Global population trajectories of tunas and their relatives

Maria José Juan-Jordá[a,b,c,1], Iago Mosqueira[d,e], Andrew B. Cooper[f], Juan Freire[a], and Nicholas K. Dulvy[c]

[a]Grupo de Recursos Marinos y Pesquerías, Facultad de Ciencias, Universidad de A Coruña, 15009 A Coruña, Spain; [b]AZTI-Tecnalia, 20110 Pasaia, Gipuzkoa, Spain; [c]Earth to Ocean Research Group, Department of Biological Sciences, Simon Fraser University, Burnaby, BC, Canada V5A 1S6; [d]Centre for Environment, Fisheries & Aquaculture Science, Lowestoft Laboratory, Lowestoft NR33 0HT, United Kingdom; [e]European Commission, Joint Research Center, Institute for the Protection and Security of the Citizen/Maritime Affairs Unit, FISHREG, 21027 Ispra Varese, Italy; [f]School of Resource and Environmental Management, Simon Fraser University, Burnaby, BC, Canada V5A 1S6

Edited by Timothy E. Essington, University of Washington, Seattle, WA, and accepted by the Editorial Board October 25, 2011 (received for review May 17, 2011)

Tunas and their relatives dominate the world's largest ecosystems and sustain some of the most valuable fisheries. The impacts of fishing on these species have been debated intensively over the past decade, giving rise to divergent views on the scale and extent of the impacts of fisheries on pelagic ecosystems. We use all available age-structured stock assessments to evaluate the adult biomass trajectories and exploitation status of 26 populations of tunas and their relatives (17 tunas, 5 mackerels, and 4 Spanish mackerels) from 1954 to 2006. Overall, populations have declined, on average, by 60% over the past half century, but the decline in the total adult biomass is lower (52%), driven by a few abundant populations. The trajectories of individual populations depend on the interaction between life histories, ecology, and fishing pressure. The steepest declines are exhibited by two distinct groups: the largest, longest lived, highest value temperate tunas and the smaller, short-lived mackerels, both with most of their populations being overexploited. The remaining populations, mostly tropical tunas, have been fished down to approximately maximum sustainable yield levels, preventing further expansion of catches in these fisheries. Fishing mortality has increased steadily to the point where around 12.5% of the tunas and their relatives are caught each year globally. Overcapacity of these fisheries is jeopardizing their long-term sustainability. To guarantee higher catches, stabilize profits, and reduce collateral impacts on marine ecosystems requires the rebuilding of overexploited populations and stricter management measures to reduce overcapacity and regulate threatening trade.

Humans have long exploited the margins of pelagic ecosystems, but only over the past half century has rapid technological development allowed fisheries to operate regularly beyond the sight of land and exploit vast populations of oceanic fishes that were relatively untouched (1, 2). Fifty or more years later, the global impact of fishing on pelagic fishes and their ecosystems is only now beginning to be understood (3, 4). Tunas and their relatives, which include 51 species of tunas, Spanish mackerels, bonitos, and mackerels (collectively known as scombrids), are major components of pelagic ecosystems, being both important predators and forage species that are widely distributed throughout the temperate and tropical epipelagic waters of the world's oceans (Table S1). The majority of tunas and their relatives are highly migratory with widespread oceanic and coastal distributions; therefore, their management and conservation are under the jurisdiction of several international management organizations, such as the tuna regional fisheries management organizations (RFMOs) (*SI Text*, Section 1.3). These predators and forage fishes support some of the largest and most valuable of the world's fisheries, sustaining industrial and artisanal fisheries throughout their ranges, and comprise 12% of global capture fisheries worth US$ 5 billion a year (5, 6) (*SI Text*, Section 1.2).

Given the ecological, social, and economic importance of tunas and their relatives, one might expect that their status and trajectories would be closely monitored and well understood, particularly in an era of monitoring progress toward global biodiversity targets (7). However, the scale and extent of the global fishing impacts on these important species are surprisingly uncertain (1, 6, 8). In 2003, one of the first syntheses brought the plight of ocean predators (mainly tuna species) to the attention of the wider scientific community, concluding that global community biomass of large pelagic fishes had been reduced by around 90% from preindustrial abundance (1). However, this work relied heavily on an analysis of catch and effort data from only one fishing gear type, resulting in an overestimation of tuna declines (8–10). Alternatively, fisheries stock assessments provide a more reliable estimate of population size and trajectory and are regarded as the preferred source of information with which to assess the effects of fishing on fish populations and ecosystems (10–13). In light of the problems with catch data, the increasing availability of stock assessments, and increasing public concern for the sustainable long-term management of natural resources, it seems timely to evaluate the global development, trajectory, and sustainability of tuna fisheries and their relatives.

Here, we evaluate the trajectory and exploitation status of 26 populations of tunas and their relatives. First, we quantify the overall impact of fishing on adult biomass globally, including the extent of the impact within major oceans, major taxonomic groups, and species with different life history strategies using two metrics: the average annual rate of change and the total extent of decline. Second, we compare the adult biomass trajectories against the current exploitation status of each population determined by two standard biological reference points: the ratio of the current adult biomass relative to the adult biomass that would provide the maximum sustainable yield (MSY; B/B_{MSY}) and the ratio of current fishing mortality relative to the fishing mortality rate that maintains MSY (F/F_{MSY}).

