Rebuilding Global Fisheries

Boris Worm,[1]* Ray Hilborn,[2]* Julia K. Baum,[3] Trevor A. Branch,[2] Jeremy S. Collie,[4]
Christopher Costello,[5] Michael J. Fogarty,[6] Elizabeth A. Fulton,[7] Jeffrey A. Hutchings,[1]
Simon Jennings,[8,9] Olaf P. Jensen,[2] Heike K. Lotze,[1] Pamela M. Mace,[10] Tim R. McClanahan,[11]
Cóilín Minto,[1] Stephen R. Palumbi,[12] Ana M. Parma,[13] Daniel Ricard,[1] Andrew A. Rosenberg,[14]
Reg Watson,[15] Dirk Zeller[15]

After a long history of overexploitation, increasing efforts to restore marine ecosystems and rebuild
fisheries are under way. Here, we analyze current trends from a fisheries and conservation
perspective. In 5 of 10 well-studied ecosystems, the average exploitation rate has recently declined
and is now at or below the rate predicted to achieve maximum sustainable yield for seven systems.
Yet 63% of assessed fish stocks worldwide still require rebuilding, and even lower exploitation
rates are needed to reverse the collapse of vulnerable species. Combined fisheries and conservation
objectives can be achieved by merging diverse management actions, including catch restrictions,
gear modification, and closed areas, depending on local context. Impacts of international fleets
and the lack of alternatives to fishing complicate prospects for rebuilding fisheries in many poorer
regions, highlighting the need for a global perspective on rebuilding marine resources.

Overfishing has long been recognized as a leading environmental and socioeconomic problem in the marine realm and has reduced biodiversity and modified ecosystem functioning (1–3). Yet, current trends as well as future prospects for global fisheries remain controversial (3–5). Similarly, the solutions that hold promise for restoring marine fisheries and the ecosystems in which they are embedded are hotly debated (4–6). Such controversies date back more than a hundred years to the famous remarks of Thomas Huxley on the inexhaustible nature of sea fisheries (7) and various replies documenting their ongoing exhaustion. Although management authorities have since set goals for sustainable use, progress toward curbing overfishing has been hindered by an unwillingness or inability to bear the short-term social and economic costs of reducing fishing (8). However, recent commitments to adopting an ecosystem approach to fisheries may further influence progress because they have led to a reevaluation of management targets for fisheries and the role of managers in meeting broader conservation objectives for the marine environment (9).

In light of this debate, we strive here to join previously diverging perspectives and to provide an integrated assessment of the status, trends, and solutions in marine fisheries. We explore the prospects for rebuilding depleted marine fish populations (stocks) and for restoring the ecosystems of which they are part. In an attempt to unify our understanding of the global fisheries situation, we compiled and analyzed all available data types, namely global catch data (Fig. 1A), scientific stock assessments, and research trawl surveys (Fig. 1B), as well as data on small-scale fisheries (10). We further used published ecosystem models (Fig. 1B) to evaluate the effects of exploitation on marine communities. Available data sources are organized hierarchically like a Russian doll: Stock assessments provide the finest resolution but represent only a subset of species included in research surveys, which in turn represent only a small subset of species caught globally. These sources need to be interpreted further in light of historical fisheries before data collection and illegal or unreported fisheries operating today (11). We focus on two leading questions: (i) how do changes in exploitation rates impact fish populations, communities, and yields, and (ii) which solutions have proven successful in rebuilding exploited marine ecosystems?

Models. A range of models is available to analyze the effects of changes in exploitation rate on fish populations, communities, and ecosystems. Exploitation rate (u_t) is defined as the proportion of biomass that is removed per year, i.e., $u_t = C_t/B_t$ where C is the catch (or yield) and B is the available biomass in year t. Single-species models are often used to determine the exploitation rate u_{MSY} that provides the maximum sustainable yield (MSY) for a particular stock. Fishing for MSY results in a stock biomass, B_{MSY}, that is substantially (typically 50 to 75%) lower than the unfished biomass (B_0). It has been a traditional fisheries objective to achieve single-species MSY, and most management regimes have been built around this framework. Recently this focus has expanded toward assessing the effects of exploitation on communities and ecosystems (9).

Multispecies models can be used to predict the effects of exploitation on species composition, size structure, biomass, and other ecosystem properties. They range from simpler community models to more-complex ecosystem models (12). Figure 2 displays equilibrium solutions from a size-based community model, which assumes that fishing pressure is spread across species according to their size and that a subset of species remains unfished (13). Results of more-complex ecosystem models across 31 ecosystems and a range of different fishing scenarios were remarkably similar (fig. S1 and table S1). With increasing exploitation rate, total fish catch is predicted to increase toward the multispecies maximum sustainable yield (MMSY) and decrease thereafter. In this example, the corresponding exploitation rate that gives maximum yield u_{MMSY} is ~0.45, and total community biomass B_{MMSY} equilibrates at ~35% of unfished biomass (Fig. 2). Overfishing occurs when u exceeds u_{MMSY}, whereas rebuilding requires reducing exploitation below u_{MMSY}. An increasing exploitation rate causes a monotonic decline in total biomass and average body size, and an increasing proportion of species is predicted to collapse (Fig. 2). We used 10% of unfished biomass as a definition for collapse. At such low abundance, recruitment may be severely limited, and species may cease to play a substantial ecological role. This model suggests that a wide range of exploitation rates ($0.25 < u < 0.6$) yield ≥90% of maximum catch but with very different ecosystem consequences: whereas at $u = 0.6$ almost half of the species are predicted to collapse, reducing exploitation rates to $u = 0.25$ is predicted to rebuild total biomass, increase average body size, and strongly reduce species collapses with little loss in long-term yield (Fig. 2). In addition to reconciling fishery and conservation objectives, setting exploitation rate below u_{MMSY} reduces the cost of fishing and increases profit margins over the long term (14). This simple model does not incorporate fishing selectivity; however, in practice the proportion of collapsed species could be reduced further by increasing selectivity through improved gear technology (15), by closing areas frequented by vulnerable species, or through offering incentives to improve targeting practices (16). Such strategies allow for protection of vulnerable or collapsed species, while allowing for more intense exploitation of others.

[1]Biology Department, Dalhousie University, Halifax, NS B3H 4J1, Canada. [2]School of Aquatic and Fishery Sciences, University of Washington, Seattle, WA 98195–5020, USA. [3]Scripps Institution of Oceanography, University of California–San Diego, La Jolla, CA 92093–0202, USA. [4]Graduate School of Oceanography, University of Rhode Island, Narragansett, RI 02882, USA. [5]Donald Bren School of Environmental Science and Management, University of California, Santa Barbara, CA 93106–5131, USA. [6]National Marine Fisheries Service, National Oceanic and Atmospheric Administration, Woods Hole, MA 02543, USA. [7]Commonwealth Scientific and Industrial Research Organisation (CSIRO) Marine and Atmospheric Research, General Post Office Box 1538, Hobart, TAS 7001, Australia. [8]Centre for Environment, Fisheries and Aquaculture Science, Lowestoft NR33 0HT, UK. [9]School of Environmental Sciences, University of East Anglia, Norwich NR4 7TJ, UK. [10]Ministry of Fisheries, Post Office Box 1020, Wellington, New Zealand. [11]Wildlife Conservation Society Marine Programs, Post Office Box 99470, Mombasa, Kenya. [12]Hopkins Marine Station, Stanford University, Pacific Grove, CA 93950, USA. [13]Centro Nacional Patagónico, 9120 Puerto Madryn, Argentina. [14]Institute for the Study of Earth, Oceans, and Space, University of New Hampshire, Durham, NH 03824–3525, USA. [15]Fisheries Centre, University of British Columbia, Vancouver, BC V6T 1Z4, Canada.

