

EEB3001 Sea Otter Homework Assignment: Due Wednesday November 11th

Name: _____

Read the attached article and answer the following questions.

C.V. Kappel. 2005. Losing pieces of the puzzle: threats to marine, estuarine, and diadromous species. *Frontiers in Ecology and the Environment* 3(5), 275-282. (“Diadromous species” migrate between salt and fresh waters, like salmon.)

Questions:

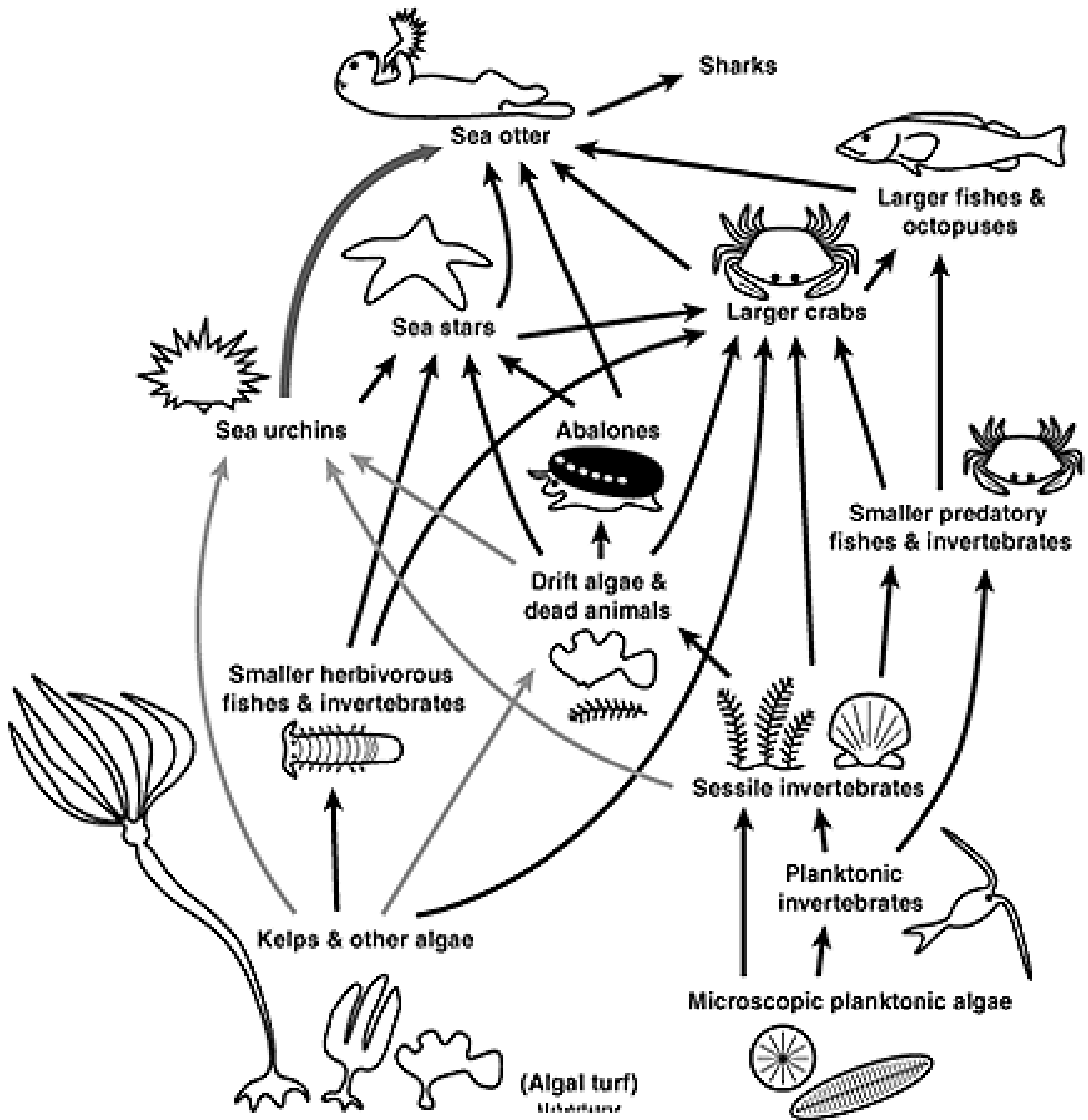
1. What are the top three categories of threats to marine species, according to ESA (the US Endangered Species Act) and IUCN (the World Conservation Union Red List)?

