Impacts of Biodiversity Loss on Ocean Ecosystem Services

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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.

That 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 longterm, 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

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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

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-

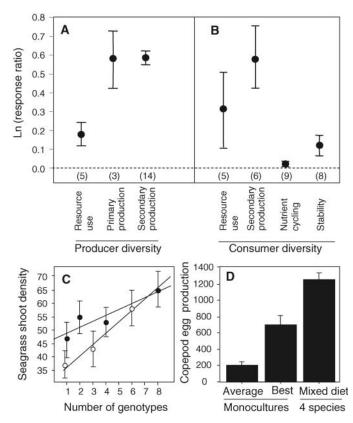
and best-performing

monocultures.

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).

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



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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.

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 km²) 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: $y = 0.0227x^{2.0035}$,

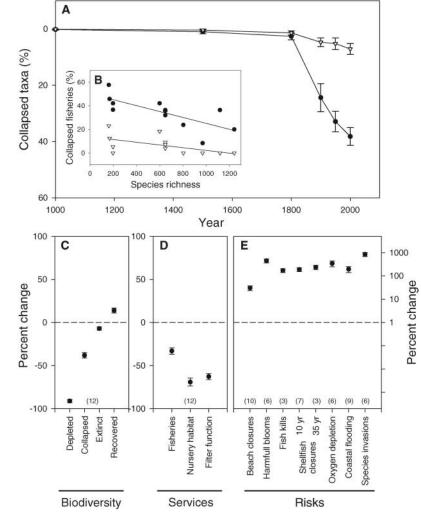


Fig. 2. Regional loss of species diversity and ecosystem services in coastal oceans. **(A)** Trends of collapse (circles, >90% decline) and extinction (triangles, 100% decline) of species over the past 1000 years. Means and standard errors are shown (n=12 regions in Europe, North America, and Australia). **(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.

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.

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

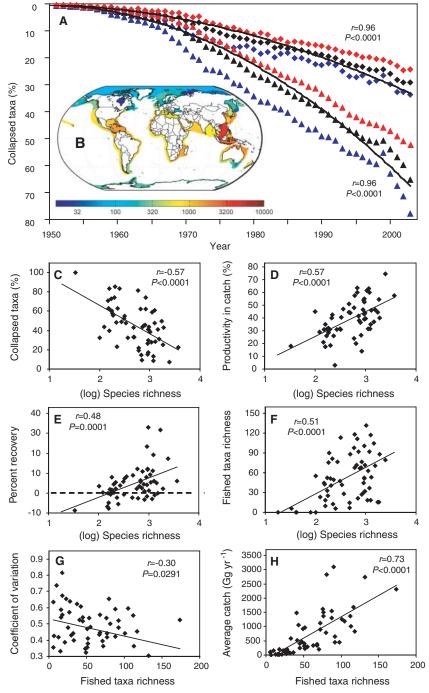


Fig. 3. Global loss of species from LMEs. (A) Trajectories of collapsed fish and invertebrate taxa over the past 50 years (diamonds, collapses by year; triangles, cumulative collapses). Data are shown for all (black), species-poor (<500 species, blue), and species-rich (>500 species, red) LMEs. Regression 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.

varied widely across LMEs, ranging from ~20 to 4000 species (Fig. 3B), and influenced fisheryrelated services in several ways. First, the proportion of collapsed fisheries decayed exponentially with increasing species richness (Fig. 3C). Furthermore, the average catches of noncollapsed 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).

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 largerscale 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.

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2 1.5 0 \overline{Q} Ln (response ratio) 0.5 δ 0 -0.5 (43)(31)(9)(6)(5)(5)(22)(138)Fished CPUE Catch Resistance Recovery Variability Dive Species richness taxa trips A Diversity **B** Productivity C Stability **D** Tourism

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 $\pm 95\%$ 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.

Supporting Online Material

www.sciencemag.org/cgi/content/full/314/5800/787/DC1 Methods and Data Sources Tables S1 to S5 References

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Supporting Online Material: Impacts of biodiversity loss on ocean ecosystem services

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Methods and data sources Supporting Tables S1-S5 Supporting references

Methods and data sources

Experiments

We systematically searched major science, ecological and marine journals from 1960 to mid2005 for experiments that (i) involved marine or estuarine organisms, (ii) conducted experiments including at least three species, (iii) measured some aspect of ecosystem functioning in mixedspecies and single-species treatments. The following journals were searched: Science journals:

Science, Nature, Proceedings of the National Academy of Sciences USA; Ecology journals:

Ecology, Ecological Monographs, Ecological Applications, Oecologia, Oikos, Ecology Letters,

Journal of Ecology, Journal of Animal Ecology; Marine journals: Limnology and Oceanography,

Marine Biology, Marine Ecology Progress Series, Journal of Experimental Marine Biology and

Ecology, Journal of the Marine Biological Association of the United Kingdom.

We grouped studies according to trophic level (primary producer or consumer) and response

We grouped studies according to trophic level (primary producer or consumer) and response variable (resource use, primary or secondary production, nutrient cycling, and resilience). For each variable, we conducted a meta-analysis comparing the log ratio of responses in the highest-diversity treatment over the average of all single-species treatments. The effect size was weighted by the sample sizes and standard deviations derived from the original study. Response ratios were combined by fixed-effects meta-analysis. Weights for the log-response ratios were estimated based on sample variance and sample size from the individual studies

$$v_{\ln R} = \frac{(S_E)^2}{N_E(\overline{X}_E)^2} + \frac{(S_C)^2}{N_C(\overline{X}_C)^2} , \qquad (1)$$

Where S, N, \overline{X} refer to the standard deviation, sample size and mean of the experimental diversity treatment (E), or control treatment (C), respectively. The mean effect size was considered significant if the parametric 95% confidence intervals did not include zero. All data sources for the meta-analysis of experimental data in Fig. 1A-B are detailed in Table S1 and references S1-S20. Fig. 1C is based on eelgrass shoot density data from S3 and S17. Copepod egg production in Fig. 1D was estimated as the product of survival and fecundity data taken from S16.