*To whom correspondence should be addressed. E-mail: bworm@dal.ca (B.W.); rayh@u.washington.edu (R.H.)

These results suggest that there is a range of exploitation rates that achieve high yields and maintain most species. To test whether current fisheries fall within this range, we evaluated trends in 10 large marine ecosystems for which both ecosystem models and stock assessments were available (*10*). Figure 3A shows exploitation rate and biomass trajectories derived from 4 to 20 assessed fish or invertebrate stocks per ecosystem. These stocks typically represent most of the catch, and we assumed that trends in their exploitation rates represent the community as a whole. Ecosystem models were used to calculate u_{MMSY} (light blue bars) and the exploitation rate at which less than 10% of the fished species are predicted to be collapsed ($u_{conserve}$, dark blue bars). Across the 10 examined ecosystems, MMSY was predicted at multispecies exploitation rates of $u_{MMSY} = 0.05$ to 0.28 (mean of 0.16), whereas avoiding 10% collapse rates required much lower exploitation rates of $u_{conserve} = 0.02$ to 0.05 (mean of 0.04).

Up to the 1990s, assessed species in 6 of the 10 ecosystems had exploitation rates substantially higher than those predicted to produce MMSY (Fig. 3A). Only the eastern Bering Sea has been consistently managed below that threshold. Since the 1990s, Iceland, Newfoundland-Labrador, the Northeast U.S. Shelf, the Southeast Australian Shelf, and California Current ecosystems have shown substantial declines in fishing pressure such that they are now at or below the modeled u_{MMSY}. However, only in the California Current and in New Zealand are current exploitation rates predicted to achieve a conservation target of less than 10% of stocks collapsed (Fig. 3A). Declining exploitation rates have contributed to the rebuilding of some depleted stocks, whereas others remain at low abundance. Averaged across all assessed species, biomass is still well below B_{MSY} in most regions. However, biomass has recently been increasing above the long-term average in Iceland, the Northeast U.S. Shelf, and the California Current, while remaining relatively stable or decreasing elsewhere (Fig. 3A).

Scientific stock assessments. Stock assessments quantify the population status (abundance, length, and age structure) of targeted fish or invertebrate stocks. We explored the status of 166 stocks worldwide for which we were able to obtain estimates of current biomass and exploitation rate (Fig. 3B). For about two-thirds of the examined stocks (63%), biomass (*B*) has dropped below the traditional single-species management target of MSY, that is, $B < B_{MSY}$. About half of those stocks (28% of total) have exploitation rates that would allow for rebuilding to B_{MSY}, that is, $u < u_{MSY}$, whereas overfishing continues in the remainder ($u > u_{MSY}$ in 35% of all stocks). Another 37% of assessed stocks have either not fallen below B_{MSY} or have recovered from previous depletion; most stocks in this category (77%) are in the Pacific. The weight of the evidence, as shown by the kernel density plot in Fig. 3B, indicates that most assessed stocks have

Fig. 1. Data sources used to evaluate global fisheries. (**A**) Global catch data; colors refer to the natural logarithm of the average reported catch (metric ton km^{-2} year^{-1}) from 1950 to 2004). (**B**) Other data: Stock assessments quantify the status of exploited populations; research trawl surveys are used to estimate fish community trends; ecosystem models are used to assess responses to fishing. Ecosystems that were analyzed in some detail are highlighted in green (not overfished), yellow (low exploitation rate, biomass rebuilding from overfishing), orange (low to moderate exploitation rate, not yet rebuilding), or red (high exploitation rate).
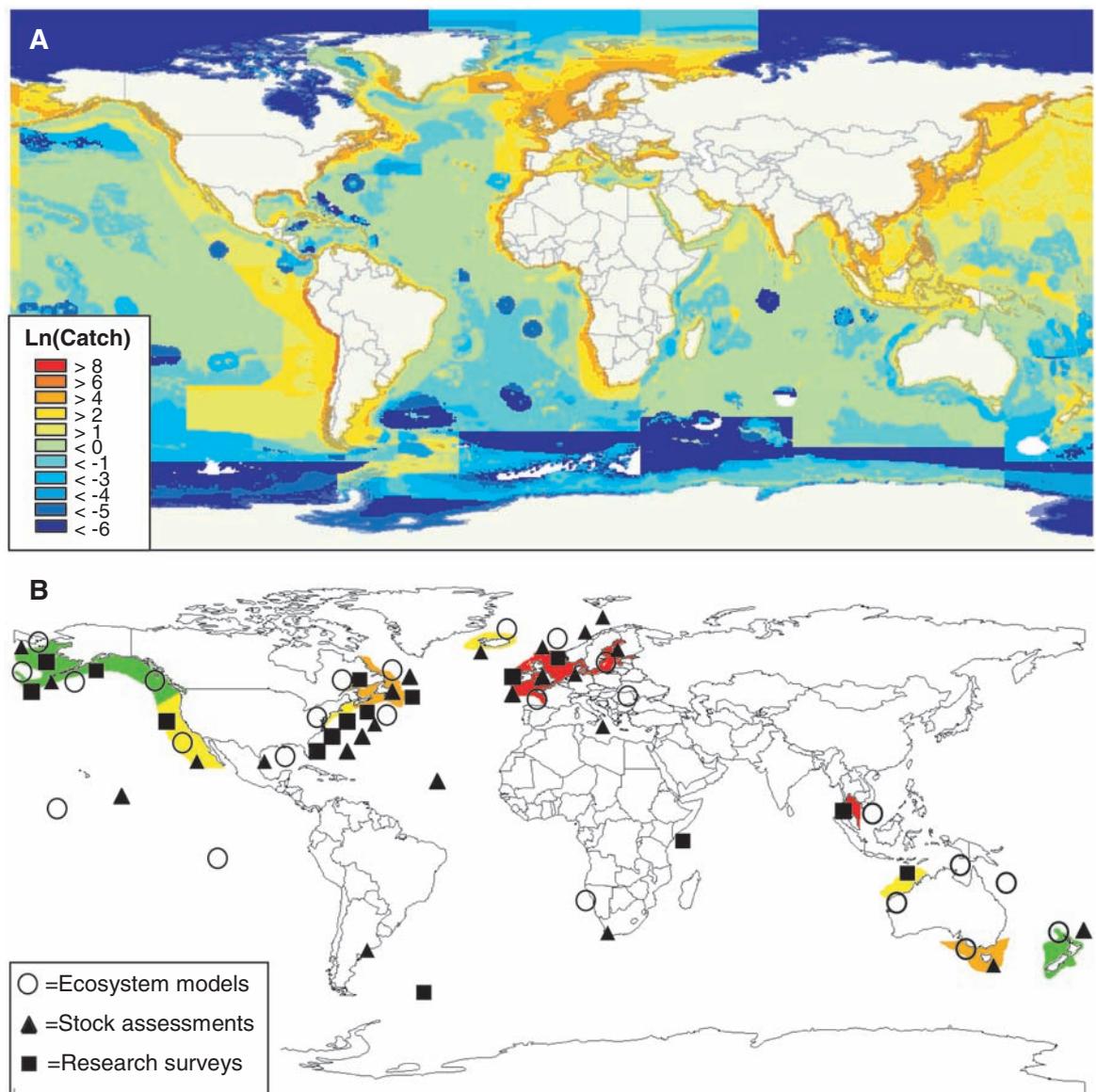
fallen below the biomass that supports maximum yield ($B < B_{MSY}$) but have the potential to recover, where low exploitation rates ($u < u_{MSY}$) are maintained. Note that most stock assessments come from intensely managed fisheries in developed countries, and therefore our results may not apply to stocks in many developing countries, which are often not assessed but fished at high exploitation rates and low biomass. Full results are provided in table S2.

