



**Resilience and Recovery of Overexploited Marine Populations**  
Philipp Neubauer *et al.*  
*Science* **340**, 347 (2013);  
DOI: 10.1126/science.1230441

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enhance the translocation and export of DBC to marine systems. The environmental consequences of this are presently unknown but may be reflected in the reduction of DOC bioavailability and associated effects on microbial loop dynamics and aquatic food webs. Our data suggest that we apply our existing knowledge on DOC production, storage, and movement in soils to ensure that biochar applications are implemented sustainably and managed in ways to minimize riverine DBC fluxes.

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**Acknowledgments:** R.J. and Y.D. thank the NSF [grant DBI-0620409; Florida Coast Everglades–LTER program], the SERC Barley Chair, and the FIU–University Graduate School for financial support. The Academy of Finland funded A.V.V. and the collection of samples from large rivers. R.G.M.S. was supported by NSF grants (ETBC-0851101, DEB-1145932, ANT-1203885, and OPP-1107774). A.S. was supported by the NSF (DEB-1146161) and a Fellowship from the Hanse Institute for Advanced Studies (HWK, Delmenhorst, Germany). R. Max Holmes, James W. McClelland, and the rest of the Arctic Great Rivers Observatory ([www.arcticgreatrivers.org](http://www.arcticgreatrivers.org)) team are thanked for providing Arctic river samples (NSF OPP-0732522, OPP-0732821, and OPP-1107774). We thank Y. Yamashita, J. Jones (Bonanza Creek–LTER), W. Dodds (Konza Prairie–LTER), C. Craft (Georgia Coastal Ecosystems–LTER), N. Jaffé, C. Nunes, K. Cawley, P. Wolski, R. Price, C. Rezende, E. M. Paolucci, E. Musibono, A. Shantz, Y. Gélinas, S. R. Khan, Q. Huang, W. Schneider, E. Petrescu and H. E. Reader for providing samples and for field support and M. Friebe and I. Ulber for analytical support. This is SERC Contribution 593. Original data will be available at [http://fclerter.fiu.edu/data/public\\_data\\_access/RJaffe\\_Global\\_DissolvedBlack\\_Corg.xls](http://fclerter.fiu.edu/data/public_data_access/RJaffe_Global_DissolvedBlack_Corg.xls).

#### Supplementary Materials

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Materials and Methods  
Supplementary Text  
References (31, 32)

15 October 2012; accepted 8 February 2013  
10.1126/science.1231476

## Resilience and Recovery of Overexploited Marine Populations

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Recovery of overexploited marine populations has been slow, and most remain below target biomass levels. A key question is whether this is due to insufficient reductions in harvest rates or the erosion of population resilience. Using a global meta-analysis of overfished stocks, we find that resilience of those stocks subjected to moderate levels of overfishing is enhanced, not compromised, offering the possibility of swift recovery. However, prolonged intense overexploitation, especially for collapsed stocks, not only delays rebuilding but also substantially increases the uncertainty in recovery times, despite predictable influences of fishing and life history. Timely and decisive reductions in harvest rates could mitigate this uncertainty. Instead, current harvest and low biomass levels render recovery improbable for the majority of the world's depleted stocks.

Recovery of overexploited marine populations would be a “win-win” outcome for fisheries and conservation, easing pressure on wild populations and associated ecosystems (1–3), and ultimately enhancing catches, revenues, and food security (4–6). Recognizing

the global importance of recovery, the United Nations (UN) 2002 World Summit on Sustainable Development proposed that global fisheries be rebuilt to maximum sustainable yield (MSY) levels by 2015 (5, 7). Echoing this call, several countries, including Australia and the United States, mandated rebuilding in their fisheries legislation. In Europe, a proposed new Common Fisheries Policy (CFP) aims to rebuild fisheries to MSY levels by 2020 (8). Although exploitation rates have been reduced and population declines halted in some regions (9, 10), stock biomass remains below that of maximum sustainable yield ( $B_{MSY}$ ) for the majority of commercially exploited fishes (6, 10, 11). By 2010, only ~1% of global

stocks requiring rebuilding had been successfully rebuilt (9), suggesting that the UN's 2015 recovery target will not be met (5). Here, we empirically examine the time frames needed to recover the world's depleted stocks.