Coastal ecosystems

The regional analysis presented in Fig. 2 focused on 12 estuarine and coastal ecosystems in North America, Europe, and Australia that form a broad temporal and spatial gradients of human impacts (Table S2). We used an existing database that combines >800 individual references on the history of human-induced ecological changes in these ecosystems covering palaeontological, archaeological, historical, fisheries and ecological records for species that have been of economical, structural, or functional significance throughout history (S21). Quantitative and qualitative records of abundance were combined to estimate relative abundance over time as pristine (100%), abundant (90%), depleted (50%), collapsed (10%), and extinct (0%) (S22). Recovery was defined as an increase of collapsed species to >10% of abundance. The database covers 30-80 species per study system from six taxonomic (marine mammals, birds, reptiles, fish, invertebrates, vegetation) and seven functional groups (large and small carnivores, large and small herbivores, suspension feeders, submerged aquatic vegetation, wetlands). The database also contains time series of water quality (mainly derived from sediment cores and water quality assessments) and species invasions (S21) thus reflecting historical changes in an ecosystem context.

To determine changes in biodiversity over historical time scales we extracted the percent of species that have collapsed (<10%) or became extinct (0%) over time (Fig. 2A). We also extracted the percent of fish taxa currently collapsed or extinct and analyzed whether regional species richness buffers against fisheries loss (Fig. 2B). We used the number of fish species per Large Marine Ecosystem (LME, *S22*) as an independent measure for regional species richness.

This measure is independent of changes in local biodiversity over time, as it captures the total recorded richness of the regional ecosystem derived from checklists, museum records, and other sources. Also there is no significant relationship between regional species richness and time since beginning of commercial exploitation (linear regression, r=0.46, P=0.313). Percent change in biodiversity (Fig. 2C) was determined as the percent of species currently depleted (<50%), rare (<10%), extinct (0%), or recovered (from 0-10% to >10%) compared to the historical baseline.

For changes in ecosystem services (Fig. 2D), we extracted the percent of fisheries, nursery habitats, and filter function collapsed compared to the historical baseline. Fisheries included all fish taxa that have been of commercial importance throughout history. Nursery habitats included all records on oyster beds, seagrass beds, and wetlands. Filter function included three functional groups: suspension feeders (oysters, mussels, polychaetes, hydrozoans, sponges, corals), all submerged vegetation (seagrasses, rockweeds, macroalgae, other macrophytes), and wetlands (saltmarshes, wetlands, mangroves). These groups are part of the estuarine filter that recycles and stores nutrients, traps sediments, and reduces phytoplankton abundance.

For the risks analysis (Fig. 2E) we extracted time series on oxygen depletion and species invasions from the same database and collected independent time series on beach closures, harmful algal blooms, fish kills, shellfish closures, and coastal flooding from the literature and published databases (Table S3). Depending on the length of the time series, we estimated the percent change between the averages of the most recent and the earliest time interval (Table S3). Because long time series for beach closures were not available, we estimated the average percent of beaches closed in recent years (Table S3). Beach closures were determined as the percent of beaches not meeting standards. For comparability among study systems, we consistently used the European Union threshold levels of elevated bacterial counts as standards with guide levels for total coliforms = 500 and coliform units (CFU) = 100. For oxygen depletion, we included independent data sets from sediment cores and water columns for the Baltic Sea and Chesapeake Bay.

Large Marine Ecosystems

The global analysis presented in Fig. 3 is based on detailed catch records for 64 Large Marine Ecosystems (LME) worldwide (Table S4). We used the spatial database of global fisheries catches of the Sea Around Us Project (SAUP, Fisheries Centre, University of British Columbia, Vancouver, Canada, according to S53). This database comprises nearly half a billion records of catch rates for global half-degree latitude and longitude spatial cells, for all reported taxa and countries from 1950 to 2003. The spatial database is based on a consolidation of several major data sources such as the FAO capture fisheries and its regional bodies, the International Council for the Exploration of the Seas (ICES) STATLANT database (www.ices.int/fish/statlant.htm), the Northwest Atlantic Fisheries Organization (NAFO; www.nafo.ca/), as well as data provided from the Canadian, United States, and other governments. We used these data to follow fisheries catch trajectories 1950-2003. Fisheries were defined by catches of unique animal taxa (usually defined by species, or genus or family in some cases) within the spatial confines of individual large marine ecosystems (LMEs, Table S4). The global system of LMEs is widely accepted as a useful way to divide coastal and shelf ecosystems (S54). Collectively, these areas comprised 83% of total commercial fisheries yields for 1950-2003. Fish diversity data by LME is available for these areas from FishBase (www.fishbase.org). Catch data were filtered by excluding all taxa that yielded less than 10kt of cumulative catch over the last 52 years. This was done to exclude minor and experimental fisheries that were not pursued over time. However, excluding these fisheries (or using 1, or 100kt filters) did not have a major effect on the results. A fishery was considered to have started when annual catches reached 10% of the annual maximum for the time series. Individual fish species i were classified as collapsed for LME k when total yield C had declined to $C_{ik} < 0.1$ relative to the maximum yield in LME k. Species were considered as recovered when their yield had increased to $C_{ik} > 0.1$ subsequent to a collapse. The terms 'collapsed' or 'recovered' as used here refer strictly to the delivery of services (fish products), not necessarily to the biological condition of the stock. The starting year of a fishery (average: 1963) did not vary systematically across the diversity gradient (linear regression, r=0.158, P=0.233), but the year it collapsed (average: 1985) did increase with diversity (r=0.272, P=0.0377), i.e. fisheries began at the same time but collapsed later, on average, in high-diversity areas. This is consistent with the proposed diversity effect.

Relationships between species richness and fisheries productivity and stability were tested using linear regression models on log-transformed data. Standard linear least squares regression and robust regression techniques gave nearly identical results; therefore we report linear least squares results in Fig. 3. Robust regression models were controlling for potential outliers in the independent variables space and in the response (dependent variable) space using the High Efficiency High Breakpoint method as proposed by Yohai, Stahel, and Zamar (*S55*) and implemented in the lmRobMM procedure in S-Plus vs. 7. Individual LMEs were considered statistically independent, as by definition they represent distinct ecosystems governed by unique biological, hydrographic and climatic conditions (*S54*). Temporally autocorrelated time series (Fig. 3A) were analyzed using the AUTOREG procedure in SAS vs. 8.

