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The Management of Fisheries and Marine Ecosystems

Louis W. Botsford, Juan Carlos Castilla, Charles H. Peterson

The global marine fish catch is approaching its upper limit. The number of overfished populations, as well as the indirect effects of fisheries on marine ecosystems, indicate that management has failed to achieve a principal goal, sustainability. This failure is primarily due to continually increasing harvest rates in response to incessant sociopolitical pressure for greater harvests and the intrinsic uncertainty in predicting the harvest that will cause population collapse. A more holistic approach incorporating interspecific interactions and physical environmental influences would contribute to greater sustainability by reducing the uncertainty in predictions. However, transforming the management process to reduce the influence of pressure for greater harvest holds more immediate promise.

F ishing the oceans is a significant human enterprise. Fisheries provide direct employment to about 200 million people (1) and account for 19% of the total human consumption of animal protein. Globally, firstsale fishery revenues produce about U.S.\$70 billion, and fishes represent important commodities in trade from developing countries, showing net exports of about U.S.\$13 billion in 1993 (2). Recent assessments by the United Nations Food and Agriculture Organization (FAO) of the state of the world's fisheries indicate a leveling off of

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Effects of Fisheries on Marine Ecosystems

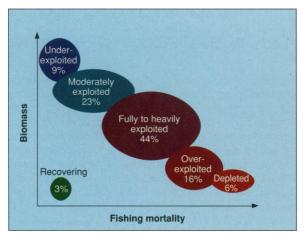
Fishing activities have altered and degraded marine ecosystems through both direct and indirect effects, especially in coastal regions where fishing and other anthropogenic perturbations are most intense. In terms of direct effects, fisheries remove the results of about 8% of the global primary production in the sea, but they require 24 to 35% of upwelling and continental shelf production (6). Fishing reduces the abundance of targeted stocks; the numerous examples worldwide of depletion through overfishing (7) are especially serious for species with high natural longevity and low reproductive rate (8). Classic examples of population collapse

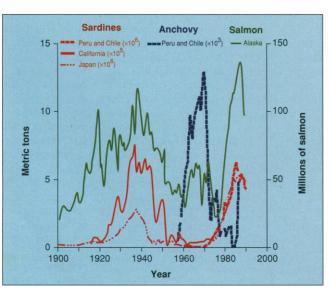
Fig. 1. Schematic view of the distribution of degree of exploitation of world fisheries with their relative biomass and fishing mortality rate indicated. Most of the data are in the range of biomass and fishing rate that indicates a fully exploited population or an overexploited population [redrawn from (2)].

Fig. 2. Catch records for several Pacific species. Catches of sardines in the California Current and off Japan increased and decreased synchronously in the early part of this century. Off Peru and Chile, the sardine increased after the decline of the anchovy in the mid-1970s. The Japanese sardine increased at the same time. The sardine off California is also increasing, but is not yet abundant enough to be harvested (not shown). Salmon catches in Alaska have been similar to the Japanese and California sardines.

where fishing may have played a role include the sardine stocks off California and Japan in the late 1940s (Fig. 2) and the anchovy off Peru and Chile in 1972 (9). Such collapses are of global importance because sardines, anchovies, and related species are a dominant part of world catches (currently 7 of the top 10 species). More recent examples of overfishing include the collapse of the Canadian cod fishery and several New England groundfish stocks (10). Even where stock abundances remain high, effects of size-selective fishing imperil future resiliency and sustainability by markedly reducing average age, size at age, and genetic diversity (11). The capture and increased mortality of less desirable, often juvenile, stages of nontarget species are substantial, exceeding catches of targeted species in many fisheries owing to use of efficient but nonselective fishing gears and high prices of a few target species that subsidize that wastage (12).

