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- RESEARCH ARTICLE

Impacts of Biodiversity Loss on Ocean Ecosystem Services

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ABSTRACT

Human-dominated marine ecosystems are experiencing accelerating loss of populations and species, with largely unknown consequences. We analyzed local experiments, long-term regional time series, and global fisheries data to test how biodiversity loss affects marine ecosystem services across temporal and spatial scales. Overall, rates of resource collapse increased and recovery potential, stability, and water quality decreased exponentially with declining diversity. Restoration of biodiversity, in contrast, increased productivity fourfold and decreased variability by 21%, on average. We conclude that marine biodiversity loss is increasingly impairing the ocean's capacity to provide food, maintain water quality, and recover from perturbations. Yet available data suggest that at this point, these trends are still reversible.

What is the role of biodiversity in maintaining the ecosystem services on which a growing human population depends? Recent surveys of the terrestrial literature suggest that local species richness may enhance ecosystem productivity and stability (*1*–*3*). However, the importance of biodiversity changes at the landscape level is less clear, and the lessons from local experiments and theory do not seem to easily extend to long-term, large-scale management decisions (*3*). These issues are particularly enigmatic for the world's oceans, which are geographically large and taxonomically complex, making the scaling up from local to global scales potentially more difficult (*4*). Marine ecosystems provide a wide variety of goods and services, including vital food resources for millions of people (*5*, *6*). A large and increasing proportion of our population lives close to the coast; thus the loss of services such as flood control and waste detoxification can have disastrous consequences (*7*, *8*). Changes in marine biodiversity are directly caused by exploitation, pollution, and habitat destruction, or indirectly through climate change and related perturbations of ocean biogeochemistry

(9–13). Although marine extinctions are only slowly uncovered at the global scale (9), regional ecosystems such as estuaries (10), coral reefs (11), and coastal (12) and oceanic fish communities (13) are rapidly losing populations, species, or entire functional groups. Although it is clear that particular species provide critical services to society (6), the role of biodiversity per se remains untested at the ecosystem level (14). We analyzed the effects of changes in marine biodiversity on fundamental ecosystem services by combining available data from sources ranging from small-scale experiments to global fisheries.

Experiments. We first used meta-analysis of published data to examine the effects of variation in marine diversity (genetic or species richness) on primary and secondary productivity, resource use, nutrient cycling, and ecosystem stability in 32 controlled experiments. Such effects have been contentiously debated, particularly in the marine realm, where high diversity and connectivity may blur any deterministic effect of local biodiversity on ecosystem functioning (1). Yet when the available experimental data are combined (15), they reveal a strikingly general picture (**Fig. 1**). Increased diversity of both primary producers (**Fig. 1A**) and consumers (**Fig. 1B**) enhanced all examined ecosystem processes. Observed effect sizes corresponded to a 78 to 80% enhancement of primary and secondary production in diverse mixtures relative to monocultures and a 20 to 36% enhancement of resource use efficiency (**Fig. 1, A and B**).

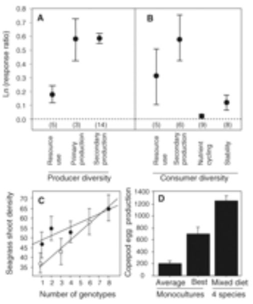

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Fig. 1.

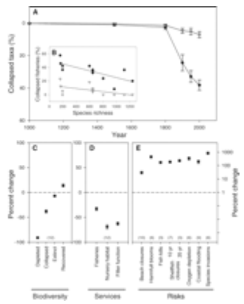
Marine biodiversity and ecosystem functioning in controlled experiments. Shown are response ratios [ln(high/low diversity) ±95% confidence interval (CI)] of ecosystem processes to experimental manipulations of species diversity of (**A**) primary producers (plants and algae), and (**B**) consumers (herbivores and predators). Increased diversity significantly enhanced all examined ecosystem functions ($0.05 > P > 0.0001$). The number of studies is given in parentheses. (**C**) Genetic diversity increased the recovery of seagrass ecosystems after overgrazing (solid circles) and climatic extremes (open circles). (**D**) Diet diversity enhanced reproductive capacity in zooplankton over both the average- and best-performing monocultures.