Marine reserves and fishery closures

We searched the literature and online databases for data collected on biological diversity and ecosystem services inside and outside or before and after an established marine reserve (n=44) or fishery closure (n=4). Marine reserves are defined here as no-take areas that are fully protected from fishing. We also used data for dive tourism in 138 Caribbean marine protected areas (MPAs). Note that not all of these Caribbean protected areas were no-take reserves, some had limited fishing allowed, and some were not well enforced. Regardless, based on the success stories of no-take reserves, there appears to be an expectation from divers of greater biodiversity inside the protected areas that drives choice of diving locations.

All data sources are detailed in Table S5 and references S56-S104. Effect sizes were calculated as the response ratio $\ln R$ of the variable within the protected over the fished area (or before-after reserve establishment). Response ratios from individual studies were combined by standard meta-analysis. Few studies reported measures of variance, and so weights for the log-response ratios were estimated based on sample size (S105). Sampling variances v for each study i were calculated including effect sizes (S105)

$$v_i = \frac{(N_c + N_E)}{(N_C N_E)} + \frac{\ln(R^2)}{2(N_C + N_E)} , \qquad (2)$$

where N_C and N_E refer to the sample size in fished and protected areas respectively. Weights were calculated as the inverse of the sampling variance. Because sample sizes varied greatly (3<N<350), this approach may weight some studies disproportionately. For comparison we present weighted and unweighted averages. The single exception was the dive trip data set (S105) which was based on complete operator records rather than samples. Therefore confidence intervals or weights could not be calculated for dive trip data. We regard our estimates of effect size as conservative, because reserve studies that used proper Before–After, Control–Impact (BACI) experimental designs showed that control and reserve sites were equivalent prior to protection and that control sites improved along with the reserves after those were established (S106). This implies that any bias in our current perception of reserve impacts introduced by inside-outside comparisons likely underestimates the effect of the reserve.

 Table S1. Studies used in the meta-analysis of experimental data.

Reference	Trophic level	Service category	Response variable	Maximum richness	Effect size (lnR)	variance (lnR)
					(====)	(====)
S1	Primary producers	Nutrient use	total N storage in plant biomass	6	0.439	0.010
S1	Primary producers	Nutrient use	litter N concentration	6	0.154	0.001
S1	Primary producers	Nutrient use	benthic microalgal N concentration	6	0.173	0.007
S2	Primary producers	Nutrient use	porewater NH4, before disturbance	8	0.092	0.052
<i>S</i> 2	Primary producers	Nutrient use	porewater NH4, after disturbance	8	0.654	0.020
S1	Primary producers	Primary production	total plant biomass	6	0.698	0.003
<i>S3</i>	Primary producers	Primary production	shoot density at ~4.5 mo	6	0.450	0.037
<i>S4</i>	Primary producers	Primary production	average of all treatments	5	0.491	0.003
S5	Primary producers	Secondary production	survival x growth (urchin)	4	0.643	0.004
S6	Primary producers	Secondary production	survival x growth (A. marcuzii)	5	0.543	0.005
S6	Primary producers	Secondary production	survival x growth (C. compta)	5	0.804	0.002
S6	Primary producers	Secondary production	survival x growth (A. valida)	5	0.227	0.002
S6	Primary producers	Secondary production	survival x growth (G. mucronatus)	5	1.173	0.004
<i>S7</i>	Primary producers	Secondary production	survival x growth (A. longimana)	12	0.583	0.003
<i>S</i> 8	Primary producers	Secondary production	copepod egg production: high food	3	-0.377	0.049
<i>S</i> 8	Primary producers	Secondary production	copepod egg production: low food	3	0.118	0.084
S9	Primary producers	Secondary production	gastropod shell growth	3	0.480	0.021
S10	Primary producers	Secondary production	copepod survival x fecundity	4	1.061	0.065
S11	Primary producers	Secondary production	growth (Amphisorus)	3	0.674	0.003
S11	Primary producers	Secondary production	growth (Amphistegina)	3	0.501	0.002
S12	Primary producers	Secondary production	copepod egg production	4	1.833	0.029
<i>S3</i>	Primary producers	Secondary production	fouling invertebrate density	6	0.341	0.006
S13	Consumers	Resource use	algal biomass (chl a)	3	0.257	0.161
S14	Consumers	Resource use	algal biomass	6	1.927	0.249
S15	Consumers	Resource use	algal biomass (predators present)	4	1.255	0.818
S16	Consumers	Resource use	space use (Botrylloides experiment)	4	0.369	0.012
S16	Consumers	Resource use	space use (Ascidiella experiment)	4	0.176	0.010

S13	Consumers	Secondary production	grazer biomass	3	-0.027	0.087
S14	Consumers	Secondary production	grazer biomass	6	0.446	0.006
S15	Consumers	Secondary production	grazer biomass (predators present)	4	0.988	0.076
S17	Consumers	Secondary production	ciliate biovolume (experiment I)	4	0.230	0.112
S17	Consumers	Secondary production	ciliate biovolume (experiment II)	7	1.569	0.050
S17	Consumers	Secondary production	ciliate biovolume (experiment III)	4	0.933	0.046
S14	Consumers	Nutrient regeneration	sediment organic carbon	6	0.426	0.036
S18	Consumers	Nutrient regeneration	NH4 flux	4	0.129	0.024
S18	Consumers	Nutrient regeneration	NH4 flux	3	0.121	0.068
S18	Consumers	Nutrient regeneration	NH4 flux	3	0.171	0.248
S19	Consumers	Nutrient regeneration	NH4 flux (with flow)	5	0.334	0.127
S19	Consumers	Nutrient regeneration	NH4 flux (no flow)	5	0.095	0.090
S20	Consumers	Nutrient regeneration	Oxygen flux	3	0.000	0.003
S20	Consumers	Nutrient regeneration	Phosphate flux	3	-0.359	0.098
S20	Consumers	Nutrient regeneration	depth-integrated pH	3	0.015	0.000
S15	Consumers	Stability	predation effect on grazer biomass	4	0.766	0.111
S15	Consumers	Stability	predation effect on algal biomass	4	0.704	0.568
S15	Consumers	Stability	predation effect on eelgrass biomass	4	1.186	0.685
S17	Consumers	Stability	UVB effect on ciliate biovolume (experiment I)	4	-0.731	0.335
S17	Consumers	Stability	UVB effect on ciliate biovolume (experiment II)	7	0.489	0.174
S16	Consumers	Stability	invader survival (Botryllus)	4	0.493	0.052
S16	Consumers	Stability	invader cover (Botrylloides)	4	0.080	0.001
S16	Consumers	Stability	invader cover (Ascidiella)	4	0.209	0.003

Table S2. Estuarine and coastal study systems.