2. Are marine species more or less vulnerable to extinction compared to terrestrial species, in your opinion?

3. Estes and Duggins (1995) found that rebounding populations of sea otters in Alaska were indirectly affecting the recovery of marine kelp forests. Figure A in next page shows the food web (i.e., a summary of the feeding relationships in a community) in kelp forests when sea otters are abundant. Taking into account the food web structure, what are possible reasons why the kelp forests in the region disappeared when sea otters were heavily hunted and mostly removed? Cross out all links that you think might be lost or severely weakened if sea otters were absent, and describe briefly your reasoning of the disappearance of the kelp forests.

4. If a large population of killer whales migrated into the region and reduced the population size of sea otters, what would happen to herbivorous fish, abalones, sea stars, and large crabs in the kelp forests? Describe your predictions using the food web diagram in Figure A.

A. With sea otters, kelp forest food web



Losing pieces of the puzzle: threats to marine, estuarine, and diadromous species

Carrie V Kappel

The number of marine species at risk of extinction is rising. Understanding the threats that contribute to extinction risk in the seas is thus critical to conservation. When major threats to marine, estuarine, and diadromous species on the US Endangered Species Act and IUCN Red lists were ranked according to the number of species they affect, strong consensus in the ranking of threats across species and between institutions emerged. Overexploitation is the most frequent threat to vulnerable marine species, with approximately half of threatened species caught as bycatch in fisheries. Habitat degradation, the primary threat to terrestrial species, ranks second in impact on marine species. Loss of listed marine species would probably affect ecosystem function and delivery of ecosystem services because many of these species are strong interactors, including ecosystem engineers, taxa that provide important nutrient links between terrestrial and marine ecosystems, and a disproportionate number of high trophic-level predators.

Front Ecol Environ 2005; 3(5): 275–282

Human history has noted the disappearance of five seabirds, three marine mammals, and four gastropods from the world's oceans. According to a recent review of marine extinctions, another 18 species may have gone extinct globally, although their taxonomic status is uncertain, while 103 species have been lost from substantial portions of their ranges (Dulvy *et al.* 2003).

Despite evidence of marine extinctions, fewer marine than terrestrial species have been flagged as vulnerable under the US Endangered Species Act (ESA), the World Conservation Union (IUCN) Red List, or the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES). However, the number of marine species on these lists has grown recently and is expected to continue to rise with mounting threats and increased attention to the status of marine populations and ecosystems (International Institute for Sustainable Development 2002; Baillie *et al.* 2004; Armsworth *et al.* in press a; Figure 1).

In part, the increase in listings represents growing recog-

nitition that marine species may be as vulnerable to extinction risk as terrestrial species, despite commonly held perceptions to the contrary (Roberts and Hawkins 1999; Dulvy *et al.* 2003; Hutchings and Reynolds 2004). In 1996, IUCN sparked a debate in the scientific literature by listing several commercially important species, including southern bluefin tuna, Atlantic cod, and North Sea haddock. Although some scientists and managers objected to the “one size fits all” decline threshold (IUCN Criterion A) that triggered the listing of these species (eg Matsuda *et al.* 1997), others have argued that there is no convincing evidence that marine species are less vulnerable to extinction than terrestrial species, and that high fecundity, naturally variable populations, and large dispersal potential do not necessarily confer resistance to over-exploitation (Hutchings 2001; Dulvy *et al.* 2003; Hutchings and Reynolds 2004).

Many recent papers have pointed to overfishing as a major cause of declines in marine populations (Pauly *et al.* 1998; Musick *et al.* 2000; Jackson *et al.* 2001; Myers and Worm 2003). Dulvy *et al.* (2003) found that 55% of known local to global marine extinctions were attributable to exploitation. However, to date no one has looked in a quantitative way at threats to the full list of vulnerable marine species. On land, the most common threat to vulnerable species is habitat loss, rather than over-exploitation (Wilcove *et al.* 1998). This difference may represent, at least in part, a temporal lag in exploitation of the seas. We have long since abandoned the harvest of substantial numbers of wild land animals or plants for human consumption, and instead have turned to domesticated biomass and industrial agriculture, which is a primary contributor to terrestrial habitat degradation (Wilcove *et al.* 1998). However, each year, over 80×10^6 tons of wild biomass are harvested from the oceans (FAO

In a nutshell:

- Most marine species face multiple threats
- Overexploitation is the most pervasive of these threats, affecting commercial and non-commercial species alike
- Bycatch is comparable in impact to targeted harvest and threatens approximately half of the listed marine species
- Habitat degradation, the second greatest threat, is particularly problematic for coastal species affected by land-based impacts
- By assessing the relative impacts of different threats and building understanding of species' ecological roles, we can develop conservation priorities

Hopkins Marine Station, Stanford University, 100 Oceanview Boulevard, Pacific Grove, CA 93950 (ckappel@stanford.edu)



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Figure 1. Humpback whale (*Megaptera novaeangliae*) breaching in Monterey Bay, CA. Humpbacks are listed as endangered under the ESA and vulnerable by the IUCN.