Indirect effects of fishing can have more important impacts on marine ecosystem





structure and dynamics than do removals of the fish themselves. Many nearshore ecosystems have been substantially altered through destruction of benthic biogenic habitat. Dredging, trawling, long-hauling, and igniting explosives have killed and removed the emergent sessile organisms that provide critical structural habitat on otherwise relatively featureless sea floors (8). The contributions of fishing activities to widespread destruction of coral reefs, temperate oyster and polychaete reefs, seagrasses, and other epibenthic organisms (13) have repercussions throughout the ecosystem because structural habitat plays an important role in recruitment, prey protection, and sustaining biodiversity (14).

Indirect trophic (food web) interactions induced by fishery removals represent a second class of important indirect effects of fishing. The few documented marine examples of top-down controls on community organization typically involve loss of a top predator such as sea otters or lobsters from coastal benthic systems; the consequent release from predation allows prey species to expand their cover on rock surfaces, leading to enhanced competition and displacement of less competitive species by a few dominants (15). Another example of this process is the overfishing of herbivorous fishes on coral reefs, which together with eutrophication allows macroalgae to overgrow and kill corals (16). In Chile, removal of a muricid gastropod, loco, permits domination of its principal prey, a mussel, instead of two local barnacles (17) (Fig. 3). Despite the paucity of documentation of analogous top-down controls of community organization in the deep ocean (9), a few nearshore pelagic examples (18) combined with the selective nature of fishing preferentially on larger, top predators in the sea imply a potential for (thus far undetected) analogous top-down indirect trophic effects in deep oceans.

Fishing is presumed to release competing species from competition with the targeted species, but this indirect response is difficult to confirm (19). Evidence suggests that the removal of baleen whales from high-latitude oceans has provided now unutilized zooplankton prey to fuel alternative energetic pathways (20). The increase of the anchovy population in the California Current after the decline of the sardine off the west coast of the United States in the late 1940s (Fig. 2) suggests an analogous competitive release, but similar covariability does not appear in longer time records. Note, however, that the sardine population off Peru and Chile increased after the decline of the anchoveta in 1972. Fishing intensively on sardines, anchovies, and other forage species also harms populations of

natural consumers of those prey, including seabirds and marine mammals (21). Critical bottlenecks in the life histories of many seabirds and marine mammals occur during the energetically demanding raising of young; this rearing is typically tied to a relatively circumscribed nearshore location, so the temporally and spatially localized depletions of forage fishes can imperil reproduction and drive population declines (22). Provision of discarded fish to scavengers, typically larger, more aggressive seabirds, also has pronounced effects on coastal marine ecosystems, in part because those aggressive seabirds disrupt and alter the broader seabird community through nest predation and aggression (12).

Physical Influences on Marine Ecosystems

Understanding the widespread, often dramatic, effects of fishing on marine ecosystem structure and dynamics requires assessing the confounding influence of the varying physical environment. Fisheries scientists have long been concerned with the effects of annual changes in weather and physical oceanographic conditions (23) to enable them to make year-to-year adjustments in management. Their traditional focus has been on variability on yearly time scales and spatial scales encompassing the range of the population of interest. For example, coupled changes in the atmosphere and the ocean occur irregularly every few years to create ENSO (El Niño-Southern Oscillation) conditions in the Pacific. These conditions involve warmer waters over a range of latitudes in the eastern Pacific (Fig. 4), which are accompanied by changes in coastal circulation. Ecological consequences of ENSO events along the coasts of South and North America include a decline in primary productivity near the equator (24), a decline in zooplankton productivity in the California Current (25), and diminished survival and growth of some fishes such as salmon, mackerel, and anchoveta (9, 26).