When we combined the biomass estimates of stocks assessed since 1977 ($n = 144$, Fig. 4A), we observed an 11% decline in total biomass. This trend is mostly driven by declines in pelagic (mid-water) species, whereas large declines in demersal (bottom-associated) fish stocks in the North Atlantic were offset by an increase in demersal biomass in the North Pacific after 1977. This shows how a global average can mask considerable regional variation. Although some ecosystems showed relative stability (e.g., the eastern Bering Sea, Fig. 4B), some experienced a collapse of biomass (e.g., eastern Canada, Fig. 4C), whereas others indicated rebuilding of some dominant target species (e.g., Northeast U.S. Shelf, Fig. 4D). These regional examples illustrate different stages of exploitation and rebuilding.

Research trawl surveys. The best sources of information to assess the state of fished communities are repeated scientific surveys that include both target and nontarget species. We analyzed research trawl survey data from 19 ecosystems where such data were available (see Fig. 1B for locations and fig. S2 and table S3 for full data set). We found that community trends averaged across all surveys (Fig. 4E) were broadly similar to the combined biomass trends seen in the recent assessments (Fig. 4A), with similar signatures of stability (Fig. 4F), collapse (Fig. 4G), and recovery (Fig. 4H) in selected regional ecosystems. Few of these surveys, however, reached back to the beginning of large-scale industrial exploitation in the 1950s and early 1960s. Where they did, for example, in the Gulf of Thailand and in Newfoundland, they revealed a rapid decline in total biomass within the first 15 to 20 years of fishing (fig. S2) as predicted by ecosystem models (Fig. 2). These declines were typically most pronounced for large predators such as gadoids (codfishes) and elasmobranchs (sharks and rays). Subsequent to the initial decline, total biomass and community composition have often remained relatively stable (fig. S2), although there may be substantial species turnover and collapses of individual stocks (see below). Across all surveys combined (10), we documented a 32% decline in total biomass, a 56% decline in large demersal fish biomass (species ≥90 cm maximum length), 8% for medium-sized demersals (30 to 90 cm), and 1% for small demersals (≤30 cm), whereas invertebrates increased by 23% and pelagic species by 143% (Fig. 4E). Increases are likely due to prey release from demersal predators (17, 18).

The trawl surveys also revealed changes in size structure that are consistent with model predictions: average maximum size (L_{max}) declined by 22% since 1959 when all communities were included (Fig. 4M). However, there were contrasting trends among our focal regions: L_{max} changed little in the eastern Bering Sea over the surveyed time period (Fig. 4N), dropped sharply in the southern Gulf of St. Lawrence, eastern Canada (Fig. 4O), as large demersal stocks collapsed, and increased because of rebuilding of large demersals (particularly haddock) on Georges Bank, Northeast U.S. Shelf (Fig. 4P). These trends included both target and nontarget species and show how changes in exploitation rates affect the broader community. Published analyses of the Gulf of St. Lawrence and adjacent areas in eastern Canada demonstrate that these community shifts involved large changes in predation regimes, leading to ecological surprises such as predator-prey reversals (19), trophic cascades (17), and the projected local extinction of formerly dominant species (20). Research on the Georges Bank closed area (21) and in marine protected areas worldwide (22) has shown how some of these changes may reverse when predatory fish are allowed to recover. This reveals top-down interactions cascading from fishers to predators and their multiple prey species as important structuring forces that affect community patterns of depletion and recovery (18).

Global fisheries catches. The benefits and costs involved in rebuilding depleted fisheries are demonstrated by an analysis of catch data. Global
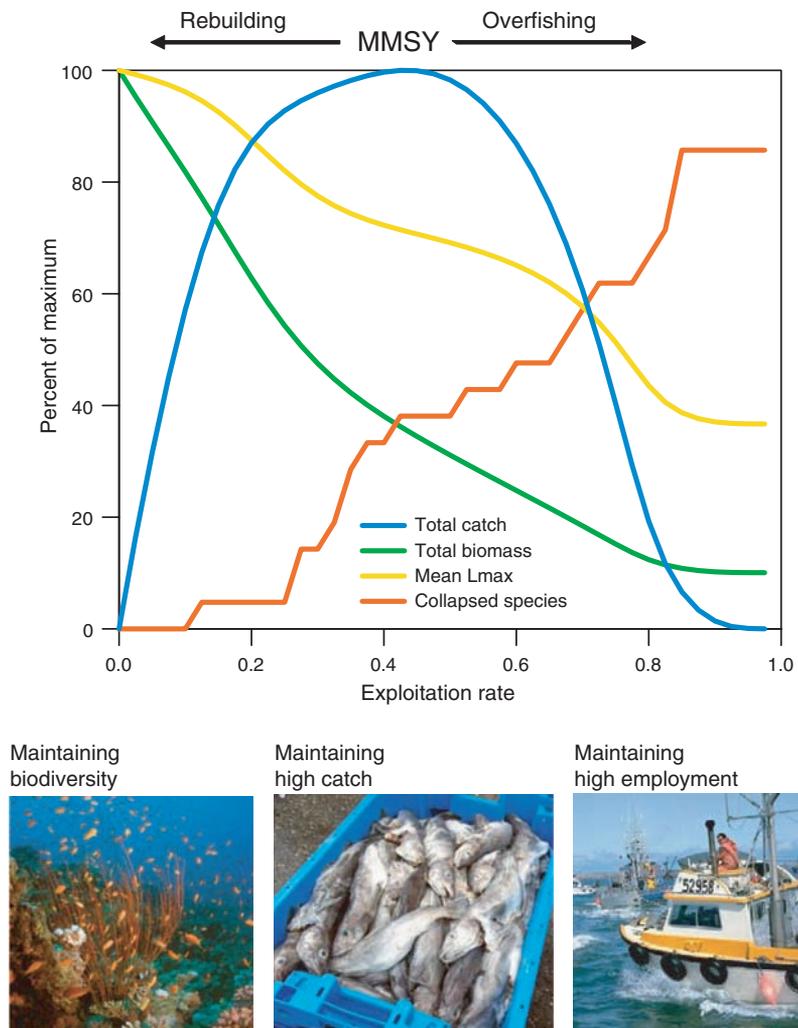

Fig. 2. Effects of increasing exploitation rate on a model fish community. Exploitation rate is the proportion of available fish biomass caught in each year. Mean L_{max} refers to the average maximum length that species in the community can attain. Collapsed species are those for which stock biomass has declined to less than 10% of their unfished biomass. This size-structured model was parameterized for 19 target and 2 nontarget species in the Georges Bank fish community (13). It includes size-dependent growth, maturation, predation, and fishing. Rebuilding can occur to the left, overfishing to the right, of the point of maximum catch. Three key objectives that inform current management are highlighted: biodiversity is maintained at low exploitation rate, maximum catch is maintained at intermediate exploitation rate, and high employment is often maintained at intermediate to high exploitation rate, because of the high fishing effort required.