System	Large Marine Ecosystem	Country
Western Baltic Sea	Baltic Sea	Europe
Wadden Sea	North Sea	Europe
Northern Adriatic Sea	Mediterranean Sea	Europe
Southern Gulf St. Lawrence	Scotian Shelf	Canada
Outer Bay of Fundy	Scotian Shelf	Canada
Massachusetts Bay	Northeast U.S. Shelf	USA
Delaware Bay	Northeast U.S. Shelf	USA
Chesapeake Bay	Northeast U.S. Shelf	USA
Pamlico Sound	Southeast U.S. Shelf	USA
Galveston Bay	Gulf of Mexico	USA
San Francisco Bay	California Current	USA
Moreton Bay	East-central Australian Shelf	Australia

Table S3. Data sources for the analysis of services and risks in coastal and estuarine ecosystems.

System Detail		Time series	Interval	Ref.
Beach closures (n=1	10)			_
Baltic	% beaches not meeting standards	1999-2002	4 yr	S23
Wadden	% beaches not meeting standards	1999-2002	4 yr	S23
Adriatic	% beaches not meeting standards	1999-2002	4 yr	S23
Massachusetts	% beaches not meeting standards	1999-2002	4 yr	S24
Delaware	% beaches not meeting standards	1999-2002	4 yr	S24
Chesapeake	% beaches not meeting standards	1999-2002	4 yr	S24
Pamlico	% beaches not meeting standards	1999-2002	4 yr	S24
Galveston	% beaches not meeting standards	1999-2002	4 yr	S24
San Francisco	% beaches not meeting standards	1999-2002	4 yr	S24
Moreton	% beaches not meeting standards	2000-2001	2 yr	S25
Harmful blooms (na	=6)			
Baltic	Concentration of cyanobacterial blooms: Aphanizomenon and Nodulari (100 µm L ⁻¹)	1887-1908 vs.	. 1981-93	S26
Wadden	Surface algal bloom events per year	1979-1995	5 yr	S27
Adriatic	Mucilage events per decade	1729-1991	50 yr	S28
Bay of Fundy	PSP toxins in clams, events per decade exceeding 100 µg per 100g tissue	1944-1983	10 yr	S29
Lawrence	Harmful algal species, mean cells L ⁻¹ per yr	1995-2004	3 yr	S30

	of all species at 11 monitoring sites			
US estuaries	Harmful algal bloom events per year	1970-1996	5 yr	S31
Fish kills (n=3)				
Chesapeake	# events / yr	1984-2003	5 yr	S32
Pamlico	# events / yr	1997-2003	3 yr	S33
Galveston	# events / yr	1970-2003	5 yr	S34
Shellfish closures 10) yr (n=7)			
Bay of Fundy	% estuarine shellfish area limited for harvest in Maine	1985-1995	5 yr	S35
Massachusetts	% estuarine shellfish area limited for harvest in Massachusetts	1985-1995	5 yr	S35
Delaware	% estuarine shellfish area limited for harvest in Delaware	1985-1995	5 yr	S35
Chesapeake	% estuarine shellfish area limited for harvest in Maryland and Virginia	1985-1995	5 yr	S35
Pamlico	% estuarine shellfish area limited for harvest in North Carolina	1985-1995	5 yr	S35
Galveston	% estuarine shellfish area limited for harvest in Texas	1985-1995	5 yr	S35
San Francisco	% estuarine shellfish area limited for harvest in California	1985-1995	5 yr	S35
Shellfish closures 35	5 vm (n=2)			
Bay of Fundy	• •	1060 1005	5	S36
Lawrence	# of shellfish closures, NB # of shellfish closures, PEI	1960-1995 1960-1995	5 yr	S36
US estuaries	% shellfish area limited for harvest in US	1960-1995	5 yr 5 yr	S35
			-	
Oxygen depletion (1	n=6)			
Baltic	Aerial extent of laminated sediments (km ²)	1900-2000	10 yr	<i>S37</i>
Baltic	Dissolved oxygen concentration Kiel Bay (mg L ⁻¹)	1950-2000	10 yr	S38
Adriatic	Dissolved oxygen concentration in bottom layer in summer (mg L ⁻¹)	1911-1984	5-10 yr	S39
Chesapeake	Anaerobic bacterial biomarker abundance, sediment core	1900-2000	20 yr	S40
Chesapeake	Water volume with low dissolved oxygen (<0.5 ml L ⁻¹)	1950-1980	4 yr	S41
Pamlico	Degree of pyritization, sediment core	1800-2000	20 yr	S42

Coastal flooding (n	=9)			
Wadden	# storm tides per decade at Cuxhaven	1850-1995	10 yr	S43
Adriatic	# positive surge anomalies >208 cm / yr	1940-2001	10 yr	S44
Lawrence	# storm surges >1m per decade at	1940-1999	10 yr	S45
	Charlottetown, Prince Edward Island			
Massachusetts	# floods / yr	1993-2004	5 yr	S46
Delaware	# floods / yr	1993-2004	5 yr	S46
Chesapeake	# floods / yr	1993-2004	5 yr	S46
Pamlico	# floods / yr	1993-2004	5 yr	S46
Galveston	# floods / yr	1993-2004	5 yr	S46
San Francisco	# floods / yr	1993-2004	5 yr	S46
Species invasions (n	n=6)			
Baltic	# invasions per decade, aquatic species	1800-2004	50 yr	S47
Wadden	# invasions per decade, North Sea, marine	1800-1996	50 yr	S48
	estuarine species			
Adriatic	# invasions per decade, Mediterranean,	1877-2000	50 yr	S49
	molluses only			
Bay of Fundy	# invasions per decade, Bay of Fundy	1817-1999	50 yr	S50
	to Long Island Sound, marine and			
	estuarine excluding cryptogenic species			
Chesapeake	# invasions per decade, marine and	1800-2002	50 yr	S51
	brackish species			
San Francisco	# invasions per decade, marine and	1850-1995	50 yr	S52
	tidal fresh species			

 Table S4. Large Marine Ecosystems (LME).