Experiments that manipulated species diversity (**Fig. 1B**) or genetic diversity (**Fig. 1C**) both found that diversity enhanced ecosystem stability, here defined as the ability to withstand recurrent perturbations. This effect was linked to either increased resistance to disturbance (16) or enhanced recovery afterward (17). A number of experiments on diet mixing further demonstrated the importance of diverse food sources for secondary production and the channeling of that energy to higher levels in the food web (**Fig. 1D**). Different diet items were required to optimize different life-history processes (growth, survival, and fecundity), leading to maximum total production in the mixed diet. In summary, experimental results indicate robust positive linkages between biodiversity, productivity, and stability across trophic levels in marine ecosystems. Identified mechanisms from the original studies include complementary resource use, positive interactions, and increased selection of highly performing species at high diversity.

Coastal ecosystems. To test whether experimental results scale up in both space and time, we compiled long-term trends in regional biodiversity and services from a detailed database of 12 coastal and estuarine ecosystems (10) and other sources (15). We examined trends in 30 to 80 (average, 48) economically and ecologically important species per ecosystem. Records over the past millennium revealed a rapid decline of native species diversity since the onset of industrialization (**Fig. 2A**). As predicted by experiments, systems with higher regional species richness appeared more stable, showing lower rates of collapse and extinction of commercially important fish and invertebrate taxa over time (**Fig. 2B**, linear regression, $P < 0.01$). Overall, historical trends led to the present depletion (here defined as >50% decline over baseline abundance), collapse (>90% decline), or extinction (100% decline) of 91, 38, or 7% of species, on average (**Fig. 2C**). Only 14% recovered from collapse (**Fig. 2C**); these species were mostly protected birds and mammals.

Fig. 2.

Regional loss of species diversity and ecosystem services in coastal oceans. (**A**) Trends of collapse (circles, >90% decline) and extinction (triangles, 100% decline) of species over the past 1000 years. Means and standard errors are shown (***n*** = 12 regions in Europe, North America, and Australia). (**B**) Percentage of collapsed (circles) and extinct (triangles) fisheries in relation to regional fish species richness. Significant linear regression lines are depicted ($P < 0.01$). (**C** to **E**) Relative losses or gains in (C) biodiversity, (D) ecosystem services, and (E) risks that are associated with the loss of services. The number of studies is given in parentheses; error bars indicate standard errors.



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These regional biodiversity losses impaired at least three critical ecosystem services (**Fig. 2D**): number of viable (noncollapsed) fisheries (–33%); provision of nursery habitats such as oyster reefs, seagrass beds, and wetlands (–69%); and filtering and detoxification services provided by suspension feeders, submerged vegetation, and wetlands (–63%). Loss of filtering services probably contributed to declining water quality (*18*) and the increasing occurrence of harmful algal blooms, fish kills, shellfish and beach closures, and oxygen depletion (**Fig. 2E**). Increasing coastal flooding events (**Fig. 2E**) are linked to sea level rise but were probably accelerated by historical losses of floodplains and erosion control provided by coastal wetlands, reefs, and submerged vegetation (*7*). An increased number of species invasions over time (**Fig. 2E**) also coincided with the loss of native biodiversity; again, this is consistent with experimental results (*19*). Invasions did not compensate for the loss of native biodiversity and services, because they comprised other species groups, mostly microbial, plankton, and small invertebrate taxa (*10*). Although causal relationships are difficult to infer, these data suggest that substantial loss of biodiversity (**Fig. 2, A and C**) is closely associated with regional loss of ecosystem services (**Fig. 2D**) and increasing risks for coastal inhabitants (**Fig. 2E**). Experimentally derived predictions that more species-rich systems should be more stable in delivering services (**Fig. 1**) are also supported at the regional scale (**Fig. 2B**).

Large marine ecosystems. At the largest scales, we analyzed relationships between biodiversity and ecosystem services using the global catch database from the United Nations Food and Agriculture Organization (FAO) and other sources (*15*, *20*). We extracted all data on fish and invertebrate catches from 1950 to 2003 within all 64 large marine ecosystems (LMEs) worldwide. LMEs are large (>150,000 km^2) ocean regions reaching from estuaries and coastal areas to the seaward boundaries of continental shelves and the outer margins of the major current systems (*21*). They are characterized by distinct bathymetry, hydrography, productivity, and food webs. Collectively, these areas produced 83% of global fisheries yields over the past 50 years. Fish diversity data for each LME were derived independently from a comprehensive fish taxonomic database (*22*).