catches have increased ~fivefold since 1950 as total biomass has been fished down (Fig. 4, A and E) then reached a plateau at ~80 million tons in the late 1980s (Fig. 4I). Catch composition with respect to the major species groups has remained relatively stable over time, with the exception of large demersal fishes, which have declined from 23 to 10% of total catch since 1950. Composition with respect to individual species, however, has fluctuated more widely owing to stock collapses (3) and expansion to new fisheries (6). Individual regions showed very different catch composition and trends, with large- and medium-sized demersal fish being historically dominant in the North Atlantic and North Pacific, small demersals being important in many tropical areas, and pelagic fish dominating the catch from oceanic and coastal upwelling systems (fig. S3). Among our focal regions, the eastern Bering Sea showed a high and stable proportion of large demersal fish (Fig. 4J), the Gulf of St. Lawrence displayed a collapse of the demersal catch and a replacement with small pelagic and invertebrate species (Fig. 4K), and Georges Bank (Fig. 4L) showed a large reduction in catch associated first with declining stocks and then with rebuilding efforts. These examples illustrate that the decline and rebuilding of fished stocks can incur significant costs because of lost

catch, whereas sustained management for lower exploitation rates may promote greater stability with respect to both biomass and catches. Part of this stability may arise from the diversity of discrete populations and species that are more likely to persist in fisheries with low exploitation rates (3, 23).

Trends in species collapses. Theory suggests that increases in fishing pressure, even at levels below MMSY, cause an increasing number of target and non-target species to collapse (Fig. 2). Reductions in fishing pressure are predicted to reverse this trajectory, at least partially. By using biomass data from stock assessments compared to estimates of unfished biomass (B_0) (10), we found an increasing trend of stock collapses over time, such that 14% of assessed stocks were collapsed in 2007, that is, $B/B_0 < 0.1$ (Fig. 4M). This estimate is in the same range as figures provided by the United Nations Food and Agriculture Organization (FAO), which estimated that 19% of stocks were overexploited and 9% depleted or recovering from depletion in 2007 (24). Collapse trends vary substantially by region: The eastern Bering Sea had few assessed fish stocks collapsed (Fig. 4N), whereas collapses strongly increased to more than 60% of assessed stocks in eastern Canada (Fig. 4O) and more than 25% on the Northeast U.S. Shelf (Fig. 4P).

It appears that recent rebuilding efforts, although successful in reducing exploitation rates in several ecosystems (Fig. 3A), have not yet reversed a general trend of increasing depletion of individual stocks (Fig. 4M). This matches the model-derived prediction that reduction of exploitation rate to the level that produces MMSY will still keep a number of vulnerable species collapsed (Fig. 2). Rebuilding these collapsed stocks may require trading off short-term yields for conservation benefits or, alternatively, more selective targeting of species that can sustain current levels of fishing pressure while protecting others from overexploitation.

Small-scale fisheries. Fish or invertebrate stocks that are scientifically assessed ($n = 177$ in our analysis) or appear in research trawl surveys ($n = 1309$ taxa-by-survey combinations in fig. S2) constitute only a fraction of fisheries worldwide, which is an important caveat to the above discussion. Moreover they represent a nonrandom sample dominated by valuable industrial fisheries with some form of management in developed countries. The information on other fisheries, particularly small-scale artisanal and recreational fisheries is scarcer, less accessible, and more difficult to interpret. This is because small-scale fisheries are harder to track, with 12 million fishers compared with 0.5 million in industrialized
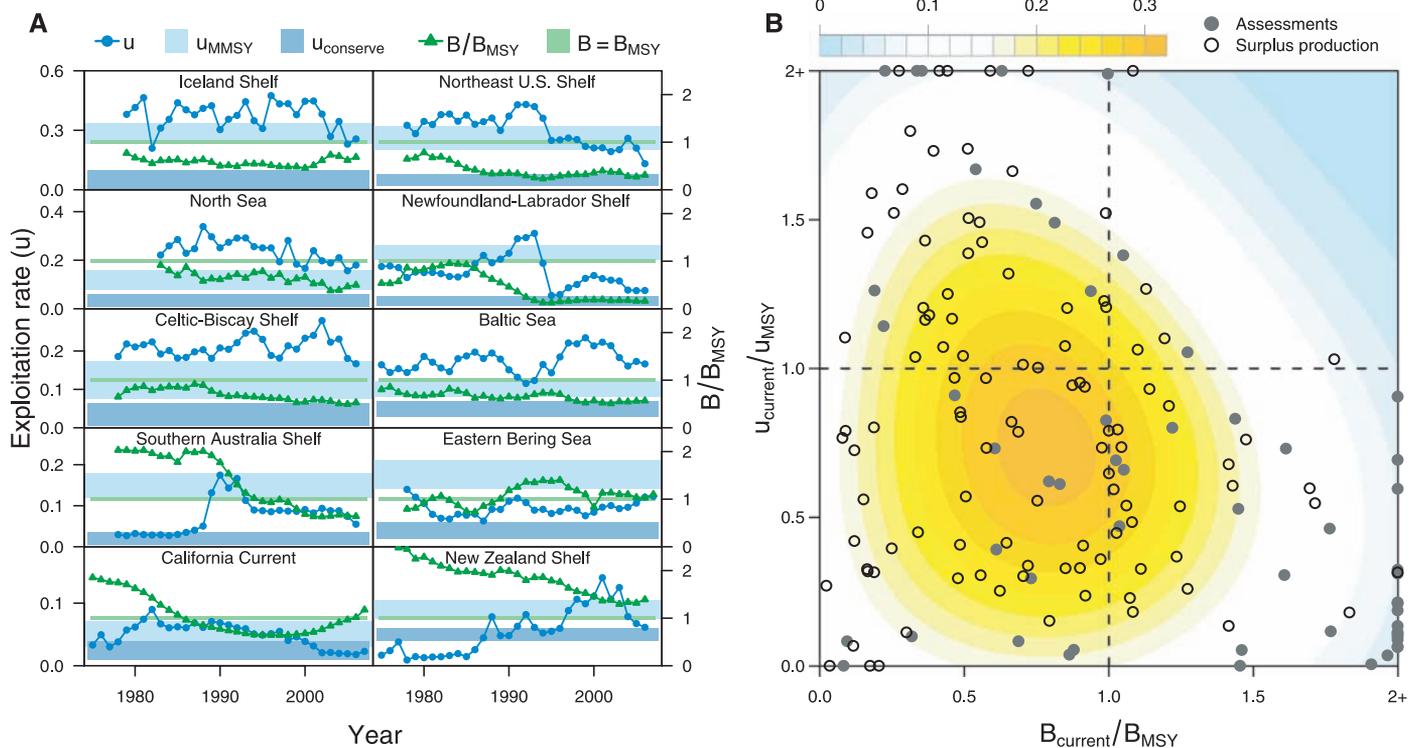
Fig. 3. Exploitation rate and biomass in large marine ecosystems and individual stocks. (**A**) Time trends of biomass (green triangles) are shown relative to the B_{MSY} (green band), exploitation rates (blue circles) relative to the u_{MMSY} (light blue band), and a hypothetical conservation objective at which less than 10% of species are collapsed ($u_{conserve}$, dark blue band). In each ecosystem, stock assessments were used to calculated average biomass relative to B_{MSY} and exploitation rate (total catch divided by total biomass) for assessed species. Reference points were calculated by using published ecosystem models; the width of the bands represents estimated uncertainty (10). (**B**) Current exploitation rate versus biomass for 166 individual stocks. Data are scaled relative to B_{MSY} and the exploitation rate (u_{MSY}) that allows for maximum sustainable yield. Colors indicate probability of occurrence as revealed by a kernel density smoothing function. Gray circles indicate that B_{MSY} and u_{MSY} estimates were obtained directly from assessments; open circles indicate that they were estimated from surplus production models (10).