Results

We assembled age-structured stock assessments with >15 y of data for 17 tuna populations (7 species), 5 mackerel populations (2 species), and 4 Spanish mackerel populations (2 species) of the 51 species of scombrids (Fig. 1, Fig. S1, and Table S2). We observe that those mackerel and tuna species with the largest number of stock assessments are the most economically important species, comprising 70% of the global reported catches (Fig. 2*A*). In contrast, the small tunnies, Spanish mackerels, and bonitos, which are mainly tropical coastal species, have a smaller number of stock assessments available. The status of these tropical coastal scombrids is mostly unknown throughout their ranges, despite the importance of their commercial fisheries for many coastal fishing

---

Author contributions: M.J.J.-J., I.M., A.B.C., J.F., and N.K.D. designed research; M.J.J.-J., I.M., A.B.C., J.F., and N.K.D. performed research; M.J.J.-J., I.M., A.B.C., J.F., and N.K.D. analyzed data; and M.J.J.-J., I.M., A.B.C., J.F., and N.K.D. wrote the paper.

The authors declare no conflict of interest.

This article is a PNAS Direct Submission. T.E.E. is a guest editor invited by the Editorial Board.

[1] To whom correspondence should be addressed. E-mail: m.juan.jorda@udc.es.

This article contains supporting information online at www.pnas.org/lookup/suppl/doi:10.1073/pnas.1107743108/-/DCSupplemental.

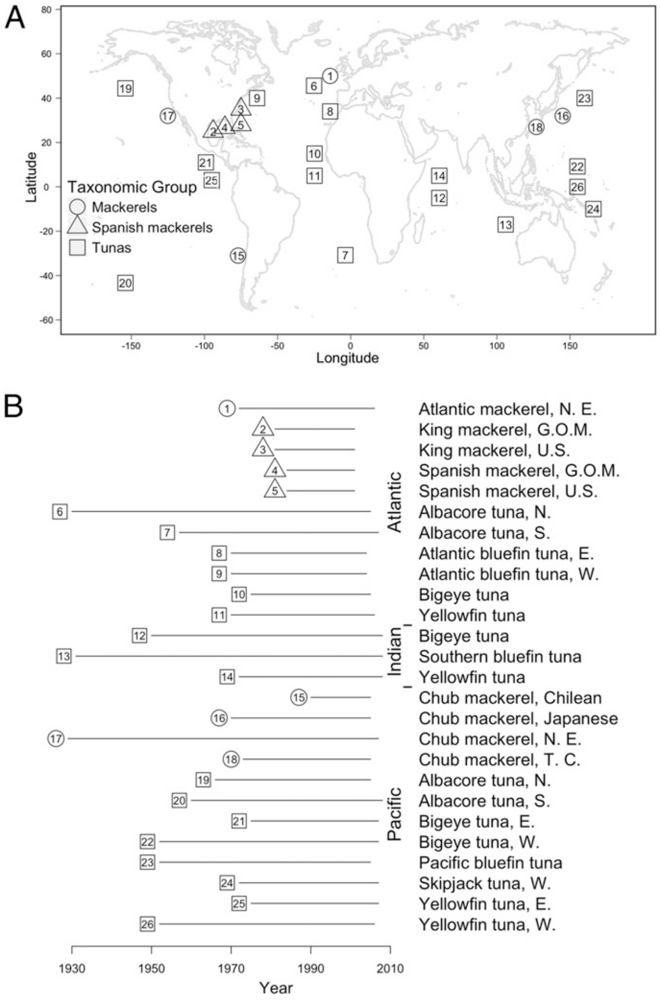

Fig. 1. Age-structured stock assessments were available for 26 populations (11 species) of tunas and their relatives. (*A*) Geographic locations. (*B*) Temporal span. Abbreviations for population names: E., east; G.O.M., Gulf of Mexico; N., north; N.E., northeast; S., south; T.C., Tsushima Current; U.S., United States; W., west.

communities in many developed and developing countries around the world (*SI Text*, Section 2).

Trajectories of Catches and Adult Biomass Across Tunas and Their Relatives. The annual catches of tuna and their relatives have risen continuously since the 1950s, reaching 9.5 million tonnes in 2008 (Fig. 2*A*). This increase in catches was achieved by halving global tuna biomass in half a century; total adult biomass summed across all monitored populations has declined globally by 52.2% from 1954 to 2006 (Fig. 2 *B* and *C*). This total extent of decline depends on the inclusion of the most abundant populations, and their contribution to the overall decline can be seen by excluding a single population at a time from the analysis and recalculating the overall trend (jackknifing). The overall extent of decline would have been 8.2% greater (60.4%) were it not for the inclusion of the abundant West Pacific skipjack tuna population. The overall annual rate of decline can be calculated from the yearly (i) changes in biomass ($r_{i,j}$) among populations (j), which accounts for temporal autocorrelation and the wide variation in the absolute size of populations (*Methods*). On average, the annual rate of change in adult biomass was −1.7% y^{-1} [95% confidence interval (CI): −2.6 to −0.9] across the 26 populations from 1954 to 2006. This global annual rate of change is equivalent to an average decline of 59.9% across all populations within the 52-y period. Moreover, the trajectories in adult biomass of tunas and their relatives vary widely across oceans, taxonomic groups, species, and life history strategies (Fig. 3 and Fig. S2).

The total extent of decline in adult biomass has been greatest in the Indian Ocean, with a 63.6% decline from 1954 to 2006, compared with a 49.6% decline and a 49.2% decline in the Atlantic and Pacific Oceans, respectively (Fig. 3 *A*–*D*). In the Pacific Ocean, the catches of tunas and their relatives are dominated by the abundant West Pacific skipjack tuna adult biomass, which comprises 64% of the total tuna catches in the western Pacific Ocean. After excluding West Pacific skipjack, the extent of decline in adult biomass in the Pacific Ocean is 66.6%. Therefore, the large observed declines in adult biomass suggest substantial impacts of fisheries in all three oceans, despite the different timing in the historical expansion of industrial fisheries. Industrial fisheries, particularly those targeting tuna species, started in the 1950s and 1960s in the Atlantic and Pacific Oceans, whereas they fully developed two decades later in the Indian Ocean. We also observed that the fastest annual rates of decline within the 52-y period occurred in the Indian Ocean (−3.2% y^{-1}, 95% CI: −4.8 to −1.6) (Fig. 3*C* and Fig. S2*A*), possibly attributable to aggressive and poorly regulated artisanal and industrial fisheries operating in a relatively lightly exploited ocean.