Fisheries operate in complex systems, and the factors driving recovery remain uncertain. Simple theoretical models predict that most overfished stocks should recover to  $B_{MSY}$  in less than a decade if fishing mortality is sufficiently reduced (12). The slow recovery of some populations, however, has led to increased investigation of their resilience to overfishing (13, 14). Allee effects (13, 15), reduced productivity attributable to adverse environmental conditions (16, 17), and the evolution of life-history traits caused by high fishing mortality (18, 19) have been proposed as causes of impaired recoveries. Although such effects may be identifiable retrospectively [e.g., (20)], it remains unclear whether recoveries are predictable, given these potentially adverse effects of long-term exploitation and altered ecosystem states.

To gain insight into the recovery process, we investigated the importance of fishing mortality relative to life history, exploitation history, and other hypothesized drivers of recovery for 153 marine fish and invertebrate stocks for which stock assessments indicated that population biomass had declined below half of  $B_{MSY}$  (table S1) (11, 21). We modeled recovery times—the number of years between depletion ( $B < 0.5 B_{MSY}$ ) and recovery to  $B_{MSY}$ —for 184 depletion events, using a Bayesian regression model based on

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stochastic population dynamics. Our models incorporate survival analysis methods to accommodate the “censored” nature of the data for stocks whose recovery is incomplete (22). From these models, we predict expected recovery times, quantify their uncertainty, and determine conditions under which population resilience is compromised.

Recovery is a multifaceted process. Our models reveal that it is driven not only by the minimum relative biomass to which stocks are depleted ( $B/B_{MSY}$ ), their relative fishing mortality during recovery ( $F/F_{MSY}$ ), and their intrinsic rate of increase ( $r$ ), but also by their exploitation history—the interplay between how long and how hard stocks are fished before their depletion (Fig. 1). On their own, exploitation time (the time between the development year of a fishery and its year of depletion) and historic fishing intensity (the long-term average relative fishing mortality during this time) are positive influences, shortening recovery time (Fig. 1). The interaction of these two variables (exploitation history) is, however, negative. Although particularly intense exploitation histories (e.g.,  $6F_{MSY}$ ) may thus slow recoveries (Fig. 2, A and C), moderate levels of overexploitation before depletion (e.g.,  $2F_{MSY}$ ) appear to enhance the resilience of stocks to such harvest regimes, resulting in shorter rebuilding times once they are depleted (all else being equal) (Figs. 1A, 2, A and C, and 3A).

Our results are consistent with the hypothesis that moderate overexploitation can generate life-history changes, which increase  $r$  to a value greater than that of a population that has not adapted to overfishing. Plastic and evolutionary changes in maturation schedules appear to compensate for initial losses in spawning output caused by selective removal of relatively large, fecund individuals (22, 23) and thus increase resilience to overfishing (22). These changes are, however, relatively slow and likely scale with applied fishing pressure and duration (22–24). Stocks that are depleted over a relatively short time (e.g., <30 years) through moderate overfishing thus exhibit substantially slower and less predictable recovery rates than those that experienced a long history of overfishing (e.g., >50 years) at the same moderate rate before depletion (Fig. 2A). The former may occur for depletions that are caused at least partly by adverse environmental regimes and/or for overfished populations that had insufficient time to adapt to fishing regimes.