A significant recent advance in the understanding of how the physical environment alters ocean ecosystems is the realization that large-scale changes called regime shifts occur across entire ocean basins every few decades. The best documented regime shift took place during the mid-1970s in the north Pacific Ocean, when intensification of the Aleutian low-pressure system was accompanied by shifts in many biologically significant physical variables (27), including the change in 1976 from cooler to warmer conditions (Fig. 4). In the subarctic Pacific, some of these changes, such as an increase in the depth of the mixed layer (28), may have been responsible for important biological changes, namely, increases in chlorophyl concentrations (29) and Alaskan salmon catches (30) (Fig. 2), and a shift from shrimp to fish (gadoids and flatfish) dominance in the northern Gulf of Alaska (31) (Fig. 5). Awareness of broadscale regime shifts has led to increased understanding of the congruence of major changes in populations of sardines and anchovy stocks in coastal ecosystems around the world (32) (Fig. 2), and support is growing for the hypothesis that these population shifts are the result of long-term, wide-scale changes in physical conditions, rather than just fishing.

Recent research efforts on the biological effects of physical oceanographic conditions are also being directed toward finer spatial and temporal scales than traditionally treated. Analysis of the effects of events at the spatial scale of individual fish during critical larval and juvenile stages has the potential to illuminate how biological productivity varies over larger spatial scales. Examples include the way in which weekly fluctuations in upwelling winds affect primary productivity (33), and the importance of occasional calm periods that allow feeding of larval fishes (34). These weekly fluctuations in upwelling winds also drive mesoscale (that is, 10 to 100 km) circulation, which determines the transport of planktonic larvae and hence recruitment to harvested populations (35). This short-term variability in recruitment to fish populations ap-

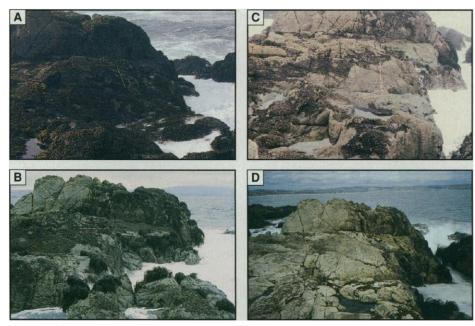


Fig. 3. The effects of harvest on community structure can be most easily seen in the rocky intertidal. In this example from the Coastal Preserve of the Estacion Costera de Investigaciones Marinas at Las Cruces, Chile, intertidal food-gathering activities were stopped in 1981. (A) One year before the Preserve was established, the mussel *Perumytilus purpuratus* covered almost 100% of the rocky shore and the keystone carnivorous gastropod *Concholepas concholepas*, "loco," was rare due to harvest (*17*, *62*). (B) Within a couple of years, loco density increased and they readily consumed the mussels. (C and D) Three and 12 years later, loco density was much higher, the mussels were almost completely eliminated, and three species of barnacles and different species of macroalgae had replaced the mussels (*17*).

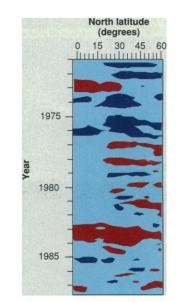


Fig. 4. Differences of $\pm 0.5^{\circ}$ C from seasonal mean 0 to 200 km from shore. ENSO (El Niño–Southem Oscillation) events cause occasional warming and cooling at various latitudes on annual time scales. A shift from a cool to a warm regime occurred in 1976 accompanied with the intensification of the Aleutian low-pressure zone [redrawn from Cole and McLain (27)].

pears to be responsible for yearly differences in the spatial pattern of recruitment, which drives the spatial dynamics of marine metapopulations (groups of populations connected by larval dispersal) (36).

Fisheries Management

For as long as fluctuations in fishery landings have been a collective human concern, various concepts of marine ecosystems have been proposed as a basis for management. Thomas Huxley's 1884 view that "probably all great sea-fisheries are inexhaustible" (37, p. 53) was countered at the same symposium by Ray Lankester's concerns for the removal of spawning stock and call for consideration of nontarget species. He maintained that the fish removed were not superfluous, as claimed, but rather had "a perfectly definite place in the complex interactions of the living beings within their area" (37, p. 54). However, despite appeals for ecosystem management of ocean fisheries (4), development of multispecies stock assessment methods (38), and new concepts of large marine ecosystems (39), few fisher-



Fig. 5. Graphic depiction of changes in species composition of catches in a small-mesh bottom trawl in Pavlof Bay, Alaska, through the regime shift of the mid-1970s. Commercial catches over a wider area reflect the same trends [reproduced from Anderson (*31*)].

ies are actually managed on a multispecies basis (40).