LME#	LME Name	Latitude (N)	Longitude (E)	Area (km²)	Fish species richness
1	East Bering Sea	57.3	-167.5	1355778	184
2	Gulf of Alaska	54.3	-139.9	1464613	309
3	California Current	34.9	-120.4	2227006	803
4	Gulf of California	33.4	-110.4	224031	363
5	Gulf of Mexico	30.2	-92.9	1535015	969
6	Southeast U.S. Continental Shelf	33.0	-81.8	324234	1118
7	Northeast U.S. Continental Shelf	48.2	-75.8	299457	648
8	Scotian Shelf	45.6	-62.1	284128	198
9	Newfoundland-Labrador Shelf	51.5	-60.6	902776	172
10	Insular Pacific-Hawaiian	23.3	-166.6	985971	829
11	Pacific Central-American Coastal	9.1	-90.5	1973475	943
12	Caribbean Sea	12.9	-75.2	3273830	1539
13	Humboldt Current	-29.1	-71.0	2547702	752
14	Patagonian Shelf	-37.6	-61.5	1153589	332
15	South Brazil Shelf	-22.5	-48.6	564789	951
16	East Brazil Shelf	-11.3	-45.6	1086782	896
17	North Brazil Shelf	1.3	-53.0	1052460	935
18	West Greenland Shelf	68.6	-55.3	373991	158
19	East Greenland Shelf	68.6	-30.1	321712	158
20	Barents Sea	66.1	42.1	1698857	201
21	Norwegian Shelf	68.2	3.5	1119675	232
22	North Sea	54.6	10.7	723171	185
23	Baltic Sea	59.6	21.1	369849	169
24	Celtic-Biscay Shelf	51.1	-5.1	759320	317
25	Iberian Coastal	40.4	-6.1	319862	586
26	Mediterranean Sea	36.4	17.7	2524934	599
27	Canary Current	23.9	-1.3	1116366	1267
28	Guinea Current	4.5	3.8	1922365	725
29	Benguela Current	-20.9	17.8	1468081	819
30	Agulhas Current	-22.1	34.9	2646502	1306
31	Somali Coastal Current	0.6	38.7	841283	689
32	Arabian Sea	28.4	51.7	3940642	933
33	Red Sea	18.5	31.9	459408	1189
34	Bay of Bengal	25.0	90.1	3665152	686
35	Gulf of Thailand	8.4	102.2	386967	606
36	South China Sea	17.2	105.5	3193252	3689
37	Sulu-Celebes Sea	7.8	121.4	1009767	1165
38	Indonesian Sea	-3.9	119.9	2286488	2437
39	North Australian Shelf	-17.8	133.8	792874	1839
40	Northeast Australian Shelf	-18.0	149.8	1284723	1733
41	East-Central Australian Shelf	-28.6	149.4	654182	1242
42	Southeast Australian Shelf	-40.5	143.2	1179619	220
43	Southwest Australian Shelf	-31.6	126.0	1063159	473