Fisheries Department 2004); thus, overexploitation has the potential to be a major threat to both target and non-target species through direct harvest, bycatch, depletion of prey, habitat alteration, or other indirect effects. To design and implement effective biodiversity conservation approaches for the oceans, we must understand the relative impacts of the full spectrum of risks facing marine species, from overexploitation to habitat loss to climate change.

Major threats to marine biodiversity in general and to vulnerable species in particular have been qualitatively reviewed elsewhere (National Research Council 1995; Pew Oceans Commission 2003; US Commission on Ocean Policy 2004; Armsworth *et al.* in press a). Table 1 briefly summarizes the threat categories evaluated here. The primary objective of this paper is to provide a synopsis of the current status of threats to vulnerable species by using two separate datasets, comprised of nearly 300 species, to evaluate the relative importance of these threats, and to rank by how many at-risk species they impact. (“Species at risk” refers to marine, estuarine, or diadromous species listed as vulnerable, endangered, or critically endangered on the IUCN Red List and/or endangered, threatened, candidate, or species of concern under the ESA.) Marine and estuarine threats are compared to terrestrial and freshwater stressors, and the potential impact that the loss of strongly interactive species or groups of species would have on ecosystem function and delivery of ecosystem goods and services is also discussed. Finally, suggestions are offered for how we should proceed with research, conservation, and management efforts to better understand and minimize extinction risk in the world’s oceans.

■ Ranking the threats

As of May 1, 2004, 168 marine, estuarine, or diadromous species from US and foreign waters were listed or being considered for listing under the ESA (Figure 2). Under the Act, subspecies and distinct population segments (DPSs) can be treated as “species” in the listing process;

“species” is thus used here to refer to any taxa listed under the ESA. Results for species defined in this manner are detailed here; however, threat rankings were also reanalyzed using biological species and subspecies rather than DPSs, in an attempt to determine whether or not species with multiple DPSs (eg salmonids) caused bias in the results.

Threats to these taxa were tallied using Federal Register rulings, status reviews, and recovery plans published by the listing agencies of the National Oceanic and Atmospheric Administration (NOAA) Fisheries and US Fish and Wildlife Service (FWS). Threats were categorized as “known” (historical or ongoing) or “potential” (uncertain or future), as indi-

cated by the listing agency (Table 1). Major and minor threats were not separated, as this information was not consistently provided. Multiple threats were recorded for most species. Single threats that could be counted in multiple categories were tallied in both. For example, habitat degradation due to destructive fishing gear was classified as both habitat loss and overexploitation.

An additional 225 species, subspecies, or stocks (55 in common with the ESA list) for which information on threats was available were compiled from the IUCN Red List (IUCN 2004a; Figure 2). This information came from assessments of taxonomic groups conducted by specialists who categorize major threats according to a common hierarchy (IUCN 2004b). Red List threats were placed into the Table 1 categories to make the two datasets comparable. For marine birds, additional information on threats and on potential correlates of vulnerability (eg ground nesting) was obtained from Birdlife International, the organization that assessed marine birds for the IUCN Red List (BirdLife International 2004). The full list of species and threats is available in Web Table 1.

These datasets have important limitations: both ESA and IUCN listings are based on expert opinion, and the biologists who prepare listing notices and status reviews may or may not use quantitative or experimental data to evaluate threats. In fact, such data are often unavailable. ESA listing notices, for instance, frequently lack important data, including information about impacts of invasive species, habitat degradation, and pollutants (Easter-Pilcher 1996). The level of detail varies considerably among taxa and with date of listing. Recent listings have resulted in more detailed documentation of status, causes of decline, and threats to recovery of petitioned species than earlier listings. Threats cited in listing documentation are partly a reflection of the scientific understanding of the time, so recently recognized impacts such as climate change are underrepresented. In addition, although the datasets cover a wide taxonomic range, they are weighted towards certain groups of species, largely because studies and management of marine