fisheries (*25*), and assessments or survey data are often lacking. Small-scale fisheries catches are also poorly reported; the best global estimate is about 21 million tons in 2000 (*25*). Conventional management tools used for industrial fisheries are generally unenforceable in small-scale fisheries when implemented in a top-down manner. More successful forms of governance have involved local communities in a co-management arrangement with government or nongovernmental organizations (*26*). An example is the rebuilding of depleted fish stocks on Kenyan coral reefs (Fig. 5A). A network of closed areas and the exclusion of highly unselective beach seines were implemented in cooperation with local communities and led to a recovery of the biomass and size of available fish (*27*). This translated into steep increases in fishers' incomes, particularly in
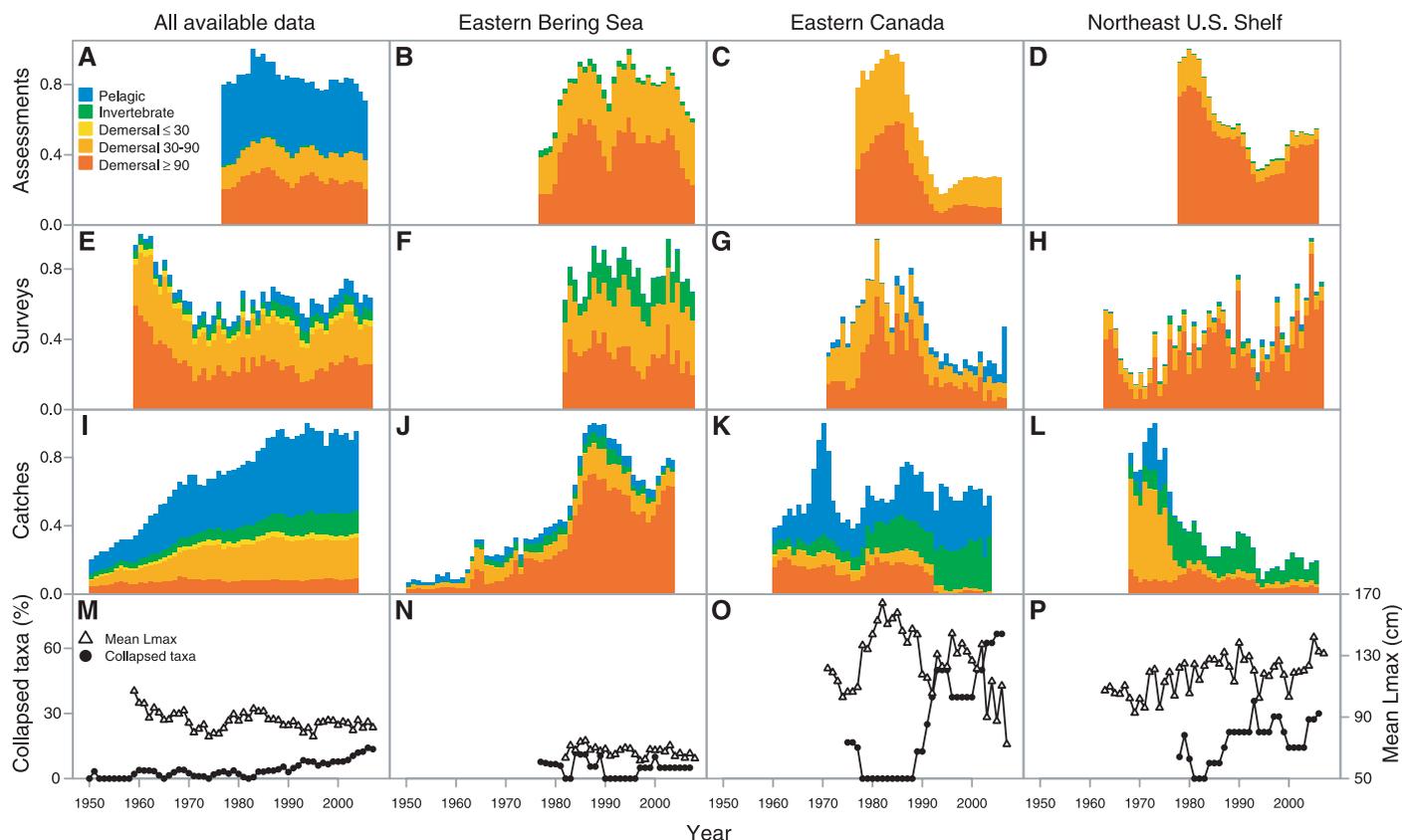

Fig. 4. Global and regional trends in fished ecosystems. Biomass trends computed from stock assessments (**A** to **D**), research surveys (**E** to **H**), as well as total catches (**I** to **L**) are depicted. Trends in the number of collapsed taxa (**M** to **P**, solid circles) were estimated from assessments, and changes in the average maximum size, L_{max} (M to P, open circles), were calculated from survey data (*10*). All data are scaled relative to the time series maximum. (G) and (K) represent the Southern Gulf of St. Lawrence (eastern Canada); (H) and (L), Georges Bank (Northeast U.S. Shelf) only. Collapsed taxa are defined as those where biomass declined to <10% of their unfished biomass. Colors refer to different species groups (demersal fish are split into small, medium, and large species based on the maximum length they can attain).
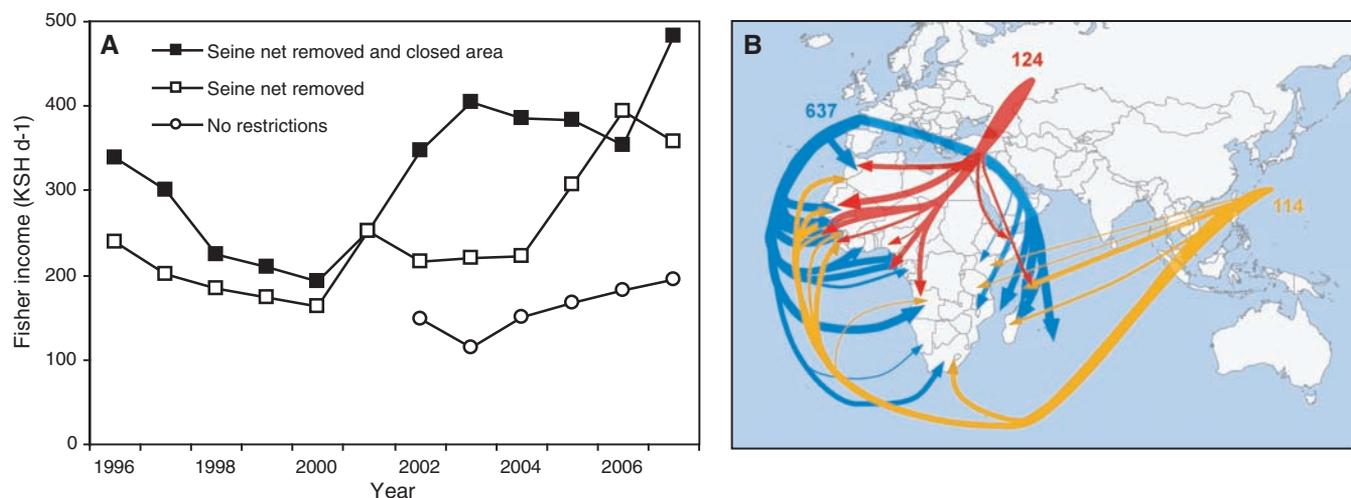

Fig. 5. Problems and solutions for small-scale fisheries. (**A**) Rebuilding of Kenyan small-scale fisheries through gear restrictions and closed area management. Updated, after (*27*). (**B**) Movement of fishing effort from developed nations to Africa in the 1990s. Data indicate total access years in distant-water fishing agreements. Updated, after (*39*).

