and protect areas within each category. The GOMIOW provides protection to a wide range of habitats based on sediment types, landscape features, and habitats of concern. The GOMIOW is therefore consistent with the precautionary principle.

The need for no-take MPAs is widely recognized because they protect coastal ecosystems and populations of exploited species, improve scientific understanding of marine ecosystems, and provide increased opportunities for other activities (Murray et al. 1999).

Recently, 161 marine scientists prepared a scientific consensus statement on marine reserves (NCEAS 2001). They concluded that marine reserves are a highly effective but under-appreciated and under-utilized tool that can help alleviate many of the problems associated with present fishery management.

No-take MPAs can be designated to protect sponges and corals where a single pass of mobile gear causes high mortality or damage (Freese et al. 1999) and recruitment of these taxa is sporadic or unpredictable. Similarly, no-take MPAs might reduce the risk of endangering species that are not assessed or sampled (Musick et al. 2000) or minimize the risk of depleting populations of non-targeted species (Casey and Myers 1998; Auster 2001). The GOMIOW achieves many of these conservation objectives.

Protection of at-risk species
In 1999, the Marine Conservation Biology Institute hosted a scientific workshop to identify priority areas in the Gulf of Maine in need of increased protection from the effects of commercial activities. While many of the areas identified in coastal areas fell outside the proposed GOMIOW, the majority of offshore sites were clustered within and around the GOMIOW, including areas having populations of species of concern: barndoor skate, Atlantic halibut, and deep-sea corals.

Protection of habitats and marine biodiversity
Fishery managers continue to manage commercial fisheries solely for maximizing economic outputs, not for the protection and maintenance of marine biodiversity. Recent studies show that present-day fisheries affect marine biodiversity in the Gulf of Maine at the local scale (Auster, 2001). By extending the GOMIOW protected area along and across the Hague Line, a representative cross-section of the habitats of the Gulf of Maine would be included, which protects the benthic biodiversity of this biologically diverse region. The GOMIOW would eliminate fishing-gear-induced changes in habitat structure and, over time, allow habitat complexity to increase (Auster et al. 1995) as areas that were chronically fished would be allowed to naturally restore. The GOMIOW also would protect pristine habitats against future impacts.

Willison (2001) has proposed a global network of MPAs, which would include "cornerstone" MPAs on international boundaries. The GOMIOW would be one of these. If cornerstone MPAs were established, each nation could develop compatible, rather than mismatched, national systems. International cornerstones therefore could act as nuclei for a multi-national system of protected areas in North America, regardless of the differing legal systems and political systems on the continent.

Creation of spawning sanctuaries

Research has been conducted on the benefits of a cross-shelf marine wilderness to commercial species. For example, a model created by McGarvey and Willison (1995) indicates that establishing a marine wilderness on Georges Bank would enhance the scallop fishery by allowing scallops to grow larger and thereby increase individual egg and larvae production. The study finds that by protecting 8 to 10% of the productive part of Georges Bank, there would be a substantial effect on scallop recruitment throughout the Bank. These areas would act as spawning sanctuaries. Portions of a cohort of postlarval and juvenile age classes, which settle or migrate to a MPA, would experience enhanced survivorship, potentially increasing recruitment to the fishable stock (Lindholm et al. 1999). Subsequent closures of areas to scallop fishing on Georges Bank have borne out this prediction.

Promote scientific research

There is inadequate information for the management of marine ecosystems in the Gulf of Maine. By implementing the GOMIOW, precautionary management is promoted by preserving pieces of undisturbed habitats, which also provide sites for a wide range of future scientific research. In order to obtain reliable data and create robust models, experiments with adequate controls are essential. Currently, lack of control areas in New England presents a significant obstacle to research on fish habitat (Dorsey and Pederson 1998).

For marine scientists, the major problem with assessing the impacts of bottom-tending mobile gear is the lack of sites that have gone unfished for long periods of time. Without control sites, scientists cannot determine the effects of fishing gear. In order to understand clearly the effects of fishing on different types of habitat, areas need to be closed so that experiments can determine effort-specific rates of impacts (Auster and Langton 1999). The GOMIOW would close portions of the five major habitat types found in the Gulf of Maine, essentially creating control sites for future habitat research.

Conclusion

The need for ocean wilderness areas in the Gulf of Maine continues. While the Clinton Administration did not designate the GOMIOW as an ocean wilderness, the National Ocean Service recognizes the need for such marine reserves in New England and is presently hosting a set of workshops to identify key areas for protection. American Oceans Campaign continues to promote the GOMIOW and other similar means to designate protected ocean wilderness areas in the Gulf of Maine. The United States and Canada should begin formal discussion on the subject of using the GOMIOW as a tool for integrating marine conservation across the artificial international boundary in the Gulf of Maine.