Globally, the rate of fisheries collapses, defined here as catches dropping below 10% of the recorded maximum (*23*), has been accelerating over time, with 29% of currently fished species considered collapsed in 2003 (**Fig. 3A**, diamonds). This accelerating trend is best described by a power relation ($y = 0.0168x^{1.8992}$, $r = 0.96$, $P < 0.0001$), which predicts the percentage of currently collapsed taxa as a function of years elapsed since 1950. Cumulative collapses (including recovered species) amounted to 65% of recorded taxa (**Fig. 3A**, triangles; regression fit: $y = 0.0227x^{2.0035}$, $r = 0.96$, $P < 0.0001$). The data further revealed that despite large increases in global fishing effort, cumulative yields across all species and LMEs had declined by 13% (or 10.6 million metric tons) since passing a maximum in 1994.

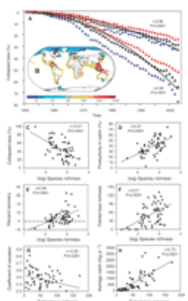

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Fig. 3.

Global loss of species from LMEs. (**A**) Trajectories of collapsed fish and invertebrate taxa over the past 50 years (diamonds, collapses by year; triangles, cumulative collapses). Data are shown for all (black), species-poor (<500 species, blue), and species-rich (>500 species, red) LMEs. Regression lines are best-fit power models corrected for temporal autocorrelation. (**B**) Map of all 64 LMEs, color-coded according to their total fish species richness. (**C**) Proportion of collapsed fish and invertebrate taxa, (**D**) average productivity of noncollapsed taxa (in percent of maximum catch), and (**E**) average recovery of catches (in percent of maximum catch) 15 years after a collapse in relation to LME total fish species richness. (**F**) Number of fished taxa as a function of total species richness. (**G**) Coefficient of variation in total catch and (**H**) total catch per year as a function of the number of fished taxa per LME.

Consistent with the results from estuaries and coastal seas (Fig. 2B), we observed that these collapses of LME fisheries occurred at a higher rate in species-poor ecosystems, as compared with species-rich ones (Fig. 3A). Fish diversity varied widely across LMEs, ranging from ~20 to 4000 species (Fig. 3B), and influenced fishery-related services in several ways. First, the proportion of collapsed fisheries decayed exponentially with increasing species richness (Fig. 3C). Furthermore, the average catches of non-collapsed fisheries were higher in species-rich systems (Fig. 3D). Diversity also seemed to increase robustness to overexploitation. Rates of recovery, here defined as any post-collapse increase above the 10% threshold, were positively correlated with fish diversity (Fig. 3E). This positive relationship between diversity and recovery became stronger with time after a collapse (5 years, r = 0.10; 10 years, r = 0.39; 15 years, r = 0.48). Higher taxonomic units (genus and family) produced very similar relationships as species richness in Fig. 3; typically, relationships became stronger with increased taxonomic aggregation. This may suggest that taxonomically related species play complementary functional roles in supporting fisheries productivity and recovery.

A mechanism that may explain enhanced recovery at high diversity is that fishers can switch more readily among target species, potentially providing overfished taxa with a chance to recover. Indeed, the number of fished taxa was a log-linear function of species richness (Fig. 3F). Fished taxa richness was negatively related to the variation in catch from year to year (Fig. 3G) and positively correlated with the total production of catch per year (Fig. 3H). This increased stability and productivity are likely due to the portfolio effect (*24*, *25*), whereby a more diverse array of species provides a larger number of ecological functions and economic opportunities, leading to a more stable trajectory and better performance over time. This portfolio effect has independently been confirmed by economic studies of multispecies harvesting relationships in marine ecosystems (*26*, *27*). Linear (or log-linear) relationships indicate steady increases in services up to the highest levels of biodiversity. This means that proportional species losses are predicted to have similar effects at low and high levels of native biodiversity.