One goal of ecosystem management, sustainability, has a long tradition in fisheries; because fish growth rates, survival rates, and reproductive rates increase when fishing reduces population density, they produce a surplus of biomass that can be harvested (41). This rationale implicitly accounts for some nontarget species in that fishing was considered to "thin" the fish population, making more prey available. Maximizing sustained yield on this basis was a goal of fisheries management through the middle of this century. The goal of maximum sustained yield (MSY) was challenged 20 years ago (42) on several grounds: It put populations at too much risk; it did not account for spatial variability in productivity; it did not account for species other than the focus of the fishery; it considered only the benefits, not the costs, of fishing; and it was sensitive to political pressure. In fact, none of these criticisms was aimed at sustainability as a goal. The first one noted that seeking the absolute MSY with uncertain parameters was risky. The rest point out that the goal of MSY was not holistic; it left out too many relevant features.

Current fisheries management depends on stock assessments to estimate population parameters of the focal species from the age or length structure of past catches, biomass of past catches, past fishing effort, and fishery-independent surveys (43). In the most common institutional format for fisheries management (44), fisheries scientists formulate potential management actions based on these estimates, then provide them to fishery managers, who weigh their sociopolitical consequences in deciding which to implement. This structure leads managers to constantly increase fishing pressure to excessive levels because of the "ratchet effect" (7, 45): Managers, under constant political pressure for greater harvests because of their short-term benefits to society (jobs and profits), allow harvests to increase when fishery scientists cannot specify with certainty that the next increase will lead to overfishing and collapse. This is a one-way ratchet effect for two reasons: There is rarely political pressure for lower harvest rates (fewer jobs and lower profits in the immediate future), and the burden of proving whether higher harvests are harmful falls on the fishery managers, not the fishing industry. The result is a continuous, unidirectional increase in fishing effort, and in some cases fishery collapse. In a few instances, mistakes in stock assessment also may have been made [for example, the Canadian cod stocks (10, 46)]. However, for the most part, overfishing is due to the ratchet effect. Proposed solutions to the lack of sustainability of fisheries must change the two elements of this root cause of overfishing, either by reducing uncertainty in predicting the effects of management or by reducing the pressure on managers for increased harvest. However, because of the limited understanding of the complexity of marine ecosystems, the difficulty and expense involved in sampling them, and their susceptibility to environmental variability, there will always be great uncertainty in predictions of the effects of harvest (7, 42). Thus, reducing harvest rates will require a reduction in the pressure for greater harvest on the management process. This could be achieved, for example, by reductions in overcapitalization of fisheries and government subsidies of fishing, and will require controlling the open-access nature of fisheries. In addition, a better understanding of, and changes in, the way that management responds to uncertainty could also reduce overfishing.

Because of recent failures to sustain catches, fishery agencies have developed specific frameworks for avoiding low abundance. In addition to targets that allow them to obtain the best harvest, they also now operate with thresholds below which emergency actions are taken to rebuild populations (44, 47). For example, in the United States, about 100 federal management plans now contain a definition of overfishing and stipulate remedial actions once a population is overfished. This shift in focus has increased awareness of another source of uncertainty, the behavior of populations at low abundance (especially when considered in the context of other induced ecosystem changes). The stock level at which recruitment to a population will decline rapidly is not known until it happens, nor is the subsequent behavior of competitors and predators. These threshold levels are therefore based on empirical comparisons with similar species that have been overfished (47). This aspect of fisheries management presents an opportunity for fishery biologists and their colleagues concerned with endangered species (48) to collaborate on the development of methods to their mutual benefit.