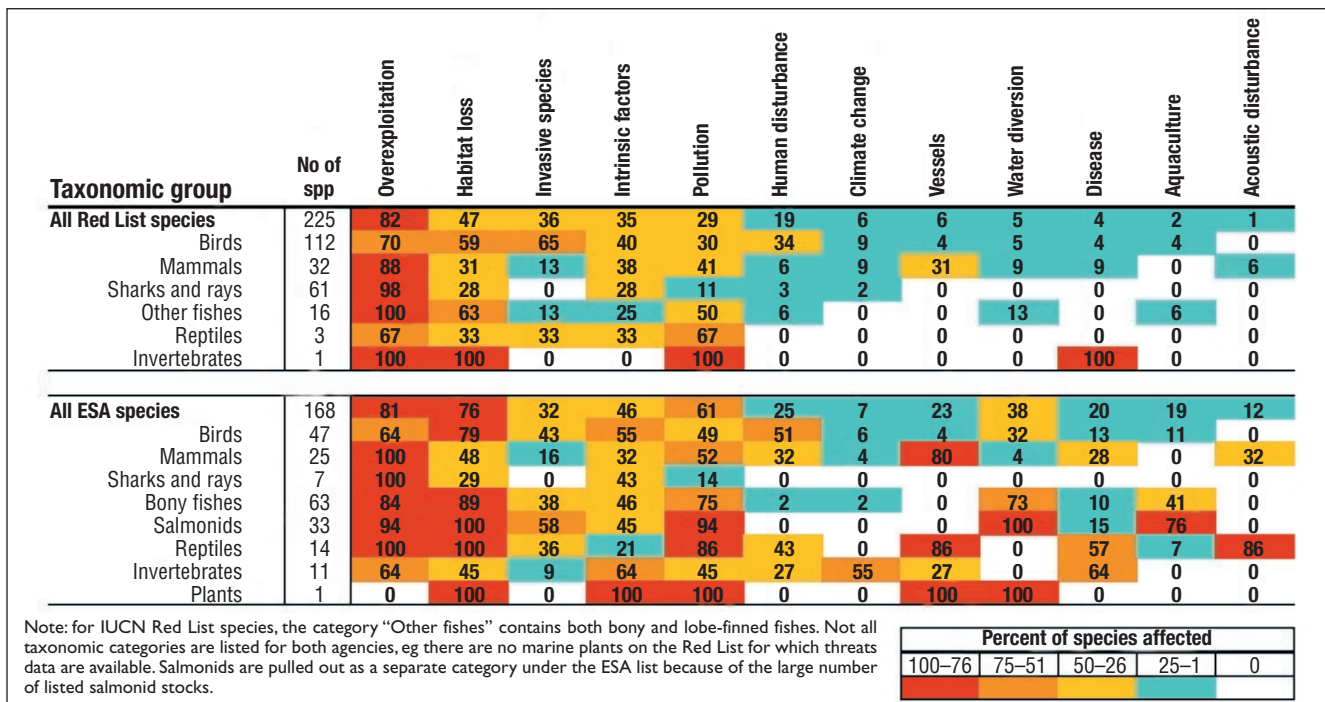


Figure 2. Impacts of threats on different taxonomic groups. The proportions of species affected by different threats were compared between the ESA and IUCN lists and within individual taxonomic groups for each list. Cells in the table are color-coded to reflect the relative magnitude of each threat to the given group.

ecosystems are similarly imbalanced; commercially important taxa are overrepresented, for instance, as are large-bodied vertebrates. Invertebrates and marine plants and algae, on the other hand, are drastically underrepresented. Despite such limitations, these datasets represent the most comprehensive and taxonomically broad assessment of the current threats to marine species and combine available data and expert opinion from a variety of sources and fields.

■ The seascape of risks

The most common threat to marine and diadromous species on both lists is overexploitation (Figures 2 and 3a). Overharvest impacts 82% of Red List and 81% of ESA species at risk, through direct harvest, incidental catch and bycatch, and indirect effects, such as trophic cascades, competition for prey, and habitat destruction due to destructive fishing gear. The relative importance of these is shown in Figure 3b: 65% of ESA species are affected by targeted harvest, 42% by incidental catch or bycatch, and 8% by indirect effects, while for IUCN species the proportions are 58%, 48%, and 17%, respectively. Habitat loss ranks second in importance on the IUCN list, affecting 47% of imperiled species, followed by invasive species, which impact 36% (Figure 3a). For ESA species, habitat degradation also ranks second (76%) and pollution third (61%). On both lists the top three threats are pervasive: overexploitation, habitat loss, and/or invasive species affect every Red List species, either singly or in combination. Similarly, 98% of ESA species are affected by overexploitation, habitat loss, and pollution, or some com-

ination of these. Results were similar whether the unit considered was a population or a biological species/subspecies (C Kappel, unpublished). Red List threat rankings were unaltered, and percentages affected differed by ≤ 1% for every threat. Considering species rather than populations had a slightly greater effect on results for ESA species. Ranks of the top four threats were unaltered, but water diversion and aquaculture both went down in rank (from fifth to a tie for sixth and from tenth to eleventh place, respectively), while human disturbance went up from seventh to fifth. Percentages affected by each threat differed, on average, by 4.4%.