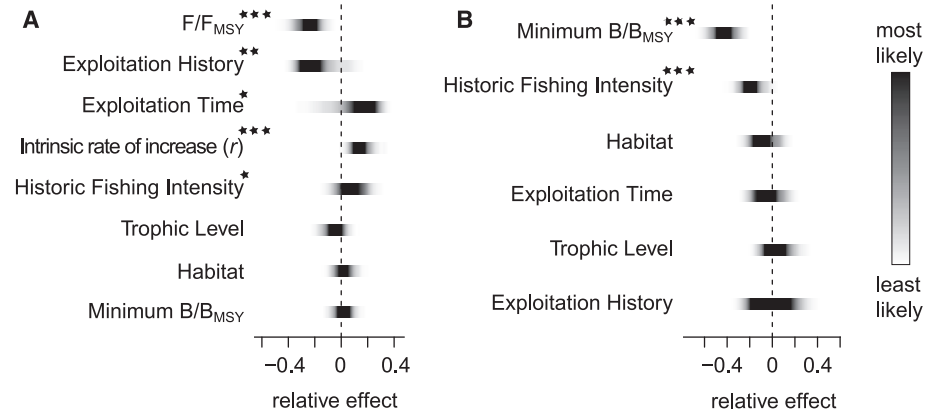
Although our analysis also provides some evidence that intense long-term overfishing eventually impedes resilience, such negative effects are predicted to manifest only at extremely high and sustained fishing mortalities, which occur rarely in our data (Fig. 3A and fig. S1). This empirical result is consistent with recent theoretical studies suggesting that maladaptive effects of fishing are likely slow to manifest and may have limited negative effect on recovery to  $B_{MSY}$  levels (22). Nonetheless, the altered phenotypic and genotypic composition resulting from continued over-

exploitation might be undesirable for reasons other than recovery per se, such as increased variability in biomass trends and decreased resilience to adverse environmental conditions that may compromise long-term productivity of these populations.

We find that recovery is generally predictable and achievable within a decade for stocks with average exploitation histories (i.e., historic fishing intensity  $\sim 2.3F_{MSY}$  and exploitation times >30 years) and intrinsic rates of increase ( $r = 0.43$ ) if fishing mortality is rapidly reduced below  $F_{MSY}$  once stocks fall below  $0.5B_{MSY}$  and collapse ( $B < 0.2B_{MSY}$ ) is avoided (Figs. 2, B and D, 3B, and fig. S3). For instance, reductions in  $F$  below  $F_{MSY}$  seem to have reversed the steady

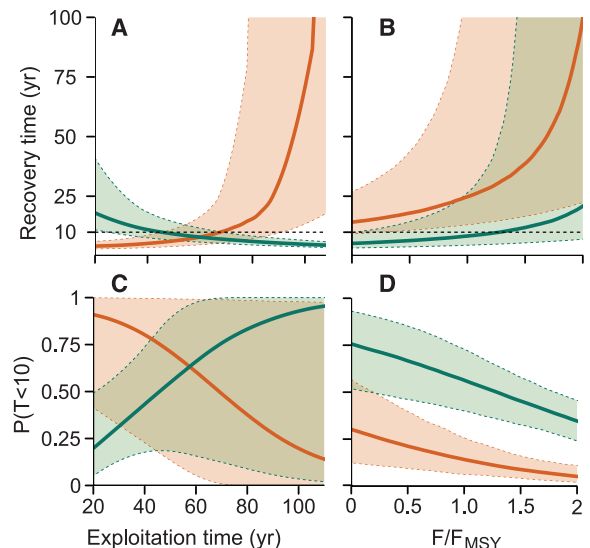
and highly publicized trend toward population collapse of Eastern Atlantic bluefin tuna (*Thunnus thynnus*), and this stock is projected to recover within this time frame under fishing reductions to  $F \leq F_{MSY}$  (Fig. 4A), a prediction supported by its most recent stock assessment (25). In general, however, uncertainty about rebuilding times is considerable if fishing rates are reduced merely to  $F_{MSY}$  once a stock is depleted. Median recovery times increase only from 5 to 8 years with a change in  $F$  from zero to  $F_{MSY}$ , but uncertainty in these times (25th and 75th percentiles of recovery times) increases from 3 to 10 up to 5 to 27 years (Fig. 2B, light green).