45 Northwest Australian Shelf -18.0 118.9 896663 1066 46 New Zealand Shelf -40.7 172.8 959623 916 47 East China Sea 37.4 105.3 779632 1014 48 Yellow Sea 41.7 110.1 439590 1906 49 Kuroshio Current 32.4 133.5 1312887 1442 50 Sea of Japan 43.6 134.0 984353 490 51 Oyashio Current 46.0 150.4 535269 37 52 Sea of Okhotsk 54.5 146.4 1556089 216 53 West Bering Sea 58.2 174.4 2005272 272 54 Chukchi Sea 70.0 -167.6 569932 81 55 Beaufort Sea 71.8 160.6 925514 41 57 Laptev Sea 65.0 110.5 504994 42 58 Kara Sea 66.3 81.1	44	West-Central Australian Shelf	-26.9	118.6	547049	472
47 East China Sea 37.4 105.3 779632 1014 48 Yellow Sea 41.7 110.1 439590 1906 49 Kuroshio Current 32.4 133.5 1312887 1442 50 Sea of Japan 43.6 134.0 984353 490 51 Oyashio Current 46.0 150.4 535269 37 52 Sea of Okhotsk 54.5 146.4 1556089 216 53 West Bering Sea 58.2 174.4 2005272 272 54 Chukchi Sea 70.0 -167.6 569932 81 55 Beaufort Sea 71.0 -140.9 773322 102 56 East Siberian Sea 71.8 160.6 925514 41 57 Laptev Sea 65.0 110.5 504994 42 58 Kara Sea 66.3 81.1 806101 18 59 Iceland Shelf 65.4 -20.0 312287 152 60 Faroe Plateau 60.4 -11.5 150	45	Northwest Australian Shelf	-18.0	118.9	896663	1066
48 Yellow Sea 41.7 110.1 439590 1906 49 Kuroshio Current 32.4 133.5 1312887 1442 50 Sea of Japan 43.6 134.0 984353 490 51 Oyashio Current 46.0 150.4 535269 37 52 Sea of Okhotsk 54.5 146.4 1556089 216 53 West Bering Sea 58.2 174.4 2005272 272 54 Chukchi Sea 70.0 -167.6 569932 81 55 Beaufort Sea 71.0 -140.9 773322 102 56 East Siberian Sea 71.8 160.6 925514 41 57 Laptev Sea 65.0 110.5 504994 42 58 Kara Sea 66.3 81.1 806101 18 59 Iceland Shelf 65.4 -20.0 312287 152 60 Faroe Plateau 60.4 -11.5 150049 174 61 Antarctica -75.1 90.0 4385933<	46	New Zealand Shelf	-40.7	172.8	959623	916
49 Kuroshio Current 32.4 133.5 1312887 1442 50 Sea of Japan 43.6 134.0 984353 490 51 Oyashio Current 46.0 150.4 535269 37 52 Sea of Okhotsk 54.5 146.4 1556089 216 53 West Bering Sea 58.2 174.4 2005272 272 54 Chukchi Sea 70.0 -167.6 569932 81 55 Beaufort Sea 71.0 -140.9 773322 102 56 East Siberian Sea 71.8 160.6 925514 41 57 Laptev Sea 65.0 110.5 504994 42 58 Kara Sea 66.3 81.1 806101 18 59 Iceland Shelf 65.4 -20.0 312287 152 60 Faroe Plateau 60.4 -11.5 150049 174 61 Antarctica -75.1 90.0 4385933 247 62 Black Sea 43.8 39.8 463322 <td>47</td> <td>East China Sea</td> <td>37.4</td> <td>105.3</td> <td>779632</td> <td>1014</td>	47	East China Sea	37.4	105.3	779632	1014
50 Sea of Japan 43.6 134.0 984353 490 51 Oyashio Current 46.0 150.4 535269 37 52 Sea of Okhotsk 54.5 146.4 1556089 216 53 West Bering Sea 58.2 174.4 2005272 272 54 Chukchi Sea 70.0 -167.6 569932 81 55 Beaufort Sea 71.0 -140.9 773322 102 56 East Siberian Sea 71.8 160.6 925514 41 57 Laptev Sea 65.0 110.5 504994 42 58 Kara Sea 66.3 81.1 806101 18 59 Iceland Shelf 65.4 -20.0 312287 152 60 Faroe Plateau 60.4 -11.5 150049 174 61 Antarctica -75.1 90.0 4385933 247 62 Black Sea 43.8 39.8 463322 148 63 Hudson Bay 53.9 -97.9 3911123	48	Yellow Sea	41.7	110.1	439590	1906
51 Oyashio Current 46.0 150.4 535269 37 52 Sea of Okhotsk 54.5 146.4 1556089 216 53 West Bering Sea 58.2 174.4 2005272 272 54 Chukchi Sea 70.0 -167.6 569932 81 55 Beaufort Sea 71.0 -140.9 773322 102 56 East Siberian Sea 71.8 160.6 925514 41 57 Laptev Sea 65.0 110.5 504994 42 58 Kara Sea 66.3 81.1 806101 18 59 Iceland Shelf 65.4 -20.0 312287 152 60 Faroe Plateau 60.4 -11.5 150049 174 61 Antarctica -75.1 90.0 4385933 247 62 Black Sea 43.8 39.8 463322 148 63 Hudson Bay 53.9 -97.9 3911123 18	49	Kuroshio Current	32.4	133.5	1312887	1442
52 Sea of Okhotsk 54.5 146.4 1556089 216 53 West Bering Sea 58.2 174.4 2005272 272 54 Chukchi Sea 70.0 -167.6 569932 81 55 Beaufort Sea 71.0 -140.9 773322 102 56 East Siberian Sea 71.8 160.6 925514 41 57 Laptev Sea 65.0 110.5 504994 42 58 Kara Sea 66.3 81.1 806101 18 59 Iceland Shelf 65.4 -20.0 312287 152 60 Faroe Plateau 60.4 -11.5 150049 174 61 Antarctica -75.1 90.0 4385933 247 62 Black Sea 43.8 39.8 463322 148 63 Hudson Bay 53.9 -97.9 3911123 18	50	Sea of Japan	43.6	134.0	984353	490
53 West Bering Sea 58.2 174.4 2005272 272 54 Chukchi Sea 70.0 -167.6 569932 81 55 Beaufort Sea 71.0 -140.9 773322 102 56 East Siberian Sea 71.8 160.6 925514 41 57 Laptev Sea 65.0 110.5 504994 42 58 Kara Sea 66.3 81.1 806101 18 59 Iceland Shelf 65.4 -20.0 312287 152 60 Faroe Plateau 60.4 -11.5 150049 174 61 Antarctica -75.1 90.0 4385933 247 62 Black Sea 43.8 39.8 463322 148 63 Hudson Bay 53.9 -97.9 3911123 18	51	Oyashio Current	46.0	150.4	535269	37
54 Chukchi Sea 70.0 -167.6 569932 81 55 Beaufort Sea 71.0 -140.9 773322 102 56 East Siberian Sea 71.8 160.6 925514 41 57 Laptev Sea 65.0 110.5 504994 42 58 Kara Sea 66.3 81.1 806101 18 59 Iceland Shelf 65.4 -20.0 312287 152 60 Faroe Plateau 60.4 -11.5 150049 174 61 Antarctica -75.1 90.0 4385933 247 62 Black Sea 43.8 39.8 463322 148 63 Hudson Bay 53.9 -97.9 3911123 18	52	Sea of Okhotsk	54.5	146.4	1556089	216
55 Beaufort Sea 71.0 -140.9 773322 102 56 East Siberian Sea 71.8 160.6 925514 41 57 Laptev Sea 65.0 110.5 504994 42 58 Kara Sea 66.3 81.1 806101 18 59 Iceland Shelf 65.4 -20.0 312287 152 60 Faroe Plateau 60.4 -11.5 150049 174 61 Antarctica -75.1 90.0 4385933 247 62 Black Sea 43.8 39.8 463322 148 63 Hudson Bay 53.9 -97.9 3911123 18	53	West Bering Sea	58.2	174.4	2005272	272
56 East Siberian Sea 71.8 160.6 925514 41 57 Laptev Sea 65.0 110.5 504994 42 58 Kara Sea 66.3 81.1 806101 18 59 Iceland Shelf 65.4 -20.0 312287 152 60 Faroe Plateau 60.4 -11.5 150049 174 61 Antarctica -75.1 90.0 4385933 247 62 Black Sea 43.8 39.8 463322 148 63 Hudson Bay 53.9 -97.9 3911123 18	54	Chukchi Sea	70.0	-167.6	569932	81
57 Laptev Sea 65.0 110.5 504994 42 58 Kara Sea 66.3 81.1 806101 18 59 Iceland Shelf 65.4 -20.0 312287 152 60 Faroe Plateau 60.4 -11.5 150049 174 61 Antarctica -75.1 90.0 4385933 247 62 Black Sea 43.8 39.8 463322 148 63 Hudson Bay 53.9 -97.9 3911123 18	55	Beaufort Sea	71.0	-140.9	773322	102
58 Kara Sea 66.3 81.1 806101 18 59 Iceland Shelf 65.4 -20.0 312287 152 60 Faroe Plateau 60.4 -11.5 150049 174 61 Antarctica -75.1 90.0 4385933 247 62 Black Sea 43.8 39.8 463322 148 63 Hudson Bay 53.9 -97.9 3911123 18	56	East Siberian Sea	71.8	160.6	925514	41
59 Iceland Shelf 65.4 -20.0 312287 152 60 Faroe Plateau 60.4 -11.5 150049 174 61 Antarctica -75.1 90.0 4385933 247 62 Black Sea 43.8 39.8 463322 148 63 Hudson Bay 53.9 -97.9 3911123 18	57	Laptev Sea	65.0	110.5	504994	42
60 Faroe Plateau 60.4 -11.5 150049 174 61 Antarctica -75.1 90.0 4385933 247 62 Black Sea 43.8 39.8 463322 148 63 Hudson Bay 53.9 -97.9 3911123 18	58	Kara Sea	66.3	81.1	806101	18
61 Antarctica -75.1 90.0 4385933 247 62 Black Sea 43.8 39.8 463322 148 63 Hudson Bay 53.9 -97.9 3911123 18	59	Iceland Shelf	65.4	-20.0	312287	152
62 Black Sea 43.8 39.8 463322 148 63 Hudson Bay 53.9 -97.9 3911123 18	60	Faroe Plateau	60.4	-11.5	150049	174
63 Hudson Bay 53.9 -97.9 3911123 18	61	Antarctica	-75.1	90.0	4385933	247
•	62	Black Sea	43.8	39.8	463322	148
64 Arctic Ocean 76.5 90.0 6854419 123	63	Hudson Bay	53.9	-97.9	3911123	18
	64	Arctic Ocean	76.5	90.0	6854419	123