Overharvest, bycatch, and the indirect effects of fishing

Tallies of threats to ESA and Red List species lead to the same conclusion: overexploitation is the most common threat to listed species. Both of these lists are biased towards commercial species; in fact, about half the listed taxa have been, or currently are, commercially exploited. At the same time, however, the vast majority of species were affected, demonstrating that impacts of exploitation go beyond target species, an assertion supported by the large proportions of species affected by bycatch and/or incidental catch (Figure 3b). The majority of the world's fisheries affect multiple species, and even sustainable levels of exploitation of a primary target species can lead to non-sustainable impacts on less valuable, non-target species taken incidentally (eg skates and rays in the Irish Sea; Dulvy *et al.* 2003).

Table 1. Threats categories used in analysis

Threat	Description	Examples of species affected
Overexploitation	Targeted harvest via fishing, hunting, or collecting; bycatch or incidental catch; and indirect effects including trophic cascades, competition for prey, and habitat degradation due to destructive fishing gear	<ul style="list-style-type: none"> • Sturgeons (Collins <i>et al.</i> 2000) • White abalone (Hobday and Tegner 2000) • Loggerhead and leatherback turtles (Lewison <i>et al.</i> 2004) • Vaquita (Rojas-Bracho and Taylor 1999; D'Agrosa <i>et al.</i> 2000)
Habitat destruction	Degradation or loss of habitat due to various causes	<ul style="list-style-type: none"> • Salmonids (Slaney <i>et al.</i> 1996) • Abbott's booby (Reville <i>et al.</i> 1990)
Climate change	Direct and indirect effects of anthropogenic global climate change (eg changes in prey availability, altered water temperature, salinity, and pH, increased storm frequency, etc)	<ul style="list-style-type: none"> • Seabirds (Croxall <i>et al.</i> 2002) • Corals (Hoegh-Guldberg 1999; Knowlton 2001) • Marine mammals (Langtimm and Beck 2003; Tynan and DeMaster 1997)
Pollution	Contamination, terrestrial runoff, and eutrophication, sedimentation, thermal pollution, and marine debris	<ul style="list-style-type: none"> • Marine mammals (MMC 1999) • Florida manatee (Beck and Barros 1991)
Vessel interaction	Boat collisions and acoustic and visual disturbance due to vessel traffic	<ul style="list-style-type: none"> • Northern right whale (Clapham <i>et al.</i> 1999, Nowacek <i>et al.</i> 2004a) • Florida manatee (Nowacek <i>et al.</i> 2004b)
Disease	Native and non-native pathogens	<ul style="list-style-type: none"> • Black abalone (Friedman <i>et al.</i> 1997) • Acroporid corals (Gladfelter 1982; McClanahan and Muthiga 1998) • Sea turtles (Aguirre <i>et al.</i> 1998)
Water diversion	Diversion of water and flow modification in rivers, streams, coastal wetlands, bays, and estuaries, for hydropower and irrigation, navigation, and coastal development (could be considered a particular type of habitat destruction)	<ul style="list-style-type: none"> • Salmonids (Slaney <i>et al.</i> 1996) • Tidewater goby (Lafferty <i>et al.</i> 1996)
Invasive species	Direct and indirect effects of non-native invaders, such as competition, predation, spread of disease, and habitat modification	<ul style="list-style-type: none"> • Sea turtles (Allen <i>et al.</i> 2001) • Seabirds (Moors and Atkinson 1984)
Aquaculture & hatcheries	Direct and indirect effects of aquaculture and hatcheries operations on wild populations, including competition for food, predation by escaped or released individuals, spread of disease, habitat destruction, genetic pollution, water quality degradation	<ul style="list-style-type: none"> • Snake River spring chinook salmon (Levin <i>et al.</i> 2001) • Pacific salmonids (Volpe <i>et al.</i> 2000)
Increased human presence	Disturbance from increased human activity, especially to marine animals that come to shore to nest, breed, or rest	<ul style="list-style-type: none"> • Hawaiian monk seal (Gerrodette and Gilmartin 1990)
Acoustic disturbance	Disturbance from underwater explosions, sonar, or other acoustic sources	<ul style="list-style-type: none"> • Marine mammals (NRC 2003)
Natural threats and Intrinsic factors	Intrinsic factors such as limited dispersal or range size, slow growth rate, or poor recruitment, and natural threats such as predation, storms, or flooding	<ul style="list-style-type: none"> • Skates and rays (Dulvy <i>et al.</i> 2002)

Habitat loss on land and in the seas

Habitat degradation, the leading driver of terrestrial endangerment, is the second most pervasive threat to marine species at risk. In fact, it may be that habitat loss is the number two threat to aquatic species, specifically because it is the primary threat on land. This is suggested by the prevalence of species for which habitat degradation was counted as a substantial threat and that spend some part of their lives associated with terrestrial, freshwater, or estuarine habitats. Over 85% of the ESA species that utilize these ecosystems in addition to marine habi-

tats – and all of the diadromous species – are impacted by habitat degradation, most likely because their life cycles expose them to the effects of terrestrial land conversion. In addition, all but one of the fully marine species affected live in coastal (nearshore or continental shelf) habitats, where activities on land and near the shore may contribute to habitat loss. Degradation of oceanic and deep-water habitats, though less commonly cited, may be increasing in frequency as a threat to marine species, particularly as advances in navigation technology allow exploitation of formerly inaccessible areas.