Of the three major taxonomic groups of tunas and their relatives, only the total adult biomass of all Spanish mackerels has recovered, increasing by 38.2% over the past half century (Fig. 3*F*). The status of the four Spanish mackerel populations off the southeastern coast of the United States is currently healthy following the implementation of a recovery program after many years of overfishing (14). Of the other two taxonomic groups, the total adult biomass of all mackerels has declined the most (58.1%), whereas tunas have declined by 49.1% (Fig. 3 *G* and *L*). However, after excluding the abundant West Pacific skipjack tuna, the total biomass of all tunas has decreased by 62.5% from 1954 to 2006.

The life history and ecology of fishes are intimately linked to their response to exploitation. Larger species tend to be preferentially targeted by fisheries over smaller species and may be intrinsically more sensitive to fishing because of their relatively less productive life histories (15). However, this ecological pattern can be overwritten by aggressive globalized fisheries (16). We observed that the total adult biomass of the largest species, bluefins, bigeye, and yellowfin tunas, and the smallest species, mackerels, has declined the most, 62.8% and 58.1%, respectively, since 1954 (Fig. 3 *I*–*L*). In addition, we only found significant and steep rates of decline in adult biomass in the largest species, −2.4% y^{-1} (95% CI: −3.5 to −1.4) (Fig. 3*J* and Fig. S2*A*). We hypothesize that the large interannual variability observed in the adult biomass trends of the smallest pelagic coastal species may be hindering the detection of significant declines in their overall annual rates of change (Fig. S3).

We also find that the biogeography of tuna life histories matters. Temperate tuna populations have declined more steeply, −3.1% y^{-1} (95% CI: −4.2 to −1.9), than tropical tuna populations, −1.7% y^{-1} (95% CI: −2.8 to −0.7) (Fig. 3*H* and Fig. S2*A*). These rates are equivalent to an average decline of 80.2% across all the temperate tuna populations and 59.5% across all the tropical tuna populations. Temperate and tropical tuna species have biogeographically distinct life history strategies: temperate species (bluefins and albacore tunas) are longer lived, reproduce later, and have a shorter breeding season and a geographically more restricted breeding site than the tropical tuna species (yellowfin, skipjack, and, to some extent, bigeye tunas), making them more accessible to fisheries, and therefore overall less productive fisheries (17).

Link Between the Adult Biomass Trajectories and the Current Exploitation Status. Population and species trajectories depend not only on life histories and ecology but on the level of exploitation. Here, we summarize the current exploitation status for the 21 populations for which we were able to obtain estimates of the two

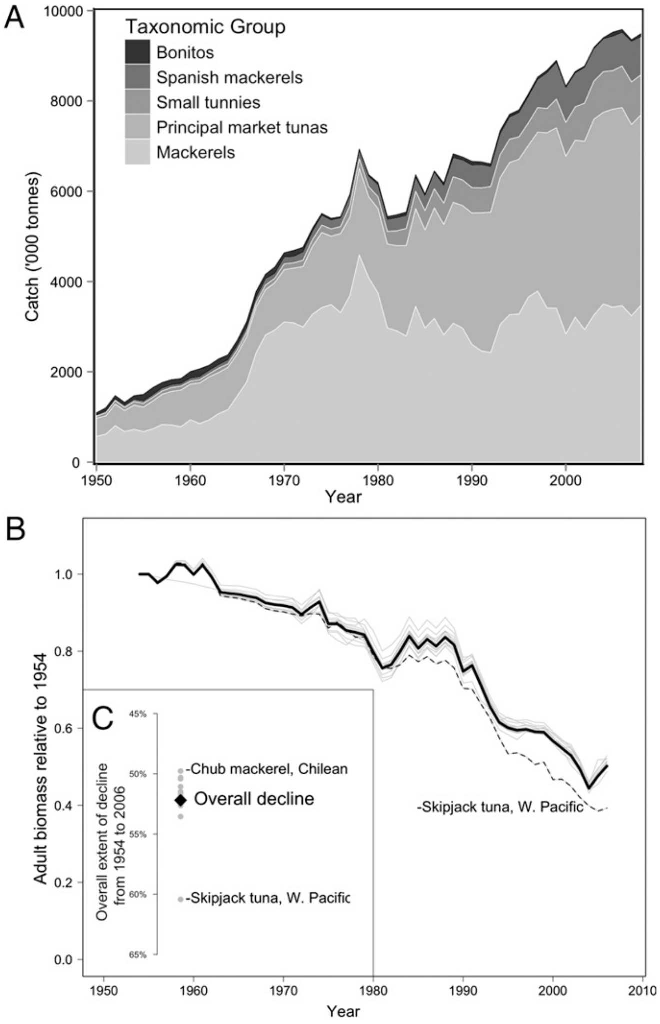

Fig. 2. Global catches and adult biomass trajectories of tunas and their relatives. (*A*) Catches of the major taxonomic groups of tunas and their relatives in the world from 1950 through 2008. (*B*) Relative adult biomass summed across 26 populations of tunas and their relatives (thick solid line), standardized to 1 in 1954. Faint gray lines and black dashed lines show the effect of excluding a single population at a time from the global trend and recalculating the relative adult biomass. The dashed line shows the effect of excluding the most influential population. (*C*) Estimated overall extent of decline in total adult biomass from 1954 to 2006 (filled diamond) and the effect of excluding a single population at a time and recalculating the total extent of decline (shaded circles).