Marine reserves and fishery closures. A pressing question for management is whether the loss of services can be reversed, once it has occurred. To address this question, we analyzed available data from 44 fully protected marine reserves and four large-scale fisheries closures (*15*). Reserves and closures have been used to reverse the decline of marine biodiversity on local and regional scales (*28*, *29*). As such, they can be viewed as replicated large-scale experiments. We used meta-analytic techniques (*15*) to test for consistent trends in biodiversity and services across all studies (Fig. 4).

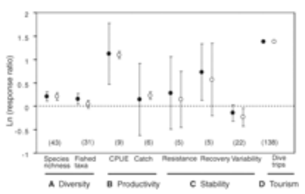

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Fig. 4.

Recovery of diversity and ecosystem services in marine protected areas and fisheries closures. Shown are the response ratios (inside versus outside the reserve or before and after protection ±95% CI) of (**A**) species diversity and (**B** to **D**) ecosystem services that correspond to fisheries productivity, ecosystem stability, and tourism revenue, respectively. Positive values identify increases in the reserve relative to the control; error bars not intersecting zero indicate statistical significance (P < 0.05). Solid circles represent unweighted averages; open circles are weighted by sample size (see supporting online methods for details). The number of studies is shown in parentheses. CPUE, catch per unit of effort.

We found that reserves and fisheries closures showed increased species diversity of target and nontarget species, averaging a 23% increase in species richness (Fig. 4A). These increases in biodiversity were associated with large increases in fisheries productivity, as seen in the fourfold average increase in catch per unit of effort in fished areas around the reserves (Fig. 4B). The difference in total catches was less pronounced (Fig. 4B), probably because of restrictions on fishing effort around many reserves. Resistance and recovery after natural disturbances from storms and thermal stress tended to increase in reserves, though not significantly in most cases (Fig. 4C). Community variability, as measured by the coefficient of variation in aggregate fish biomass, was reduced by 21% on average (Fig. 4C). Finally, tourism revenue measured as the relative increase in dive trips within 138 Caribbean protected areas strongly increased after they were established (Fig. 4D). For several variables, statistical significance depended on how studies were weighted (Fig. 4, solid versus open circles). This is probably the result of large variation in sample sizes among studies (*15*). Despite the inherent variability, these results suggest that at this point it is still possible to recover lost biodiversity, at least on local to regional scales; and that such recovery is generally accompanied by increased productivity and decreased variability, which translates into extractive (fish catches around reserves) and nonextractive (tourism within reserves) revenue.

Conclusions. Positive relationships between diversity and ecosystem functions and services were found using experimental (Fig. 1) and correlative approaches along trajectories of diversity loss (Figs. 2 and 3) and recovery (Fig. 4). Our data highlight the societal consequences of an ongoing erosion of diversity that appears to be accelerating on a global scale (Fig. 3A). This trend is of serious concern because it projects the global collapse of all taxa currently fished by the mid-21st century (based on the extrapolation of regression in **Fig. 3A** to 100% in the year 2048). Our findings further suggest that the elimination of locally adapted populations and species not only impairs the ability of marine ecosystems to feed a growing human population but also sabotages their stability and recovery potential in a rapidly changing marine environment.

We recognize limitations in each of our data sources, particularly the inherent problem of inferring causality from correlation in the larger-scale studies. The strength of these results rests on the consistent agreement of theory, experiments, and observations across widely different scales and ecosystems. Our analysis may provide a wider context for the interpretation of local biodiversity experiments that produced diverging and controversial outcomes (*1*, *3*, *24*). It suggests that very general patterns emerge on progressively larger scales. High-diversity systems consistently provided more services with less variability, which has economic and policy implications. First, there is no dichotomy between biodiversity conservation and long-term economic development; they must be viewed as interdependent societal goals. Second, there was no evidence for redundancy at high levels of diversity; the improvement of services was continuous on a log-linear scale (**Fig. 3**). Third, the buffering impact of species diversity on the resistance and recovery of ecosystem services generates insurance value that must be incorporated into future economic valuations and management decisions. By restoring marine biodiversity through sustainable fisheries management, pollution control, maintenance of essential habitats, and the creation of marine reserves, we can invest in the productivity and reliability of the goods and services that the ocean provides to humanity. Our analyses suggest that business as usual would foreshadow serious threats to global food security, coastal water quality, and ecosystem stability, affecting current and future generations.

Supporting Online Material

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Methods and Data Sources

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