The persistent and pervasive problem of pollution

Pollution affects large numbers of ESA species. However, strong causal links between pollution and population level effects in marine species have generally been difficult to demonstrate (Nisbet 1994; Marine Mammal Commission 1999). Clear evidence comes from catastrophic and chronic oil spills (eg Peterson *et al.* 2003; Wiese and Robertson 2004) and selected organochlorine impacts (eg links between DDT, DDE, and PCBs, and bird declines; Nisbet 1994). Evidence for a link between persistent organic pollutants and decreased health and reproductive success in turtles and marine mammals is emerging (Marine Mammal Commission 1999; Keller *et al.* 2004). The large numbers of species thought to be vulnerable to pollution is in keeping with the ubiquity of the problem. Even remote ecosystems are plagued by pollutants: for example, over 111 metric tons of derelict fishing gear and other debris were removed from the uninhabited Northwest Hawaiian Islands in 2003 (NOAA Fisheries 2003b). The Arctic Ocean is now a net source for contaminants such as the pesticide lindane (HCH), deposited from the atmosphere in the 1940s–1980s (MacDonald *et al.* 2000). The widespread distribution and long-term persistence of these pollutants, combined with the small population sizes of many species at risk, could translate to population-level impacts.

Invasive species impacts and the IUCN Red List

A major difference between ESA and IUCN threat rankings is the greater importance of invasive species impacts to IUCN Red List taxa. This difference is probably driven by several factors. First, half the Red List species assessed for the purposes of this review are birds. Of these, 65% are affected by invasive species (Figure 2). By contrast, birds make up less than 30% of marine and coastal ESA species, and invasive species were highlighted as a cause of decline or a threat to recovery in only 43% of these taxa. Breeding traits of many marine birds may explain their vulnerability to invasive species. Eighty-two percent of Red List marine birds are ground nesting, and three-quarters are adapted to breeding on oceanic islands, which often lack native predators, leaving them vulnerable to introductions of rats, cats, and other predators of eggs, nestlings, and adults.

Why wasn't climate change ranked higher?

Surprisingly, climate change was not frequently listed as a threat, despite recent modeling which suggests that as many as 15–37% of terrestrial species may go extinct due to global warming by 2050 (Thomas *et al.* 2004). One would expect that factors such as climate change that have only recently gained attention would be underrepresented in earlier listings. In keeping with this, pollution, climate change, invasive species, and disease, in particular, have been cited more frequently in recent ESA listings. It is likely that reporting of these threats will

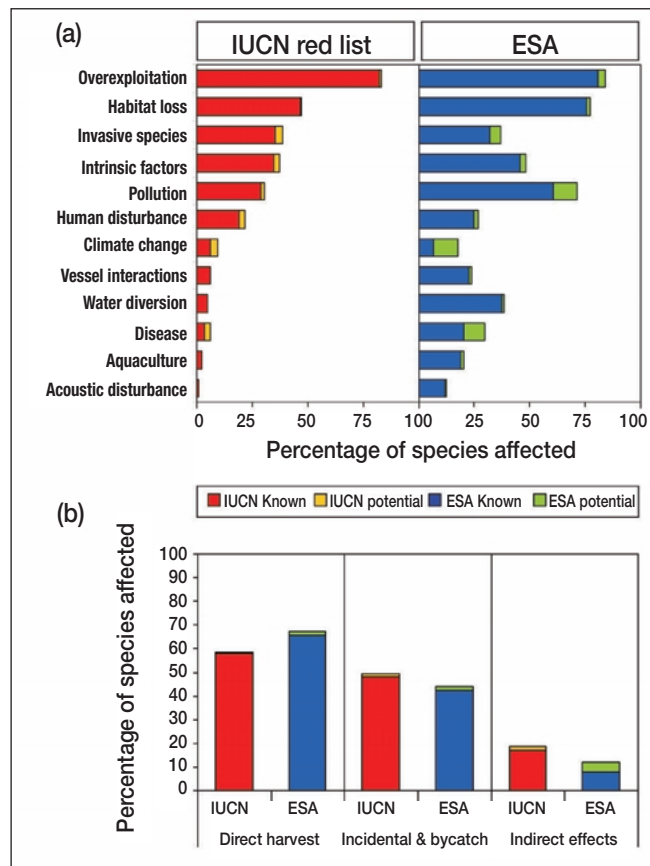


Figure 3. Results of assessment of relative importance of different threats to marine species at risk. (a) Comparison of proportions of IUCN ($n=225$) and ESA ($n=168$) species affected by each threat. (b) Breakdown of the top threat, overexploitation, into the percentages of species affected by direct, targeted harvest versus incidental catch and bycatch, or indirect effects such as habitat degradation, competition for prey, or trophic cascades.