biological reference points, B/B_{MSY} and F/F_{MSY} (Fig. 4*A*). We define "overfished" to mean that the biomass of the population has been reduced to a level less than that which would provide the MSY ($B < B_{MSY}$) and the term "overfishing" to mean that a population is being subjected to a fishing effort greater than that required to produce the MSY ($F > F_{MSY}$), a definition used by the majority of the tuna RFMOs (18). First, there are a total of 4 overexploited temperate tuna populations that are overfished and are experiencing overfishing: East and West Atlantic bluefin tunas, Southern bluefin tuna, and North Atlantic albacore tuna (Fig. 4*A*). Second, there are 12 populations, mostly tropical tunas and Spanish mackerels, currently considered healthy ($B > B_{MSY}$ and $F < F_{MSY}$). Finally, there are 5 populations of tunas and mackerels in an intermediate state that either have a biomass below healthy levels or a fishing mortality exceeding healthy levels but not both ($B < B_{MSY}$ or $F > F_{MSY}$). Although the current exploitation status of tunas and their relatives can be easily categorized according to their biological reference points, it is important to highlight that the majority of tunas and their relatives, despite their assigned exploitation status, have been fished down to around MSY levels, and are therefore fully exploited (Fig. 4*A* and *SI Text*, Section 4.1). The extent of the declines in adult biomass is consistent with the current exploitation status of the populations; the populations having experienced the largest declines in biomass are either fully exploited or overexploited (Figs. S4 and S5 and *SI Text*, Section 4.2).

Discussion

The global adult biomass of tunas and their relatives has been halved over the past half century but not without yielding considerable catches, income, and food for the benefit of humanity. However, these population declines cannot continue without compromising yields in the near future: The majority of populations are fully exploited, which limits the further expansion of catches from these fisheries. Currently, fisheries catch around 10–15% of the tunas and their relatives each year globally (Fig. 4*B* and *SI Text*, Section 3.5). The global demand for tunas and their relatives is still increasing (19), as is the trajectory of fishing mortality (Fig. 4*B*).

The largest declines in adult biomass have occurred in two groups of species with distinct life histories, the largest and less productive temperate tunas and the smallest and more productive mackerel species. Mackerels would, a priori, be considered intrinsically resilient to overfishing because of their "fast" life histories, being fast-growing, early-maturing, and short-lived; yet, mackerels exhibit some of the steepest declines. However, it has been shown that within the past 50 y of industrial fisheries, the collapse of small-and fast-growing pelagic species has been more frequent than in larger species (16). Since fisheries developed in the 1950s, they have preferentially targeted large-biomass, shallow-water species, such as small pelagics (20). This historical pattern of fisheries development, combined with the increasing global market demand for small pelagic fish as food, fishing bait, fish meal, and oil (21), has probably contributed to their massive declines. The role of life histories is more apparent in tunas. The less productive temperate tuna species have been affected the most by fishing, exhibiting steeper and larger declines than the more productive tropical tuna species, suggesting that low productivity and slower life histories might be an important factor, together with catchability, accessibility, and market price and demand, in determining the vulnerability of the species to fishing (22).

The reductions in adult biomass of tuna populations estimated in our global analysis differ from the more pessimistic interpretations of the global status of tuna fisheries described by Myers and Worm (1). Although the two studies are not strictly comparable, Myers and Worm (1) found a 90% decline, on average, in the catch per unit effort of large pelagic fish species and we found a 59.9% decline, on average, in the adult biomass of tunas and their relatives. Notwithstanding the gross differences, both studies agree on the steep declines of three bluefin populations and one albacore population, which are clearly overfished with current biomasses below B_{MSY}. Instead, our results present a wide range of trajectories across tuna populations, which are more consistent with the findings of a study by Sibert et al. (3), which reports declines ranging from 11–88% from baseline adult biomass across the Pacific tuna populations. Moreover, our findings are consistent with those of a recent evaluation of the global conservation status of scombrid species carried out by the International Union for Conservation of Nature (IUCN), which showed that 68% (35 of 61 species) of scombrids are not considered to be threatened with extinction but that a few (5 species) have declined sufficiently to trigger listing under the IUCN Red List Threatened categories, notably the Southern and Atlantic bluefin tunas (22). We caution that our estimates of total and average declines in adult biomass are almost certainly an underestimate, because fishing began long before the start of many of the time series summarized here. Stock assessments often begin years after the start of a fishery and may even be triggered