Greater Holism

Greater holism in fisheries management can be achieved by consideration of multiple species interactions, broad-scale physical forcing, and the response of management to pressure for greater harvests under uncertainty. To the extent that lack of sustainability of fisheries is due to the ratchet effect, whether such an expanded focus improved sustainability would depend on

whether the first two of these reduced the uncertainty in prediction, and whether the third reduced the effects of political pressure for short-term gain in the management process.

Multiple species approaches. Virtually all fisheries in the world target more than one species or affect secondary species. Yet fisheries science has diverged from traditional oceanography and limnology, as well as community ecology, in maintaining a focus on single-species descriptions. Presumably, the rationale for this was to simplify the system by omitting the details of ecosystem complexity. That trend has been questioned in recent years; new assessment methods and management approaches account for both biological and technological (for example, through nets harvesting several species) interactions among species (38, 39). However, ecosystem management of marine systems requires a sophisticated understanding of ecosystem dynamics and the organization of component communities. The development of marine ecosystem management lags significantly behind management of terrestrial and freshwater systems (39) due to undersampling of the oceans, their three-dimensional nature, and the difficulty in replicating and controlling experiments. Thus far, the value of multispecies approaches in marine fisheries has been in terms of post hoc explanations of long-term changes, rather than year-to-year predictions (38). Even in cases of replacement of collapsed species by competitors, it is not clear whether knowing the dynamics of the competitive interaction would have prevented the collapse.

At present, the ability of marine ecology to incorporate multispecies and ecosystem information into a model that would reduce uncertainty in forecasting the effects of alternative management choices is limited. Food web descriptions and even energy-flow models (6) represent static descriptions of the past and do not predict dynamics arising from future perturbations such as alternative exploitation scenarios. Dynamic models of interacting species are uncertain in their predictions, and factoring in physical forcing, such as the effects of local turbulence on feeding success, of mesoscale circulation on metapopulation structure, and of global regime shifts on entire communities, will add further complications. One promising, but challenging, protocol for the development of ecosystem models for management involves use of adaptive management (7, 41)to identify strong interactors and erect interaction webs (49) that include physical as well as biological components.

Only in coastal regions, where habitat alteration, water pollution, and other serious anthropogenic influences are pervasive, are the costs of such a holistic, multispecies approach likely to be compensated by shortterm benefits to the fisheries industry. Nevertheless, if sustainability over the long term depends on retention of the integrity of ecosystem structure (50), then there may be long-term payoffs, even to pelagic fisheries, of adoption of an ecosystem approach. Furthermore, because fishing represents such a significant disruptor of ocean ecosystems, wildlife conservation objectives on behalf of seabirds, marine mammals, and sea turtles also require and justify an immediate commitment to progress in multispecies management.

Physical forcing. Recent identification of the dramatic effects of basin-scale, decadal variability on marine ecosystems and component species, such as small pelagics and salmon in the north Pacific, have reduced the uncertainty surrounding some fluctuations in fish stocks. However, in most instances the mechanisms of physical-biological coupling have not been identified, a necessary step to greater utilization of this understanding for prediction. Because optimal management and expected catch will vary with climatic regime, such knowledge should improve management. However, knowledge of the potential effects of regime shifts can also introduce ambiguity. For example, the regime shift in the north Pacific in the mid-1970s has been proposed as an alternative to the completion of the last several dams on the upper reaches of the Columbia River as an explanation for the dramatic decline in chinook salmon stocks. An understanding of the mechanisms underlying regime shifts is needed to differentiate between causes. Such information will also provide clues as to the possible effects on marine ecosystems of changes in climate due to global warming. Physical effects on weekly time scales and mesoscale spatial scales have the potential to provide better explanations of annual variability in the abundance and distribution of fish and invertebrates than currently used monthly averages (51). Better understanding of the effects of mesoscale circulation on dispersal within coastal metapopulations will provide information for rational management of populations distributed along coastlines, especially important for those crossing jurisdictional boundaries (36).