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News from Zoos

Oregon Silverspot Population Supplementation

Habitat loss and degradation has greatly affected the Oregon silverspot (*Speyria zerene hyppolyta*) and the six different locations where this butterfly lives in the Pacific Northwest. The greatest affect has been on the silverspot's larval host plant, which now has to compete with non-native grasses. In 1980, the US Fish and Wildlife Service (USFWS) listed the Oregon silverspot as a threatened species. In 1998, the silverspot population at The Nature Conservancy's Cascade Head Preserve dropped to 57 individuals. This prompted the Oregon Zoo, The Nature Conservancy, Lewis & Clark University and USFWS to join forces and begin working on a captive rearing and release program to supplement the current populations.

The rapidly declining population at the Cascade Head Preserve made it the perfect location for the first supplementation. In September 1999, Nature Conservancy volunteers captured 10 adult butterflies. These 10 adults produced enough eggs that volunteers rereleased 107 adult butterflies into the wild. A survey of Cascade Head's silverspot population in 2000 showed a 21% increase over the 1999 population. Based on the success of the first release, the four organizations are planning additional releases at Cascade Head and possibly another site in 2002. [Source: Blair Csuti and David Shepherdson, Oregon Zoo]

Saint Louis Zoo Receives Leadership Gift for New Exhibit

The Saint Louis Zoo received a commitment of $1.5 million from the David B. Lichtenstein Foundation for the construction of its new Penguin & Puffin Coast exhibit. The Lichtenstein Penguin Cove will feature the first walk-through Antarctic penguin exhibit in North America. The exhibit will also offer two large indoor habitats, one for Antarctic penguins and one for puffins. Both will give visitors underwater viewing in a rugged, naturalistic coastline exhibit.

Penguin & Puffin Coast will also feature puffins and Humboldt penguins. The completion of Puffin Bay will bring the colorful birds to the zoo for the first time. The exhibit is slated to open in 2002. [Source: Communique]

Asian Otter Survey and Awareness Program

Throughout most of Asia, the otter is the top freshwater and wetland carnivore, but conservation efforts in this region have placed more emphasis on larger mammals. Increased industrialization and population have altered the otter's habitat as well as reduced the otter population. In more industrialized countries, the otter has almost disappeared and in other countries, there is no reliable information on the status of their populations.

AZA's Small Carnivore Taxon Advisory Group (TAG) and Asian Small-clawed Otter Species Survival Plan (SSP) are working closely with Asian officials, such as the IUCN Asian Otter Secretariat in Sri Lanka, on a series of projects. One project is to survey Cambodia, Laos, Myanmar, Malaysia, Thailand, Vietnam and Indonesia for hairy-nosed otters. Another project is to conduct a general survey in western Asia and create awareness programs about otters and their importance in countries like Pakistan, Nepal and India. The results of the surveys are now coming back to the Secretariat, the TAG and the SSP. Once the size and locations of the populations are determined, these groups will determine a course of action. [Source: AZA in Action]

Information for News from Zoos *is provided by the American Zoo and Aquarium Association*

News & Events

Society for Conservation Biology, 16th Annual Meeting

Co-hosted by the British Ecological Society (BES), the theme for the upcoming SCB annual meeting will be: People and Conservation. This meeting will be held July 14 to 18, 2002, at the Durrell Institute of Conservation and Ecology, University of Kent at Canterbury, Canterbury, UK. For more information, contact Nigel Leader-Williams, SCB 2002 Programme Chair (scb2002@ukc.ac.uk), or Andrew Pullin, BES (a.s.pullin@bham.ac.uk). Conference web site: http://www.ukc.ac.uk/anthropology/dice/scb2002/

Conservation Maps Online

The Library of Congress offers a new web site, *Conservation and Environmental Maps*, which provides historic and recent maps of land use and exploration in the United States. These maps will be of great interest to ecologists as they show "changes in the landscape, including natural and man-made features, recreational and wilderness areas, geology, topography, wetland area, vegetation, and wildlife." http://lcweb2.loc.gov/ammem/gmdhtml/cnsvhome.html.

New Journal Announcement

Ecological Indicators, a new international website and corresponding journal, has been launched. The ultimate goal of Ecological Indicators is to integrate the monitoring and assessment of ecological and environmental indicators with management practices. The journal is intended for scientists, decision-makers, and resource managers working with or using ecological and environmental indicators for the long-term goals of assessing extent, condition and trends within the environment. http://www.ecologicalindicators.org.

Ecological Society of America

The ESA announces its 87th Annual Meeting in Tuczon, Arizona, on August 5-8, 2002. Keynote address to be given by E.O. Wilson. For more information: http://www.esa.org/tuczon.

Tahoe-Baikal Exchange Program

The twelfth annual summer environmental exchange program between Lake Tahoe in California and Lake Baikal in Russia will be held from July to August 2002. For an application packet, call (530) 542-5599, or email tbi@etahoe.com. For more information: http://tahoe.ceres.ga.gov/tbi.

Announcements for the Bulletin Board are welcomed. Some items have been provided by the Smithsonian Institution's Biological Conservation Newsletter.

Endangered Species UPDATE

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