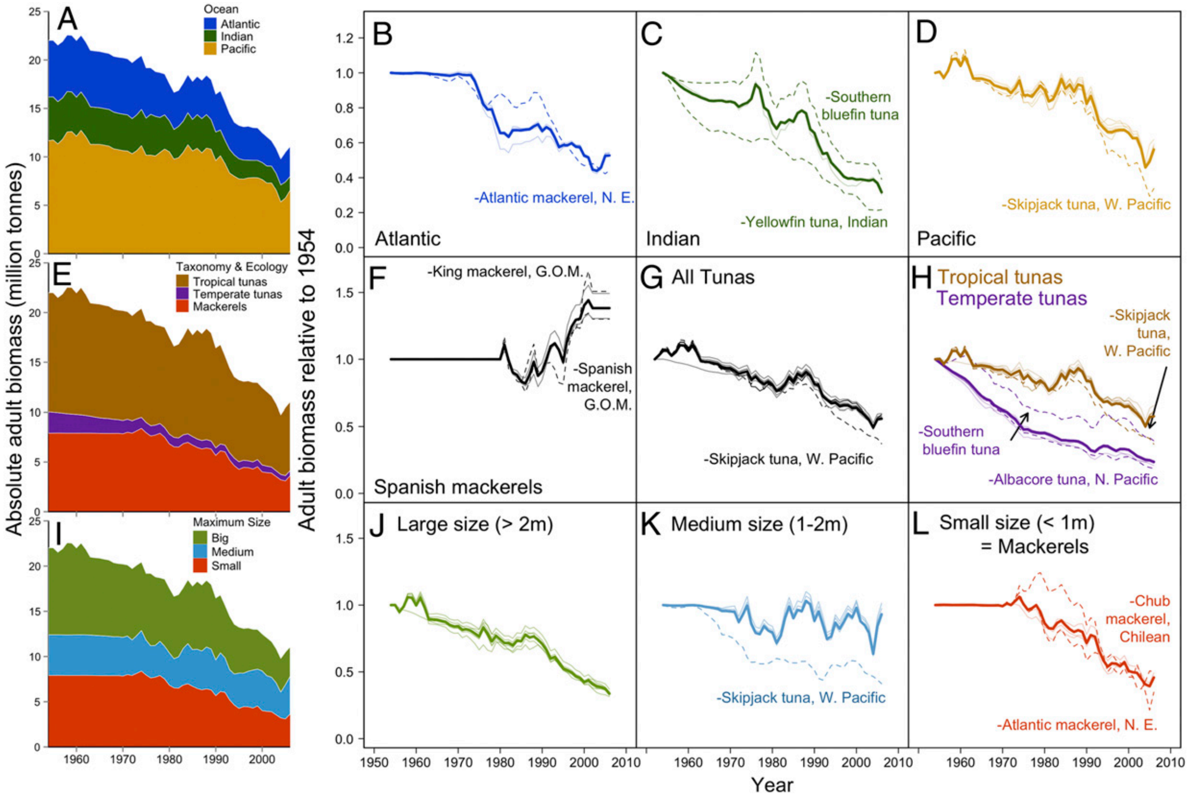

Fig. 3. Adult biomass trajectories of tunas and their relatives within oceans (*A*–*D*), taxonomic and ecological groups (*E*–*H* and *L*), and life histories (*I*–*L*). (*A*, *E*, and *I*) Total adult biomass in million tonnes. (*B*–*D*, *F*–*H*, and *J*–*L*) Relative adult biomass across all populations (thick solid line) standardized to 1 in 1954. Faint gray and dashed lines show the effect of excluding a single population at a time and recalculating the relative adult biomass. Dashed lines show the effect of excluding the most influential populations. The adult biomass of Spanish mackerels was eliminated from *E* because their absolute adult biomass was negligible relative to the other groups. Albacore tuna and the Atlantic, Pacific, and Southern bluefin tunas are considered temperate tunas, and skipjack, yellowfin, and bigeye tunas are considered tropical tunas. The maximum body size of a particular species is provided in Table S1. Abbreviations for population names: G.O.M., Gulf of Mexico; N., north; N.E., northeast; W., west.

by declining catches, as, for example, in the case of the Atlantic bluefin tuna, which was essentially fished out in the South Atlantic in the 1960s before formal assessment (23). Finally, we also show that, globally, the majority of the tunas have been already fished down to near MSY-related levels (Fig. S6). From a fisheries management perspective, MSY is usually obtained when the biomass of a population has been reduced by 60–70% (24). Nonetheless, from a conservation perspective, the 52.2% global decline in total adult biomass and the average population declines of 59.9% across tunas and their relatives increase the probability of ecological and economic extinctions of target populations, with considerable biodiversity consequences for bycatch species (22). In addition, the magnitude of these declines creates concerns about the potential unknown ecosystem effects of removing large amounts of biomass from the pelagic food webs (25).

MSY is the explicit or de facto target yield level for most tuna RFMOs (18). Given that 4 of the 26 populations are substantially below B_{MSY} (Fig. 4*A*) and the others are all at target levels larger than $0.9B_{MSY}$, most fisheries managers would consider these to be extremely well managed (with the exception of the 3 bluefin and 1 albacore populations). However, there is little room for complacency. We highlight three issues to be tackled with urgency to reduce the risk of tropical tunas and other scombrid populations deteriorating in the same way as the bluefin tunas and to minimize the considerable collateral damage and biodiversity consequences of these fisheries. First, tuna productivity is apparently declining; the current estimates of MSY for some tuna populations are lower than in the past, partly a result of the increased mortality of immature tunas in the past two decades from purse seine fisheries, which has consequently decreased the maximum potential yield of the fisheries (19). Second, their high value and global demand, and the rising fishing capacity and mortality (18, 24) (Fig. 4*B*), are exacerbating the pressure on populations that are already fully exploited or, in some cases, overexploited. Management of tuna populations under the single-species approach appears to be largely successful for the less valuable tropical species but has not been effective for high-value bluefin tunas driven by the scale of international demand for and trade of high-valued tunas. In those cases, additional measures seem to be required. Here, we have a case where trade is overwhelming the, normally effective, scale of fisheries management. Hence, there appears to be a role for conservation tools, such as the Convention on International Trade in Endangered Species (CITES), to work alongside the existing management framework to ensure the recovery and future sustainable fishing of the most exploited populations. Third, exploitation of productive species, such as tunas, at MSY is driving steep population declines and elevating the risk of extinction of some unmanaged and less productive bycatch species. Tuna fisheries are directly responsible for endangering a wide range of oceanic pelagic sharks, billfishes, seabirds, and turtles (26, 27).