Table S5. Data sources for marine reserves and fishery closures (lnR=Response ratio; N_C =Sample size in fished area; N_E =Sample size in protected area).

Variable	Location	Ecosystem type	ln <i>R</i>	Time (yr)	N_C	N_E	Reference
Spp. richness	Amedee, New Caledonia	coral reef	0.742	5.0	3	3	S56
Spp. richness	Apo, Philippines	coral reef	0.336	1.0	5	5	S57
Spp. richness	Bailly, New Caledonia	coral reef	0.236	5.0	3	3	S56
Spp. richness	Balicasag, Philippines	coral reef	0.149	14.0	3	3	S58
Spp. richness	Balicasag, Philippines	coral reef	0.336	1.0	5	5	S57
Spp. richness	Banyuls, France	rocky reef	0.154	1.0	8	8	S62
Spp. richness	Barbados	coral reef	0.063	12.0	21	13	S59
Spp. richness	Carry-le-Rouet, France	rocky reef	0.151	14.0	24	24	S63
Spp. richness	Castellamare, Sicily	groundfish	0.266	4.0	21	30	<i>S60</i>
Spp. richness	English Channel	soft sediment	0.724	23.0	9	6	S61
Spp. richness	English Channel	soft sediment	0.983	2.0	9	6	S61
Spp. richness	French Reef, Florida, USA	coral reef	-0.132	21.0	130	40	S65
Spp. richness	Georges Bank, New England, USA	groundfish	0.104	9.0	350	350	S66
Spp. richness	Goat Island, New Zealand	kelp forest	0.336	13.0	50	85	S67
Spp. richness	Governor Island, Tasmania	kelp forest	0.155	28.0	23	23	S68
Spp. richness	Haunama, Hawaii	coral reef	0.042	18.0	3	3	S69
Spp. richness	Hol Chan, Belize	coral reef	0.091	2.0	24	25	S70
Spp. richness	Honolua, Hawaii	coral reef	0.200	16.0	3	3	S69
Spp. richness	Kealakakua, Hawaii	coral reef	0.020	16.0	3	3	S69
Spp. richness	Kenya	coral reef	0.652	2.0	28	28	S71
Spp. richness	Laregnere, New Caledonia	coral reef	0.626	5.0	3	3	S56
Spp. richness	Maitre, New Caledonia	coral reef	0.370	5.0	4	4	S56
Spp. richness	Manele, Hawaii	coral reef	-0.036	17.0	3	3	S69
Spp. richness	Maria Island, Tasmania	kelp forest	0.155	28.0	23	23	S68
Spp. richness	Mayotte Island, Comoros	coral reef	0.006	3.0	3	3	S72
Spp. richness	Molasses Reef, Florida	coral reef	-0.029		130	63	S65
Spp. richness	Molokini, Hawaii	coral reef	0.133	17.0	3	3	S69
Spp. richness	Ninepin Pt, Tasmania	kelp forest	0.179	9.0	23	23	S68
Spp. richness	Pamilican, Philippines	coral reef	-0.036		3	3	S58
Spp. richness	Pamilican, Philippines	coral reef	0.223	1.0	5	5	S57
Spp. richness	Red Sea	coral reef	-0.078	11.0	9	9	S73
Spp. richness	Scandola, France	rocky reef	0.214	17.0	10	10	S64
Spp. richness	Scotian Shelf, Canada	groundfish	0.540	14.0		350	S74
Spp. richness	Signal, New Caledonia	coral reef	0.280	5.0	3	3	S56
Spp. richness	South Africa	intertidal	-0.306		42	28	S75
Spp. richness	South Africa	intertidal	-0.187		29	28	S75
Spp. richness	South Africa	intertidal	-0.461	2.0	28	34	S75
Spp. richness	St. Lucia, Caribbean	coral reef	0.080	6.0	12	12	S76
Spp. richness	Sumilon, Philippines	coral reef	0.265	10.0	6	6	S77
Spp. richness	Sumilon, Philippines	coral reef	0.377	4.0	6	6	S77
Spp. richness	Tinderbox, Tasmania	kelp forest	-0.018	9.0	23	23	S68
Spp. richness	Transkei, South Africa	rocky shore	1.034	13.0	4	4	S78
Spp. richness	Transkei, South Africa	rocky shore	0.528	13.0	4	4	\$78
Fishable species	Apo, Philippines	coral reef	-0.095	1.0	5	6	S77
•	Apo, Philippines	coral reef	0.620	1.0	5	5	S57
_	Balicasag, Philippines	coral reef	0.484	1.0	5	5	S57
1 isliance species	Danousus, i imppines	201411001	J.70 1	1.0	5	5	037