Pressure for greater harvests. The influence of political pressure for short-term gain on the fishery management process needs to be reduced. Greater holism in this case involves expanding our view of fisheries management to include aspects of economics and political science. One approach to combating the common property, open access nature of fisheries (52) has been to provide a sense of ownership to fishermen,

either through individual transferable quotas (53) or greater involvement in management through comanagement schemes (54, 55). Both of these still require estimates of the effects of different levels of harvest (46), but they are designed to reduce pressure for short-term gain by increasing vested interest in the long term. In practice, this is effective only under certain conditions. Basing management on a degree of ownership by fishermen works best in small-scale, artisanal fisheries in coastal zones, where overcapitalization is not present and short-term economic interests can be overcome by appeals for cooperation based on clear scientific demonstration of the utility of such an approach (55). However, it will be more difficult to change large, overcapitalized fisheries. Particularly challenging are large international fisheries, where existing institutional structures are inadequate to overcome short-term economic interests, and where socially and culturally diverse participants have little tradition of cooperation.

Greater management involvement of stakeholders who do not have an actual long-term interest in the fishery may even have negative effects on sustainability. The concept of optimum sustained vield, allowing for economic, social, and other considerations, rather than simply maximizing biological yield, emerged at a United Nations oceans convention in Geneva in 1958 and was used in subsequent management. In the United States, for example, the Magnuson Act of 1976, which created the current federal management structure, charged regional councils with taking into account socioeconomic consequences of management actions, and added the possibility of industry participation in management. The record of management since then, evidenced especially by collapses of New England groundfish stocks, has led to charges of foxes having too great a role in guarding the henhouse (56). The definition of optimal sustainable yield in the Magnuson Act was changed in 1996 to be MSY or less as determined by economic, social, and ecological considerations. Changes such as these that counteract the ratchet effect will occur more frequently with increasing public education and awareness of fishery problems. Responsible public policy demands inclusion of all stakeholders in the decision-making process, but more effective means of implementing comanagement so that biological judgments are not compromised need to be devised (56). Political forces for short-term economic gain are present in countries at all levels of development of management capability and operate through local, national, and international channels. For example, Third

World countries under pressure to repay their external debt may increase allowable catches to do so.

Better Management

Several changes in the way fisheries are managed would improve sustainability without changes in scientific approach. Using a precautionary approach to fishery management is one example (57). The precautionary principle, as applied in other areas of environmental law, involves taking a conservative approach to management issues until there is compelling evidence that a less conservative approach would pose no added risk. The burden of proof that it is safe to be less conservative is then shifted to those favoring that option (58). Another policy option, spatially explicit management, has great potential to improve sustainability of ocean ecosystems. Harvest refugia can preserve a specified fraction of an exploited population by shielding that fraction of the population's range instead of specifying a certain fishing effort. That approach removes the dependence on uncertain assumptions about the link between fishing effort and future biomass. Use of marine reserves also reduces uncertainty regarding the effects of harvest on ecosystems because portions of the ecosystem remain intact (59). Spatial variability in management also provides the potential for more efficient harvest (60), as well as the possibility of experimental harvesting and adaptive management, which is the most direct empirical way to reduce uncertainty in fisheries (7). Finally, closures and moratoria should be used more liberally to protect and allow recovery of declining stocks or stressed marine ecosystems well before, instead of after, collapse has occurred.

A holistic, ecosystem approach to fishery management requires the integration of information from a wide range of disciplines, levels of ecological organization, and temporal and spatial scales. New, expanded mathematical models that synthesize multiple processes are critical to the scientific basis of ecosystem management of marine fisheries. Such modeling should integrate the many anthropogenic influences on ocean ecosystems, now treated in isolation: eutrophication and induction of nuisance algal blooms; habitat destruction, fragmentation, and degradation; species introductions, extinctions, and endangerments; chemical pollution of the sea; and effects of anthropogenic and natural global change on ocean physics (14).