Many of these issues could be alleviated if fisheries management organizations treated MSY as an upper limit rather than a target reference point in their management objectives, a longstanding recommendation of several international United Nations Food and Agricultural Organization agreements and guidelines over the past 15 y (28). Most tuna RFMOs have vague management objectives and have not adopted or implemented specific targets and limits (29, 30). We recommend the development of well-defined management strategies involving harvest control rules and the associated decision rules that can keep the fishery within defined limits. These would potentially facilitate the crea-

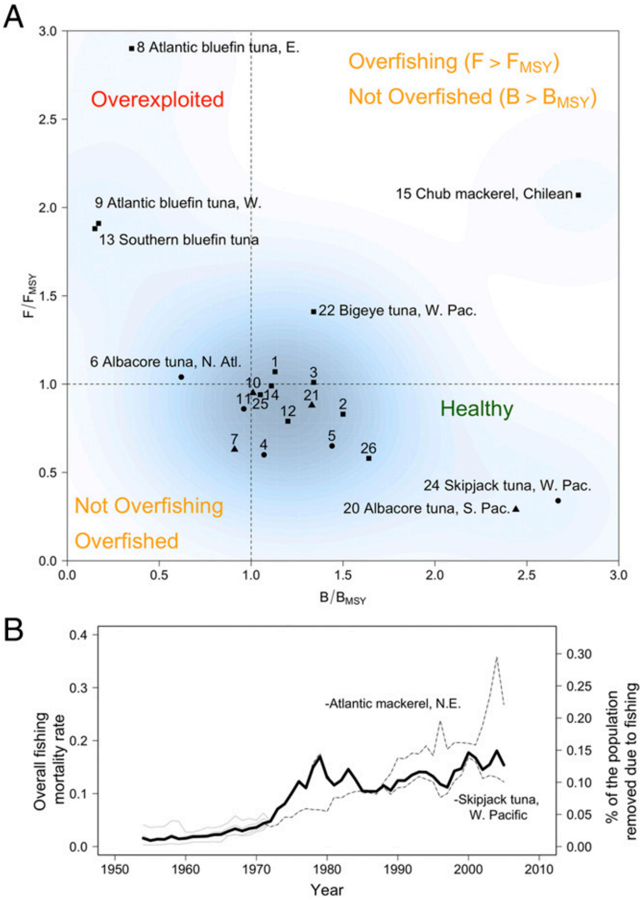

Fig. 4. Current exploitation status and fishing mortality rate over time of tunas and their relatives. (*A*) Reference points for tunas and their relatives: current adult biomass relative to B$_{MSY}$ (*x* axis) vs. current exploitation rate relative to F$_{MSY}$ (*y* axis). Codes follow Fig. 1 and Table S2. Colors represent the kernel density of the points. (*B*) Fishing mortality rate over time across tunas and their relatives. Faint gray lines and black dashed lines show the effect of excluding a single population at a time and recalculating the overall fishing mortality rate. Dashed lines represent the most influential populations. E., east; N.E., northeast; Pac., Pacific; S., south; W., west.

tion of well-defined and specific targets and limits for each population (and therefore management objectives), improving the decision-making process and speeding the implementation of appropriate management measures (29–31). The use of upper limits and lower targets would improve profitability and reduce the impacts on ocean biodiversity (13).

The long-term sustainability of tunas and their relatives can only come from stricter management measures to treat MSY-related levels as a limit rather than a target management objective, to reduce the overall fishing capacity, and to rebuild overexploited populations, as well as further implementing regulations to minimize the collateral impacts of these fisheries on marine ecosystems.

Methods

Data. We compiled age-structured stock assessments with more than 15 y of data for 26 populations and 11 species of tunas and their relatives from a total of 51 species of scombrids (Table S2 and *SI Text*, Section 2). We extracted the trajectories of the adult biomass; fishing mortality; and standard biological reference points, B/B$_{MSY}$ and F/F$_{MSY}$, if available from the assessments. We use the term "population" instead of "stock."

Statistical Analysis. We used two metrics to quantify fishing impacts on the population trajectories of adult biomass. First, we estimated the average annual rate of change across all the populations and its equivalent average percent decline over time globally, within oceans (Atlantic, Pacific, and Indian Oceans), within the main taxonomic groups (tunas, mackerels, and Spanish mackerels), within species, and within groups with different life history strategies. Second, we estimated the overall extent of decline in total adult biomass summed across all the populations over time within the same spatial and taxonomic levels. Although the overall extent of decline is an indicator of ecosystem removals, it might be sensitive to the populations with the largest abundances, which we tested with a jackknife analysis. On the other hand, the estimated average annual rates of change and the equivalent average percent declines are not influenced by the few most abundant populations and can be used to address how well management is working.

Fishing impacts were quantified from 1954 to 2006 to maximize the coverage of data (Fig. 1*B*). The majority of the industrial tuna fisheries began in this period, typically in the 1950s and 1960s. However, it should be acknowledged that there were already fisheries targeting tuna species and their relatives before the 1950s, for centuries in some cases, such as in the case of the Atlantic bluefin tuna in the Mediterranean or skipjack in the Pacific Islands (6); therefore, our analysis does not account for these earlier effects of exploitation. In our analyses, for those time series starting after 1954, we assumed that from 1954 to the first year with data, there have been no major fisheries targeting the populations, and the adult biomass has therefore not changed over time. We retrospectively extended the adult biomass time series to 1954 using the mean of the first 3 y of data and truncated time series that began before 1954. For those time series finishing before 2006, we also extended them forward to 2006, assuming that the most recent estimate, an average of the past 3 y, is projected forward to the future. This imputation approach is conservative in the sense that it is more likely to underestimate the rate and extent of decline (Section 3.1). The maximum observed body sizes of the species were used as a proxy to group species into different life histories because they correlate with other life history traits as well as with intrinsic sensitivity to fishing (32). Populations with a maximum body size (measured as fork length) larger than 2 m were categorized as large, those with a maximum body size between 1 and 2 m as medium, and those with a maximum body size smaller than 1 m as small (Table S1).