Not only does uncertainty about recovery time increase exponentially with applied fishing pres-



**Fig. 1. Scaled posterior distributions of the effect of regression covariates on two components of recovery time.** (A) Recovery rate and (B) relative distance from the recovery target (relative to time-series variance) (21). Dashed lines mark (A)  $\beta = 0$  and (B)  $\gamma = 0$ , where covariates have no effect; one, two, and three stars denote 80, 90, and 99% probabilities that the effect is different from 0, respectively. In (A) a negative effect of a covariate (indicative of a lower recovery rate) delays recovery, whereas in (B) a negative effect of a covariate (indicative of a shorter relative distance) shortens recovery. Habitat is a categorical variable for pelagic and demersal stocks, coded to show the effect for pelagic stocks.

**Fig. 2. Effect of selected covariates on recovery.** Median predicted recovery times (A and B) and probability of recovering within 10 years (C and D) as a function of [(A) and (C)] exploitation time before depletion for stocks recovering from collapse ( $0.2B_{MSY}$ ), with moderate ( $2F_{MSY}$ , green) or high ( $6F_{MSY}$ , orange) historic fishing intensity; [(B) and (D)] relative fishing mortality for stocks recovering from low ( $0.4B_{MSY}$ , green) versus high ( $0.2B_{MSY}$ , orange) depletion levels. Areas of overlap between scenarios appear as olive green. For (A) and (C), relative fishing mortality during the recovery phase is set to zero; all remaining covariates in each plot were fixed at their mean value. For (A) and (B), solid lines are point estimates of median predicted recovery times, shaded regions delimit the 25th to the 75th percentile of predicted recovery times, and dashed black lines show a 10-year recovery time. For (C) and (D), solid lines are median estimates; shaded regions are 95% credible intervals.



sure during the recovery phase but also recovery times are prolonged and less predictable for collapsed stocks (Fig. 2, B and E). For some collapsed Atlantic cod (*Gadus morhua*) stocks, for example, although median predicted rebuilding times are ~10 years, there is substantial uncertainty about these rebuilding times (Fig. 4B). When stocks are driven to severely low abundances, recovery can take decades and recovery projections become uncertain. Georges Bank/Gulf of Maine Atlantic halibut (*Hippoglossus hippoglossus*)—a stock that had been overfished and at low biomass levels ( $B \sim 0.01B_{MSY}$ ) for about a century before rebuilding began—exemplifies such slow and uncertain recoveries (Fig. 4C). Delays in recovery also are pronounced for stocks with low intrinsic rates of increase (e.g.,  $r < 0.2$ ). Species with such “slow” life histories constitute a group that is at particular risk of long-term depletion, especially if the fishing mortality rate is not sufficiently reduced (Fig. 3B and fig. S2).

The stochastic nature of the recovery process means that with longer recovery times comes much greater uncertainty. Patterns in productivity attributable to adaptive processes, trophic interactions, or environmental regimes can dictate the impact of a particular fishing regime and are thus important unknowns in projected recovery times (20, 26–29). For instance, when overfishing continues after depletion, cumulative recovery probabilities for individual stocks still increase over

time (Fig. 4). Thus, despite a marked increase in predicted recovery times and their uncertainty (especially for collapsed stocks) (Fig. 2B), median predicted recovery times remain finite even at fishing mortalities as high as  $2F_{MSY}$ , which, in theory, should not result in recovery. Recovery in these cases might well depend on the adaptive potential of each stock and/or the occurrence of conditions favorable to high recruitment, neither of which can, in general, be predicted with much certainty.