increase in the future, as indicated by the proportions of species for which these were listed as a “potential” threat: pollution 11%, climate 13%, disease 10%, and invasive species 5%.

The science of threats assessment

Simple lists of threats cannot predict population or ecosystem effects of combining multiple stressors. A key challenge for ecologists is to develop statistical, modeling, and experimental techniques to build our capacity to predict how threats combine and interact to affect vulnerable species. For biodiversity conservation planning, we require spatially explicit data, preferably collected over the long term, so that spatiotemporal trends in threats can be evaluated. These data should derive from assessments of multiple species and ecosystems and should be evaluated within the context of species and ecosystem vulnerability to particular threats.

Threats assessment aimed at endangered species recovery requires quantitative data and experimental evidence to reveal causes of declines and roadblocks to recovery. For

example, Peery *et al.* (2004) used a multi-pronged approach to test multiple competing hypotheses about causes of marbled murrelet declines in California. Like elasticity analyses of population matrix models, which highlight the life stages of vulnerable species that exert the greatest effect on population growth rates, mechanistic tests of the relative importance of different threats can direct us towards effective recovery strategies (Caswell 2000; Peery *et al.* 2004).

■ Functional roles of vulnerable species

It is sometimes assumed that loss of threatened species would not lead to ecosystem-level changes because these species were probably rare to begin with and therefore unlikely to have played important roles in ecosystem function. However, examination of the currently listed marine and estuarine species indicates that the world might indeed feel the loss of these species, many of which are top predators, ecosystem engineers, and key links between marine and terrestrial ecosystems. Soulé *et al.* (2003, 2005) term these species “strongly interactive” and provide guidelines for assessing the types and degree of interaction that include promotion of species diversity, provision or modification of habitat, and alteration of nutrient dynamics, among other factors. As the authors point out, the ESA contains language that provides a rationale for attending to species interactions: “The purposes of this Act [the ESA] are to provide a means whereby the ecosystems upon which threatened and endangered species depend may be conserved” (section 16 USC § 1531 [b]). They recommend that the goal for recovery of strongly interactive species should be “ecological effectiveness”, with a particular desired ecosystem state as the management endpoint (Soulé *et al.* 2005).

The average trophic level of the taxa reviewed here is 3.7, indicating that most of these species are secondary or tertiary predators (Web Table 2). Species within top trophic

levels have been shown to be more susceptible to extinction than lower level species (Pauly *et al.* 1998; Duffy 2003; Petchey *et al.* 2004), and tend to be more heavily exploited and more vulnerable to bioaccumulation of pollutants and temperature shifts as well (Pauly *et al.* 1998; Myers and Worm 2003; Petchey *et al.* 2004). Top-down effects of predators have been shown to be critical in structuring some marine ecosystems (eg Menge 2000). For example, rebounding populations of over-hunted sea otters, a keystone predator in Pacific kelp forest ecosystems, reversed large-scale declines in kelp cover by eating urchins which had been overgrazing the kelp (Estes and Duggins 1995). We know little about the exact ecological roles of most listed species, and the impacts of their loss would doubtless be varied and context-dependent. Nonetheless, strongly interactive top predators should be priority targets for recovery efforts.

Species at lower trophic levels may also provide key ecosystem functions. Caribbean acroporid corals, (*Acropora palmata*, *A. cervicornis*, and *A. prolifera*), which are currently candidates for listing under the ESA and are at present listed under CITES, were once the ecological dominants on shallow-water reefs in Florida and the Caribbean (Goreau 1959; NOAA Fisheries 2003a; Figure 4). These corals, which represent the only staghorn and tall tabular corals in this region, provided important biogenic habitat for many species of fish and invertebrates (Bellwood *et al.* 2004). Live coral cover and habitat complexity provided by these species is positively correlated with abundance and diversity of fishes (Gladfelter and Gladfelter 1978). The elkhorn (*A. palmata*) and staghorn (*A. cervicornis*) zones have virtually been eliminated from the Caribbean through disease, hurricanes, bleaching, and algal overgrowth (NOAA Fisheries 2003a). The number of obligate species that depend on these corals is unknown, as is the extent of diversity loss that would result from extinction of Caribbean acroporids.