We used mixed-effect models to perform a metaanalysis of population trends in adult biomass to estimate annual rates of change within the several spatial and taxonomic levels and within populations with similar life histories. We also tested if the average annual rate of change in adult biomass across all the populations (global estimate) was accelerating or decelerating over time (*SI Text*, Section 3.2). Most of the time series of adult biomass showed nonlinearity and autocorrelation over time; therefore, we converted the raw time series of adult biomass of each population to annual rates of change (r$_i$), $r_i = \ln(AB_{i+1}/AB_i)$, where AB$_i$ is the adult biomass in year i (Fig. S7). Such differencing or taking the ratios in log-space is a common method of removing temporal autocorrelation from a time series (33). The annual rate of change in adult biomass, r$_i$, was the dependent variable in the analyses of adult biomass trends. We used the following full mixed-effect model and several submodels of the full model, depending on the objective of the analysis to estimate the overall annual rates of change in adult biomass:

Level 1: $y_{ij} = \beta_{0j} + \beta_{1j} X_{ij} + \varepsilon_{ij}$, where $\varepsilon_{ij} \sim N(0, \sigma_\varepsilon^2 I)$

$$\text{Level 2:}\quad \begin{array}{l} \beta_{0j} = \gamma_{00} + \gamma_{01} W_j + \delta_{0j} \\ \beta_{1j} = \gamma_{10} + \gamma_{11} W_j + \delta_{1j,} \end{array} \quad \text{where} \quad \begin{bmatrix} \delta_{0j} \\ \delta_{1j} \end{bmatrix} \sim N\left(\begin{bmatrix} 0 \\ 0 \end{bmatrix}, \begin{bmatrix} \sigma_0^2 & \sigma_{01} \\ \sigma_{10} & \sigma_1^2 \end{bmatrix} \right)$$

Level 1 is a linear regression model in which the intercepts and the slopes are allowed to vary by group (here, populations), where *j* indexes the populations modeled as random effects and *i* indexes the years. Level 2 describes the variability of the relationship between the dependent variable y (here, the annual rates of change in adult biomass) and the covariate variable *X* (here, years) among all the populations *j*. Level 2 has one categorical predictor variable, *W*, which can be any of the categorical variables grouping populations geographically or taxonomically (e.g., oceans, taxonomic groups). The β's and the γ's are the fixed effects coefficients, and the δ's and ε's are the random effects coefficients. We assume the random effects (δ) are normally distributed with the given variance-covariance matrix, and we assume that the residual errors (ε) follow an $\varepsilon_t \sim N(0, \sigma_\varepsilon^2)$. In addition, we estimated the average of the annual rates of change in adult biomass across all the years for each population (*SI Text*, Section 3.3).

We used restricted maximum likelihood to fit all the mixed models utilizing the lme function in the NLME package in R (34). We examined the residuals of all the models and corrected for temporal autocorrelation with AR1 and AR2 processes when necessary. In addition, we allowed each population to have a different variance. The Akaike Information Criterion was used to determine the autocorrelation process and the variance structure most suitable for the time series under investigation. We show the model validation plots of one analysis, although all the analyses had similar validation plots (Fig. S8). The significance of the fixed terms of the models was assessed by computing the CIs for each fixed effect and then considering them significant if the 95% CIs did not include zero.

To calculate the overall extent of decline in total adult biomass summed across all the populations over time within the several spatial and taxonomic levels, we first summed the values of adult biomass across all the populations for the years 1954 and 2006 using the mean of the first and last 3 y of data. We then estimated the total percent change in adult biomass between 1954 and 2006 globally across all the populations, within each ocean, within each taxonomic group, within species, and within populations with similar life histories. In addition, we estimated the extent of decline for each individual population (*SI Text*, Section 3.3).

ACKNOWLEDGMENTS. We are grateful to Trevor Branch and two anonymous reviewers for their constructive comments. We are very grateful to many scientists and national and international organizations for providing access to stock assessment fisheries data to carry out this work. The stock assessments were provided by the National Oceanic and Atmospheric Administration-National Marine Fisheries Service, International Commission for the Conservation of Atlantic Tunas, Inter-American Tropical Tuna Commission, Western and Central Pacific Fishery Commission, and Indian Ocean Tuna Commission. We particularly thank Miguel Herrera, Ana Parma, Cristian Canales, Simon Hoyle, Mauricio Ortiz, Carolla Kirchner, Francois Gregoire, Richard Hillary, Alexandre Aires-Da-Silva, Alejandro Perez, Marc Maunder, Beatriz Roel, Carlos Palma, Pilar Pallares, Haritz Arrizabalaga, Chikako Watanabe, and Paul Crone for their help and advice in using the stock assessment data. We gratefully acknowledge the constructive comments and suggestions from John Reynolds, Jennifer Sunday, Maria Calvo Uyarra, Sean Anderson, and Loren McClenachan on earlier versions of this manuscript. This work was supported, in part, by European Union Marie Curie Early Stage Training Project METAOCEANS, MEST-CT-2005-019678 (to M.J.J.-J.); a Maria Barbeito Scholarship from Xunta de Galicia, Spain (to M.J.J.-J.); the Natural Environment Research Council of Canada (N.K.D. and A.B.C.); and the United Kingdom's Department for the Environment, Food, and Rural Affairs under Contract M1205 "Data-poor fisheries" (I.M.).