In conclusion, ocean ecosystems are influenced as much by changes in the physical environment as by humans, but it would be a fallacy to conclude that the effects of fishing can be dismissed as unimportant (61). The effects of the physical environment on marine ecosystems make it difficult to define sustainability in the context of ecosystem management, but it is clear that the root cause of the lack of sustainability is the sociopolitically biased response of management to intrinsic uncertainty. A more holistic approach involving expanded consideration of other strongly interacting species, marine habitats, and the physical environment has the potential for incrementally improving sustainability by reducing uncertainty. However, attention to changing the institutions and processes by which fisheries management is implemented will have more immediate payoffs in improving fishery sustainability. The challenge for the next century lies in crafting new local and regional institutions, not just in filling the scientific gaps. The best hope for greater sustainability of marine ecosystems is to insulate management from pressure for greater harvest while attempting to reduce uncertainty through a comprehensive ecosystem view.

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Hopes for the Future: Restoration Ecology and Conservation Biology

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Conversion of natural habitats into agricultural and industrial landscapes, and ultimately into degraded land, is the major impact of humans on the natural environment, posing a great threat to biodiversity. The emerging discipline of restoration ecology provides a powerful suite of tools for speeding the recovery of degraded lands. In doing so, restoration ecology provides a crucial complement to the establishment of nature reserves as a way of increasing land for the preservation of biodiversity. An integrated understanding of how human population growth and changes in agricultural practice interact with natural recovery processes and restoration ecology provides some hope for the future of the environment.

The impact of humans on the natural environment occurs at a variety of temporal and spatial scales. Industrial accidents, such as the *Exxon Valdez* oil spill or the meltdown at Chernobyl, often dominate the world's headlines and produce sudden dramatic ecological change over a large, but usually restricted, area of the landscape. Other changes—such as industrial pollution, deforestation, and conversion of natural habitats into agricultural and industrial

land—occur chronically over large sections of each continent. All of these anthropogenic activities alter the habitat available for most other species and usually lead to a reduction in biodiversity.

Where catastrophic environmental changes occur, their major impact on biodiversity occurs instantaneously, although residual effects may last for several years. In contrast, the impacts of long-term habitat conversion may occur over a much longer time scale as individual species become threatened and eventually go extinct. Moreover, the disruptions in community structure and ecosystem function that occur as species are lost will exacerbate this accumulated extinction debt (1). Yet the scale and magnitude of these disturbances is often comparable with the

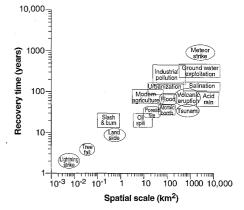


Fig. 1. The relation between the spatial scale of natural and anthropogenic disasters and their approximate expected time to recovery. Natural disasters are depicted in ellipses, and anthropogenic disasters are represented by rectangles. The data used to construct the figure were taken from a number of sources (*6, 13, 32*).

"natural" disasters from which ecosystems usually recover (Fig. 1). In this review we describe how developments in restoration ecology and phytoremediation can be integrated with conservation biology to speed the recovery of natural ecosystems from local and more widespread anthropogenic changes. From the perspective of conservation biology, it is essential that restoration is undertaken before substantial losses of biodiversity have occurred. It is also crucial that the cleanup of industrial accidents have a minimum impact on biodiversity. In both cases, many of the more innovative and cost-effective approaches to solving these problems rely on harnessing natural ecosystem processes that are mediated by the different components of biodiversity.

Habitat Conversion and Loss of Biodiversity

Habitat conversion is the major threat to biodiversity. In particular, tropical forests (2), along with temperate forests, savannas, and coastal marshes, are being converted into land for agriculture, private homes, shopping malls, and cities. The length of time that the habitat remains viable for agricultural use is determined by the duration of soil productivity, or the rate of accumulation of weeds and other pest and pathogen species. Similarly, in areas of industrial activity, such as mining, use of an area commonly persists only until the mineral resource is exhausted; where there is manufacturing, use often comes to an end when the industry becomes outdated.

Throughout human history, habitat conversion has taken place at different rates and on different spatial scales (3). In

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