Table 1. Management tools for rebuilding fisheries. Symbols indicate the contributions of a range of management tools to achieving reductions in exploitation rate: + tool contributed, ++ an important tool, or +++ an essential tool. Note that these examples are for industrialized fisheries, except Kenya, Chile, and Mexico. Ratings were supplied and checked by local experts.

Region	Gear restrictions	Capacity reduced	Total allowable catch reduced	Total fishing effort reduced	Closed areas	Catch shares	Fisheries certification	Community co-management
Bering Sea, Gulf of Alaska	+	++	+++		++	+++	+	+
California Current	+	++	+++		+++			
Northeast U.S. Shelf	+	++		+++	++			
North Sea, Celtic-Biscay	+	+	+++	++	+	+		+
Iceland	+	+	+++			+++		
Southeast Australian Shelf	+	+	+++		++	+++	+	
Northwest Australian Shelf	++				++			
New Zealand	+	+	+++			+++	+	
Kenya (Artisanal)	++				++			+++
Chile and Mexico (Artisanal)	+++				+			+++
Count	10	7	6	2	8	5	3	4
Total score	14	10	18	5	15	13	3	8

regions that had both closed areas and gear restrictions in place (Fig. 5A). Other examples of successful rebuilding come from Latin America, particularly Chile and Mexico, where open-access fisheries for valuable invertebrates were transformed by the establishment of spatial management units that had exclusive access by local fishing organizations (26). Despite these successes, rebuilding small-scale fisheries remains a significant challenge in developing countries where most fishers do not have access to alternative sources of food, income, and employment.

Tools for rebuilding. Management actions in a few ecosystems have prevented overfishing or, more commonly, reduced exploitation rates after a period of overfishing (Figs. 3 to 5). Diverse management tools have helped to achieve reductions in exploitation rates (Table 1). The most commonly used tools overall are gear restrictions, closed areas, and a reduction of fishing capacity, followed by reductions in total allowable catch and catch shares. Reductions in fishing capacity and allowable catch directly reduce the exploitation rate of target species by limiting catches. Gear modifications may be used to increase selectivity and reduce by-catch of nontarget species. Closed areas are either fully protected marine reserves (as in the Kenyan example discussed above) or are designed to exclude specific fisheries from certain areas. They can initiate recovery by providing refuge for over-

fished stocks (21, 28), restoring community structure (22) and biodiversity (3), protecting important habitat features, and increasing ecosystem resilience (29). Assigning dedicated access privileges, such as catch shares or territorial fishing rights, to individual fishers or fishing communities has often provided economic incentives to reduce effort and exploitation rate (30) and may also improve compliance and participation in the management process (31). Likewise, the certification of sustainable fisheries is increasingly used as an incentive for improved management practices. Realigning economic incentives with resource conservation (rather than overexploitation) is increasingly recognized as a critical component of successful rebuilding efforts (8).

We emphasize that the feasibility and value of different management tools depends heavily on local characteristics of the fisheries, ecosystem, and governance system. For example, the most important element of small-scale fisheries success has been community-based management (Table 1), in which local communities develop context-dependent solutions for matching exploitation rates to the productivity of local resources (26). A combination of diverse tools, such as catch restrictions, gear modifications, and closed areas, is typically required to meet both fisheries and conservation objectives.

Here we have only identified the proximate tools, not the ultimate socioeconomic drivers that

have enabled some regions to prevent or reduce overfishing while others remained overexploited. Yet it is generally evident that good local governance, enforcement, and compliance form the very basis for conservation and rebuilding efforts (32). Legislation that makes overexploitation illegal and specifies unambiguous control rules and rebuilding targets has also been critically important, for example, in the United States (8, 28).

Most rebuilding efforts only begin after there is drastic and undeniable evidence of overexploitation. The inherent uncertainty in fisheries, however, requires that agencies act before it comes to that stage (33); this is especially true in light of accelerating global change (34). We found that only Alaska and New Zealand seemed to have acted with such foresight, whereas other regions experienced systemic overexploitation. The data that we have compiled cannot resolve why inherently complex fish-fisher-management systems (35) behaved differently in these cases; possible factors are a combination of abundant resources and low human population, slow development of domestic fisheries, and little interference from international fleets. It would be an important next step to dissect the underlying socioeconomic and ecological variables that enabled some regions to conserve, restore, and rebuild marine resources.

Problems for rebuilding. Despite local successes, it has also become evident that rebuilding efforts can encounter significant problems and

short-term costs. On a regional scale, the reduction of quotas, fishing effort, and overcapacity eliminates jobs, at least in the short term. Initial losses may create strong resistance from fisheries-dependent communities through the political process. For instance in the United States, where 67 overfished stocks have rebuilding plans, 45% of those were still being overfished in 2006, whereas only 3 stocks had been rebuilt at that time (*36*). This problem is exacerbated by the fact that the recovery of depleted stocks can take years or even decades (*28, 37*), and during this time catches may be dramatically reduced (e.g., Fig. 4L). Furthermore, government subsidies often promote overfishing and overcapacity and need to be reduced against the interests of those who receive them (*38*). Lastly, there is the problem of unreported and illegal fishing, which can seriously undermine rebuilding efforts (*11*). Illegal and unreported catches vary between regions, ranging between an estimated 3% of total catch in the Northeast Pacific to 37% in the East Central Atlantic, with a global average of 18% in 2000–2003 (*11*).

On a global scale, a key problem for rebuilding is the movement of fishing effort from industrialized countries to the developing world (Fig. 5B). This north-south redistribution of fisheries has been accelerating since the 1960s (*39*) and could in part be a perverse side effect of efforts to restore depleted fisheries in the developed world, as some fishing effort is displaced to countries with weaker laws and enforcement capacity. The situation is particularly well documented for West Africa (*39*) and more recently East Africa, where local fisheries have seen increasing competition from foreign fleets operating under national access agreements (Fig. 5B) and where illegal and unreported catches are higher than anywhere else (*11*). Almost all of the fish caught by foreign fleets is consumed in industrialized countries and may threaten regional food security (*39*) and biodiversity (*40*) in the developing world. Clearly, more global oversight is needed to ensure that rebuilding efforts in some regions do not cause problems elsewhere. For example, fishing vessels removed in effort-reduction schemes would ideally be prohibited from migrating to other regions and exacerbating existing problems with overcapacity and overexploitation.