1. Myers RA, Worm B (2003) Rapid worldwide depletion of predatory fish communities. *Nature* 423:280–283.
2. Swartz W, Sala E, Tracey S, Watson R, Pauly D (2010) The spatial expansion and ecological footprint of fisheries (1950 to present). *PLoS ONE* 5:e15143.
3. Sibert JR, Hampton J, Kleiber P, Maunder M (2006) Biomass, size, and trophic status of top predators in the Pacific Ocean. *Science* 314:1773–1776.
4. Worm B, et al. (2006) Impacts of biodiversity loss on ocean ecosystem services. *Science* 314:787–790.
5. FAO (2010) *The State of World Fisheries and Aquaculture 2010* (FAO, Rome).
6. Majkowski J (2007) Global fishery resources of tuna and tuna-like species. FAO Fisheries Technical Paper No. 483 (FAO, Rome), p 55.
7. Butchart SHM, et al. (2010) Global biodiversity: Indicators of recent declines. *Science* 328:1164–1168.
8. Hampton J, Sibert JR, Kleiber P, Maunder MN, Harley SJ (2005) Fisheries: Decline of Pacific tuna populations exaggerated? *Nature* 434:E1–E2, discussion E2.
9. Walters CJ (2003) Folly and fantasy in the analysis of spatial catch rate data. *Can J Fish Aquat Sci* 60:1433–1436.
10. Polacheck T (2006) Tuna longline catch rates in the Indian Ocean: Did industrial fishing result in a 90% rapid decline in the abundance of large predatory species? *Mar Policy* 30:470–482.
11. Branch TA, Jensen OP, Ricard D, Ye Y, Hilborn R (2011) Contrasting global trends in marine fishery status obtained from catches and from stock assessments. *Conserv Biol* 25:777–786.
12. Hutchings JA, Minto C, Ricard D, Baum JK, Jensen OP (2010) Trends in the abundance of marine fishes. *Can J Fish Aquat Sci* 67:1205–1210.
13. Worm B, et al. (2009) Rebuilding global fisheries. *Science* 325:578–585.
14. Ortiz M (2004) Stock assessment analysis on Gulf of Mexico king mackerel. SEDAR5-2004 Miami Lab Sustainable Fisheries Division Contribution 2004-004, National Marine Fisheries Service, South East Fisheries Science Center, Miami.
15. Reynolds JD, Dulvy NK, Goodwin NB, Hutchings JA (2005) Biology of extinction risk in marine fishes. *Proc Biol Sci* 272:2337–2344.
16. Pinsky ML, Jensen OP, Ricard D, Palumbi SR (2011) Unexpected patterns of fisheries collapse in the world's oceans. *Proc Natl Acad Sci USA* 108:8317–8322.
17. Fromentin JM, Fonteneau A (2001) Fishing effects and life history traits: A case study comparing tropical versus temperate tunas. *Fish Res* 53:133–150.
18. Aranda M, de Bruyn P, Murua H (2010) A report review of the tuna RFMOs: CCSBT, IATTC, IOTC, ICCAT and WCPFC. EU FP7 Project No. 212188 TXOTX, Deliverable 2.2, p 171.
19. Allen R (2010) International management of tuna fisheries. Arrangements, challenges and a way forward. FAO Fisheries and Aquaculture Technical Paper No. 536 (FAO, Rome), p 47.
20. Sethi SA, Branch TA, Watson R (2010) Global fishery development patterns are driven by profit but not trophic level. *Proc Natl Acad Sci USA* 107:12163–12167.
21. Deutsch L, et al. (2007) Feeding aquaculture growth through globalization: Exploitation of marine ecosystems for fishmeal. *Glob Environ Change* 17:238–249.
22. Collette BB, et al. (2011) Conservation. High value and long life—Double jeopardy for tunas and billfishes. *Science* 333:291–292.
23. Fromentin JM, Powers JE (2005) Atlantic bluefin tuna: Population dynamics, ecology, fisheries and management. *Fish Fish* 6:281–306.
24. Hilborn R (2010) Pretty good yield and exploited fishes. *Mar Policy* 34:193–196.
25. Polovina J, Abecassis M, Howell EA, Woodworth P (2009) Increases in the relative abundance of mid-trophic level fishes concurrent with declines in apex predators in the subtropical North Pacific, 1996-2006. *Fish Bull* 107:523–531.
26. Dulvy NK, et al. (2008) You can swim but you can't hide: The global status and conservation of oceanic pelagic sharks and rays. *Aquatic Conservation: Marine and Freshwater Ecosystems* 482:459–482.
27. Wallace BP, et al. (2010) Global patterns of marine turtle bycatch. *Conservation Letters* 3:131–142.
28. Caddy JF, Mahon R (1995) Reference points for fisheries management. FAO Fisheries Technical Paper No. 347 (FAO, Rome), p 83.
29. Maunder MN, Harley SJ (2006) Evaluating tuna management in the eastern Pacific Ocean. *Bull Mar Sci* 78:593–606.
30. Mooney-Seus ML, Rosenberg AA (2007) Best practices for high seas fisheries management: Lessons learned (Chatham House Briefing Paper, Energy, Environment and Development Programme EEDP BP 07/03, London).
31. Kell LT, et al. (2003) An evaluation of management strategies for Atlantic tuna stocks. *Sci Mar* 67:353–370.
32. Jennings S, Reynolds JD, Mills SC (1998) Life history correlates of responses to fisheries exploitation. *Proc R Soc Lond B Biol Sci* 265:333–339.
33. Shumway RH, Stoffer DS (2006) *Time Series Analysis and Its Applications: With R Examples* (Springer, New York).
34. Pinheiro J, Bates D (2000) *Mixed Effects Models in S and S-Plus* (Springer, New York).