Many vulnerable marine species use terrestrial, freshwater, and estuarine habitats at points in their life histories, and thus have the potential to serve as important conduits for nutrient flux between marine and terrestrial systems. Guano production by seabirds, for example, can greatly affect community structure on or around seabird colonies (eg Bosman and Hockey 1986; Anderson and Polis 1999). Similarly, the return of spawning salmon to Pacific Northwest streams represents a tremendous annual input of marine nutrients to freshwater and riparian ecosystems and has cascading effects (Gende *et al.* 2002; Schindler *et al.* 2003). Loss of either seabirds or salmonids, two groups that are nearly universally threatened, could have ecosystem-level ramifications.

The consequences of marine extinctions will remain a black box until more is known about the natural histories, interactions, and



Figure 4. *Acropora palmata*, commonly known as elkhorn coral, in the Bahamas. *A. palmata*, which once formed dense stands, has declined precipitously throughout the Caribbean and is now listed as a candidate species under the ESA, along with *Acropora cervicornis* and *Acropora prolifera*.

ecological roles of marine species. Nonetheless, the roles played by top predators, ecosystem engineers, and species that link marine and terrestrial systems may be essential to marine ecosystem function. Unfortunately, for some species, we may not learn what pieces of the puzzle they represent until it is too late.

■ Conservation implications

The results of this analysis are clear: marine species face a gauntlet of threats, chief among which are overexploitation, habitat degradation, pollution, and invasive species. Bycatch, in particular, is a major risk to nearly half the species examined. In one sense, these results are hopeful; the leading cause of endangerment, overharvest, is also the most controllable. Furthermore, unlike pollution, which may persist long past the point where its production has stopped, or habitat degradation, where recovery to pristine levels is unlikely, the threat of overharvest is removed (though alterations to habitats and food webs may persist) once halted. Then, of course, the hard business of recovery must begin.

Unfortunately, despite the potential for control, we have a poor track record of managing overexploitation (Hutchings and Reynolds 2004). Fisheries around the world have undergone serial depletion and collapses of species from ever-lower trophic levels as we “fish down marine food webs” (Pauly *et al.* 1998). The recent shift towards ecosystem-based management in fisheries holds promise for slowing and potentially reversing this trend, but we currently lack both the data and the governance structures needed to successfully account for environmental forcing, habitat dynamics, and species interactions in fisheries management (Pew Oceans Commission 2003; Pikitch *et al.* 2004; US Commission on Ocean Policy 2004). Conservation of vulnerable marine species presents a similar challenge, as data on life-history traits, habitat requirements, and interactions with other species and with the environment are nearly always lacking. However, this analysis suggests that a high priority first line of action would be to reduce non-target catch in the world’s fisheries through bycatch quotas and mandatory observer programs, changes to fishing gear and practices, and international agreements to halt destructive fishing practices (Hall *et al.* 2000; Melvin and Parrish 2001). Programs that provide incentives to fishermen to devise innovative bycatch reduction methods (for example changing the depth at which hooks are set or using thawed bait that sinks rather than floating, to avoid seabird mortality), show promise (Figure 5). No-take marine reserves, which could be used to reduce impacts on sensitive species by providing spatial refugia from overharvest and other threats have, so far, seldom been applied to marine endangered species conservation (Armsworth *et al.* in press b).



Figure 5. Seabird–fisheries interactions off the coast of Argentina. Some current fishing practices lead to high seabird mortality.

In addition, we must address the fundamental problem of overcapitalization in the world’s fisheries and establish governance structures that provide incentives for fishermen (eg via property rights) to promote conservation and sustainable fishing of portfolios of species (Edwards *et al.* 2004; Hilborn *et al.* 2004). Finally, it is critical to recognize that impacts of fishing do not act in isolation, even in populations for which overexploitation is the primary threat. Habitat degradation, pollution, and invasive species interact with disease, climate change, and other stressors to exacerbate existing problems in many populations. An effective conservation program for the oceans must address the threats on all fronts.

Species-by-species conservation is difficult, expensive, and inefficient. It is likely to be even more so in marine systems, where the implementation and monitoring of restoration and conservation measures are logistically challenging. What is needed is a broader approach to biodiversity conservation – one aimed at preventing species from collapsing to the point where extinction is imminent – and a means to prioritize how limited funds should be spent. A threats-based approach, wherein we focus first on alleviating the most serious threats to the strongly interactive species that play key ecosystem roles is recommended. A clear understanding of the nature of the threats, and of their separate and joint effects on multiple species, habitats, and ecological interactions, is vital if we are to develop effective conservation strategies to prevent the loss of a significant portion of marine biodiversity.

■ Acknowledgements

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