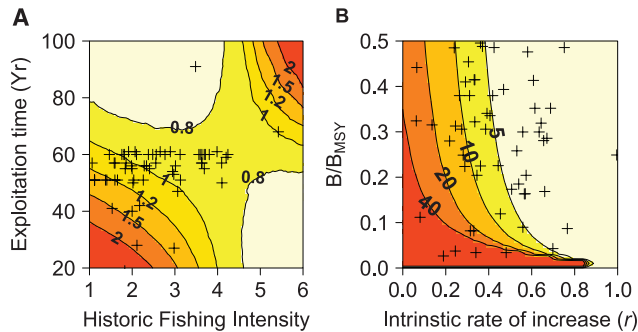
Our analysis suggests that the majority of stocks are resilient to moderate overfishing and have a good chance of recovering within 10 years if fishing pressure is reduced rapidly and substantially once a stock has been determined to be depleted ( $B \approx 0.5 \times B_{MSY}$ ). For many currently depleted stocks, however, rebuilding efforts have been slow to be enacted, and continued overfishing has led to their collapse. At present, a third remain collapsed. Even if fishing mortality rates were reduced to  $F_{MSY}$ , recovery would likely take several decades for many of these stocks (Fig. 3B). Regardless of their depletion level, at current fishing mortality rates, recovery to  $B_{MSY}$  remains a distant target for the majority of stocks that are now depleted ( $n = 62$  stocks in our analysis). Only 23% of these stocks are fished below  $F_{MSY}$ , and only 10% are fished below  $0.5F_{MSY}$ . Recent evidence that production from wild-capture fisheries around the world could be increased were

these stocks to be rebuilt (5, 6) should provide an economic incentive to implement policy and management decisions that accelerate and expand rebuilding efforts.

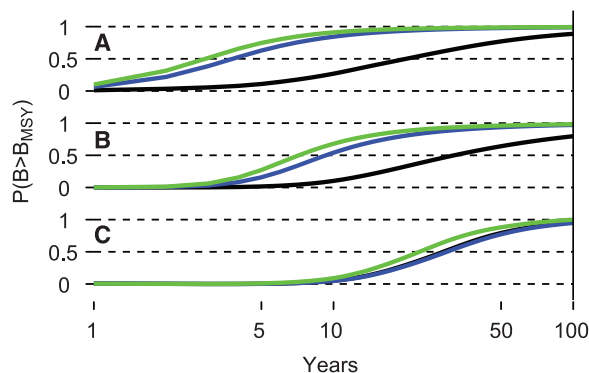
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**Fig. 3. Rebuilding expectations for currently depleted stocks.** (A) Ratio of predicted rebuilding times without fishing for depleted stocks to theoretical rebuilding times as predicted by a Graham-Schaefer model (12), as a function of historic fishing intensity and exploitation time. (B) Expected rebuilding times for depleted stocks fished at  $F_{MSY}$ , as a function of intrinsic rate of increase ( $r$ ) and depletion level, and all other variables set to the mean values for currently depleted stocks. In each panel, black crosses denote currently depleted individual stocks, shown at current levels of the plotted variables.



**Fig. 4. Predicted (cumulative) recovery probability as a function of time (log number of years).** Panels show predictions for (A) Eastern Atlantic bluefin tuna (*T. thynnus*), (B) Irish Sea Atlantic cod (*G. morhua*), and (C) Georges Bank/Gulf of Maine Atlantic halibut (*H. hippoglossus*) at mean fishing mortality rates over the last 3 years in the time series (black lines), fishing at  $F_{MSY}$  (blue lines), and no fishing (green lines). Greater spread in the cumulative probability along the x axis corresponds to greater uncertainty in (log) recovery times.



**Acknowledgments:** We acknowledge financial support from NFS/National Oceanic and Atmospheric Administration Comparative Analysis of Marine Ecosystem Organization (CAMEO) grant 1041678, Natural Sciences and Engineering Research Council Discovery Grants to J.A.H. and J.K.B., and a Sloan Fellowship to J.K.B. We thank R. Hilborn, T. Branch, and the Jensen Laboratory group for insightful comments. Comments by three anonymous reviewers substantially improved the manuscript. Source data are available at <http://ramlegacy.marinebiodiversity.ca>.

**Supplementary Materials**  
[www.sciencemag.org/cgi/content/full/340/6130/347/DC1](http://www.sciencemag.org/cgi/content/full/340/6130/347/DC1)  
 Figs. S1 to S7  
 Tables S1 and S2  
 References (30–42)

19 September 2012; accepted 4 March 2013  
 10.1126/science.1230441