Fishable species		coral reef	0.000	11.0	48	30	S59
Fishable species	California (BC)	kelp forest	-0.105	1.0	11	12	S79
Fishable species	California (HMS)	kelp forest	0.154	11.0	12	31	S79
Fishable species	California (PL)	kelp forest	0.251	22.0	15	6	S79
Fishable species	Florida Cays, USA	coral reef	0.000	20.0	130	40	S65
Fishable species	Florida Cays, USA	coral reef	0.054	20.0	130	63	S65
Fishable species	Cape Canaveral, Florida, USA	coral reef	0.000	25.0	402	251	S80
Fishable species	Hol Chan, Belize	coral reef	-0.087	2.0	24	25	S70
Fishable species	Kenya	coral reef	0.654	20.0	20	14	S71
Fishable species	Kenya	coral reef	0.379	1.0	20	19	S71
Fishable species	Kenya	coral reef	0.174	6.0	20	10	S81
Fishable species	Mayotte Island (Comoros)	coral reef	0.000	3.0	9	9	S72
Fishable species	Mediterranean, France	rocky reef	0.080	1.0	8	8	S62
Fishable species	Mediterranean, France	rocky reef	0.041	13.0	8	8	S82
Fishable species	Mediterranean, France	rocky reef	0.000	13.0	63	63	S83
Fishable species	Mediterranean, France	rocky reef	1.386	1.0	8	8	S62
Fishable species	Mediterranean, Italy	rocky reef	0.000	5.0	72	72	S84
Fishable species	Mediterranean, Italy	rocky reef	0.000	5.0	72	72	S84
Fishable species	Mediterranean, Italy	rocky reef	0.000	10.0	24	24	S85
Fishable species	Mediterranean, Spain	rocky reef	0.031	6.0	25	15	S86
Fishable species	New Caledonia	coral reef	0.000	5.0	56	32	S56
Fishable species	New Zealand	kelp forest	0.118	13.0	17	30	S67
Fishable species	Pamilican, Philippines	coral reef	0.464	1.0	5	5	S57
Fishable species	Red Sea	coral reef	0.018	11.0	9	9	S73
Fishable species	Red Sea	coral reef	-0.154	15.0	27	27	S87
Fishable species	St. Vincent-Grenadines, St. Lucia	coral reef	0.049	4.0	40	37	S87
Fishable species	St. Vincent-Grenadines, St. Lucia	coral reef	0.095	6.0	40	38	S87
Fishable species	Sumilon, Philippines	coral reef	0.241	10.0	6	6	S77
CPUE	Apo, Philippines	coral reef	2.303	10.0	NA	NA	S88
CPUE	Castellammare del Golfo, Italy	ground fish	3.194	10.0	NA	NA	S89
CPUE	Georges Bank, New England, USA	ground fish	1.003	6.0	NA	NA	S90
CPUE	Mombasa, Kenya	coral reef	0.748	2.0	NA	NA	S91
CPUE	Mombasa, Kenya	coral reef	0.942	2.0	NA	NA	S91
CPUE	Red Sea	coral reef	0.509	5.0	80	80	S92
CPUE	Scotian Shelf, Canada	ground fish	0.493	14.0	NA	NA	S74
CPUE	St. Lucia, Caribbean	coral reef	0.588	5.0	33	51	S93
CPUE	St. Lucia, Caribbean	coral reef	0.305	5.0	59	133	S93
Catch	Apo, Philippines	coral reef	1.863	10.0	NA	NA	S88
Catch	Georges Bank, New England, USA	ground fish	-0.643	6.0	NA	NA	S90
Catch	Mombasa, Kenya	coral reef	-0.427	2.0	NA	NA	S91
Catch	Scotian Shelf, Canada	groundfish	-0.491	14.0	NA	NA	S94
Catch	St. Lucia, Caribbean	coral reef	0.428	5.0	NA	NA	S93
Catch	St. Lucia, Caribbean	coral reef	0.160	5.0	NA	NA	S93
Resistance	Kenya, 4 reserves	coral reef	-0.313	0.5	7	9	S95
Resistance	Kenya, 4 reserves	coral reef	0.000	0.5	7	9	S95
Resistance	Kenya, 4 reserves	coral reef	1.161	3.0	3	3	S96
Resistance	St. Lucia, Caribbean	coral reef	-0.473	5.0	12	12	S97
Resistance	St. Lucia, Caribbean	coral reef	1.036	1.0	12	12	S97
Recovery	Balicasag, Philippines	coral reef	1.224	14.0	3	3	S58
Recovery	Mayotte Island, Comoros	coral reef	1.018	1.5	4	4	S98

Recovery	Mayotte Island, Comoros	coral reef	1.346	1.5	4	4	S98
Recovery	Pamilican, Philippines	coral reef	-0.206	14.0	3	3	S58
Recovery	St. Lucia, Caribbean	coral reef	0.277	5.0	12	12	S97
Variability	Apo, Philippines	coral reef	-0.153	6.0	5	5	S99
Variability	Apo, Philippines	coral reef	-0.091	6.0	5	5	S99
Variability	Apo, Philippines	coral reef	-0.282	6.0	5	5	S99
Variability	Apo, Philippines	coral reef	-0.503	6.0	6	6	S100
Variability	Channel Islands, California	kelp forest	-0.547	18.0	NA N	NA	S101
Variability	Channel Islands, California	kelp forest	-0.123	18.0	NA N	NA	S101
Variability	Channel Islands, California	kelp forest	-0.153	18.0	NA N	NA	S101
Variability	Channel Islands, California	kelp forest	-0.114	18.0	NA N	NA	S101
Variability	Channel Islands, California	kelp forest	0.299	18.0	NA N	NA	S101
Variability	Georges Bank, New England, USA	groundfish	-1.135	9.0	5	5	S66
Variability	Georges Bank, New England, USA	groundfish	0.873	9.0	5	5	S90
Variability	NA	seagrass	-0.463	11.0	10	10	S102
Variability	NA	seagrass	0.049	7.0	6	6	S102
Variability	Scotian Shelf, Canada)	groundfish	-0.515	14.0	5	5	S74
Variability	Transkei, South Africa	rocky shore	0.175	13.0	10	10	<i>S7</i> 8
Variability	Transkei, South Africa	rocky shore	-0.095	13.0	10	10	<i>S7</i> 8
Variability	Transkei, South Africa	rocky shore	0.116	13.0	10	10	<i>S7</i> 8
Variability	Transkei, South Africa	rocky shore	-0.025	13.0	10	10	<i>S78</i>
Variability	Glovers Reef, Belize	coral reef	0.526	6.0	4	4	S103
Variability	Glovers Reef, Belize	coral reef	-0.199	6.0	4	4	S103
Variability	Glovers Reef, Belize	coral reef	-0.421	6.0	4	4	S103
Variability	St. Lucia, Caribbean	coral reef	-0.376	3.0	83 1	14	S76
Dive trips	Caribbean (138 sites)	coral reef	1.386	NA	138 1	138	S104

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