Open questions. Rebuilding efforts raise a number of scientific questions. Recovery of depleted stocks is still a poorly understood process, particularly for demersal species (*37*). It is potentially constrained by the magnitude of previous decline (*37*), the loss of biodiversity (*3, 23*), species life histories (*37*), species interactions (*17, 18, 20*), and climate (*28, 34*). Yet, many examples of recovery exist, both in protected areas (*3, 21, 22*) and in large-scale ecosystems where exploitation was substantially reduced (Fig. 3A). A better understanding of how to predict and better manage for recovery will require insight into the resilience and productivity of individual populations and their communities.

This could be gained by more widespread spatial experimentation, involving proper controls, good monitoring, and adaptive management. Some of the most spectacular rebuilding efforts, such as those undertaken in California (*41*), the northeast United States (*21*), and northwest Australia (*42*), have involved bold experimentation with closed areas, gear and effort restrictions, and new approaches to catch allocation and enforcement. Science has a key role to play in guiding such policies, analyzing the effects of changes in management and advancing toward more general rules for rebuilding.

A second area of inquiry relates to the question of how to avoid contentious trade-offs between allowable catch and the conservation of vulnerable or collapsed species. Recovering these species while maintaining global catches may be possible through improved gear technology and a much more widespread use of ocean zoning into areas that are managed for fisheries benefits and others managed for species and habitat conservation. Designing appropriate incentives for fishers to avoid the catch of threatened species, for example, through tradable catch and by-catch quotas, has yielded good results in some regions (*16*). Temporary area closures can also be effective but require detailed mapping of the distribution of depleted populations and their habitats.

Conclusions. Marine ecosystems are currently subjected to a range of exploitation rates, resulting in a mosaic of stable, declining, collapsed, and rebuilding fish stocks and ecosystems. Management actions have achieved measurable reductions in exploitation rates in some regions, but a significant fraction of stocks will remain collapsed unless there are further reductions in exploitation rates. Unfortunately, effective controls on exploitation rates are still lacking in vast areas of the ocean, including those beyond national jurisdiction (*6, 8, 32*). Ecosystems examined in this paper account for less than a quarter of world fisheries area and catch, and lightly to moderately fished and rebuilding ecosystems (green and yellow areas in Fig. 1B) comprise less than half of those. They may best be interpreted as large-scale restoration experiments that demonstrate opportunities for successfully rebuilding marine resources elsewhere. Similar trajectories of recovery have been documented in protected areas around the world (*3, 21, 22*), which currently cover less than 1% of ocean area. Taken together, these examples provide hope that despite a long history of overexploitation (*1, 2*) marine ecosystems can still recover if exploitation rates are reduced substantially. In fisheries science, there is a growing consensus that the exploitation rate that achieves maximum sustainable yield (u_{MSY}) should be reinterpreted as an upper limit rather than a management target. This requires overall reductions in exploitation rates, which can be achieved through a range of management tools. Finding the best management tools may depend on the local context. Most often,

it appears that a combination of traditional approaches (catch quotas, community management) coupled with strategically placed fishing closures, more selective fishing gear, ocean zoning, and economic incentives holds much promise for restoring marine fisheries and ecosystems. Within science, a new cooperation of fisheries scientists and conservation biologists sharing the best available data, and bridging disciplinary divisions, will help to inform and improve ecosystem management. We envision a seascape where the rebuilding, conservation, and sustainable use of marine resources become unifying themes for science, management, and society. We caution that the road to recovery is not always simple and not without short-term costs. Yet, it remains our only option for insuring fisheries and marine ecosystems against further depletion and collapse.

References and Notes
1. J. B. C. Jackson *et al.*, *Science* **293**, 629 (2001).
2. H. K. Lotze *et al.*, *Science* **312**, 1806 (2006).
3. B. Worm *et al.*, *Science* **314**, 787 (2006).
4. R. Hilborn, *Ecosystems (N. Y., Print)* **10**, 1362 (2007).
5. S. Murawski *et al.*, *Science* **316**, 1281b (2007).
6. D. Pauly *et al.*, *Science* **302**, 1359 (2003).
7. T. H. Huxley, *Inaugural Meeting of the Fishery Congress: Address by Professor Huxley* (William Clowes and Sons, London, 1883).
8. J. R. Beddington, D. J. Agnew, C. W. Clark, *Science* **316**, 1713 (2007).
9. S. M. Garcia, A. Zerbi, C. Aliaume, T. Do Chi, G. Lasserre, "The ecosystem approach to fisheries" (FAO, Rome, 2003).
10. Details on methods and data sources are available as supporting online material on *Science* Online.
11. D. J. Agnew *et al.*, *PLoS One* **4**, e4570 (2009).
12. E. A. Fulton, A. D. M. Smith, C. R. Johnson, *Mar. Ecol. Prog. Ser.* **253**, 1 (2003).
13. S. J. Hall *et al.*, *Can. J. Fish. Aquat. Sci.* **63**, 1344 (2006).
14. R. Q. Grafton, T. Kompas, R. W. Hilborn, *Science* **318**, 1601 (2007).
15. S. Jennings, A. S. Revill, *ICES J. Mar. Sci.* **64**, 1525 (2007).
16. T. A. Branch, R. Hilborn, *Can. J. Fish. Aquat. Sci.* **65**, 1435 (2008).
17. K. T. Frank, B. Petrie, J. S. Choi, W. C. Leggett, *Science* **308**, 1621 (2005).
18. J. K. Baum, B. Worm, *J. Anim. Ecol.* **78**, 699 (2009).
19. D. P. Swain, A. F. Sinclair, *Can. J. Fish. Aquat. Sci.* **57**, 1321 (2000).
20. D. P. Swain, G. A. Chouinard, *Can. J. Fish. Aquat. Sci.* **65**, 2315 (2008).
21. S. A. Murawski, R. Brown, H.-L. Lai, P. J. Rago, L. Hendrickson, *Bull. Mar. Sci.* **66**, 775 (2000).
22. F. Micheli, B. S. Halpern, L. W. Botsford, R. R. Warner, *Ecol. Appl.* **14**, 1709 (2004).
23. R. Hilborn, T. P. Quinn, D. E. Schindler, D. E. Rogers, *Proc. Natl. Acad. Sci. U.S.A.* **100**, 6564 (2003).
24. FAO, *The State of World Fisheries and Aquaculture 2008* (FAO, Rome, 2009).
25. D. Pauly, *Marit. Stud.* **4**, 7 (2006).
26. O. Defeo, J. C. Castilla, *Rev. Fish Biol. Fish.* **15**, 265 (2005).
27. T. R. McClanahan, C. C. Hicks, E. S. Darling, *Ecol. Appl.* **18**, 1516 (2008).
28. J. F. Caddy, D. J. Agnew, *Rev. Fish Biol. Fish.* **14**, 43 (2004).
29. J. A. Ley, I. A. Halliday, A. J. Tobin, R. N. Garrett, N. A. Gribble, *Mar. Ecol. Prog. Ser.* **245**, 223 (2002).
30. C. Costello, S. D. Gaines, J. Lynham, *Science* **321**, 1678 (2008).
31. NRC, *Cooperative Research in the National Marine Fisheries Service* (National Research Council Press, Washington, DC, 2003).
32. C. Mora *et al.*, *PLoS Biol.* **7**, e1000131 (2009).

33. D. Ludwig, R. Hilborn, C. Walters, *Science* **260**, 17 (1993).
34. K. M. Brander, *Proc. Natl. Acad. Sci. U.S.A.* **104**, 19709 (2007).
35. P. A. Larkin, *Annu. Rev. Ecol. Syst.* **9**, 57 (1978).
36. A. A. Rosenberg, J. H. Swasey, M. Bowman, *Front. Ecol. Environ* **4**, 303 (2006).
37. J. A. Hutchings, J. D. Reynolds, *Bioscience* **54**, 297 (2004).
38. U. R. Sumaila *et al.*, *Fish. Res.* **88**, 1 (2007).
39. J. Alder, U. R. Sumaila, *J. Environ. Dev.* **13**, 156 (2004).
40. J. S. Brashares *et al.*, *Science* **306**, 1180 (2004).
41. M. Dalton, S. Ralston, *Mar. Resour. Econ.* **18**, 67 (2004).
42. K. J. Sainsbury, R. A. Campbell, R. Lindholm, A. W. Whitelaw, in *Fisheries Management: Global Trends*, E. K. Pikitch, D. D. Huppert, M. P. Sissenwine, Eds. (American Fisheries Society, Bethesda, MD, 1997), pp. 107–112.
43. This work was conducted as part of the "Finding common ground in marine conservation and management" Working Group supported by the National Center for Ecological Analysis and Synthesis funded by NSF, the University of California, and the Santa Barbara campus. The authors acknowledge the Natural Sciences and Engineering Research Council (NSERC) and the Canadian Foundation for Innovation for funding database development, the Sea Around Us Project funded by Pew Charitable Trusts for compiling global catch data, and numerous colleagues and institutions around the world for sharing fisheries assessment, catch, access, and survey data, and ecosystem models (see SOM for full acknowledgments).

Pre-Target Axon Sorting Establishes the Neural Map Topography

Takeshi Imai,[1]* Takahiro Yamazaki,[1]* Reiko Kobayakawa,[1] Ko Kobayakawa,[1] Takaya Abe,[2] Misao Suzuki,[3] Hitoshi Sakano[1]†

Sensory information detected by the peripheral nervous system is represented as a topographic map in the brain. It has long been thought that the topography of the map is determined by graded positional cues that are expressed by the target. Here, we analyzed the pre-target axon sorting for olfactory map formation in mice. In olfactory sensory neurons, an axon guidance receptor, Neuropilin-1, and its repulsive ligand, Semaphorin-3A, are expressed in a complementary manner. We found that expression levels of Neuropilin-1 determined both pre-target sorting and projection sites of axons. Olfactory sensory neuron–specific knockout of Semaphorin-3A perturbed axon sorting and altered the olfactory map topography. Thus, pre-target axon sorting plays an important role in establishing the topographic order based on the relative levels of guidance molecules expressed by axons.

In the vertebrate nervous system, sensory information is spatially encoded in the brain, forming topographic maps that are fundamental for cognition and higher-order processing of sensory information (*1*, *2*). Molecular mechanisms of topographic map formation have been extensively studied in the visual system. The visual image on the retina is roughly preserved in the tectum, which receives retinal ganglion cell axons. Nearly 50 years ago, Sperry proposed the "chemoaffinity hypothesis," in which target cells present chemical cues to guide axons to their destinations (*3*). Axonal projection of retinal ganglion cells is instructed by several pairs of axon guidance molecules that demonstrate graded expression in the retina and tectum (*1*, *2*).

Olfactory information is also encoded in a topographic map formed on the olfactory bulb (OB), a part of the forebrain. In rodents, odors are detected with ~1000 types of odorant receptors (ORs) expressed in olfactory sensory neurons

(OSNs) in the olfactory epithelium (*4*). Each OSN expresses only one functional OR gene (*5*, *6*). Furthermore, OSNs expressing a given type of OR converge their axons to a specific glomerulus on each glomerular map in the OB (*7–9*). During olfactory development, OSN axons are guided to approximate locations in the OB by the combination of dorsal-ventral patterning, based on anatomical locations of OSNs in the olfactory epithelium (*10*), and anterior-posterior patterning, regulated by OR-derived cyclic adenosine monophosphate (cAMP) signals (*11*, *12*). The glomerular arrangement along the dorsal-ventral axis appears to be determined by axon guidance molecules expressed in a graded manner along the dorsomedial-ventrolateral axis in the olfactory epithelium, such as Robo-2 (*13*) and Neuropilin-2 (*14*). Unlike dorsal-ventral positioning, anterior-posterior positioning of glomeruli is independent of positional information in the olfactory epithelium. Instead, OR-specific cAMP signals determine the expression levels of Neuropilin-1 (Nrp1) in OSN axon termini, forming a gradient of Nrp1 (*11*). Thus, the olfactory system also uses gradients of axon guidance molecules to form the topographic map.

How then do guidance molecules regulate topographic map formation? Does map formation solely depend on axon-target interaction? Topographic order emerges in axon bundles, well before they reach the target (*15*, *16*). Here, we studied the pre-target sorting of OSN axons and

its role in topographic map formation in the mouse olfactory system.

Nrp1 regulates axonal projection of OSNs along the anterior-posterior axis. OR-derived cAMP signals regulate the axonal projection of OSNs along the anterior-posterior axis in the OB; low cAMP leads to anterior positioning and high cAMP leads to posterior positioning (*11*). Furthermore, the levels of Nrp1 in OSN axon termini correlated with the level of cAMP signals (*11*).

We found that the Nrp1 levels determine the glomerular positioning along the anterior-posterior axis. When Nrp1 was overexpressed in OR-I7–expressing OSNs (fig. S1), projection sites shifted posteriorly relative to the control (Fig. 1A and fig. S2). In contrast, when Nrp1 was knocked out specifically in I7 OSNs, the projection sites shifted anteriorly relative to the control (Fig. 1A and fig. S2). In the pan-OSN Nrp1 knockout, however, projection sites for I7 often split into anterior and posterior areas (fig. S3). If absolute Nrp1 levels determine glomerular positioning, all glomeruli should form in the anterior OB in the pan-OSN knockout, and the results for I7 OSNs should be the same between the I7-specific knockout and pan-OSN knockout. These results indicate that the relative Nrp1 levels among axons determine the OSN projection sites.

Pre-target axon sorting in the bundle. How do the relative levels of Nrp1 determine the anterior-posterior positioning of glomeruli in the axonal projection of OSNs? To determine where the organization occurs for the olfactory map topography, we analyzed the axon bundles of dorsal-zone (D-zone) OSNs that project to the dorsal domain (D domain) of the OB. The D domain OB comprises two regions, DI and DII; DI is represented by class I ORs, and DII is represented by class II ORs. Class I and class II ORs are phylogenetically distinct and their glomeruli are segregated in the OB (*17*). We subdivided DII into two areas on the basis of Nrp1 expression level (*18*): DII-P is the posterior portion innervated by Nrp1-high axons, and DII-A is the anterior region innervated by Nrp1-low axons. Thus, the D domain can be divided into three areas: DI, DII-A, and DII-P (Fig. 1B).

Axon bundles that project to the D-domain OB were analyzed in neonatal mice by staining serial coronal sections from the anterior olfactory epithelium through the OB. Within the bundle,

[1]Department of Biophysics and Biochemistry, Graduate School of Science, University of Tokyo, Tokyo 113-0032, Japan. [2]Laboratory for Animal Resources and Genetic Engineering, Center for Developmental Biology, RIKEN, Kobe 650-0047, Japan. [3]Division of Transgenic Technology, Center for Animal Resources and Development, Kumamoto University, Kumamoto 860-0081, Japan.

*These authors contributed equally to this work.
†To whom correspondence should be addressed. E-mail: sakano@mail.ecc.u-tokyo.ac.jp