Predicting overfishing and extinction threats in multispecies fisheries

Matthew G. Burgess[a,1], Stephen Polasky[b,1], and David Tilman[a,c]

Departments of [a]Ecology, Evolution, and Behavior and [b]Applied Economics, University of Minnesota, St. Paul, MN 55108; and [c]Bren School of the Environment, University of California, Santa Barbara, CA 93106

Contributed by Stephen Polasky, July 30, 2013 (sent for review November 21, 2012)

Threats to species from commercial fishing are rarely identified until species have suffered large population declines, by which time remedial actions can have severe economic consequences, such as closure of fisheries. Many of the species most threatened by fishing are caught in multispecies fisheries, which can remain profitable even as populations of some species collapse. Here we show for multispecies fisheries that the biological and socioeconomic conditions that would eventually cause species to be severely depleted or even driven extinct can be identified decades before those species experience high harvest rates or marked population declines. Because fishing effort imposes a common source of mortality on all species in a fishery, the long-term impact of a fishery on a species is predicted by measuring its loss rate relative to that of species that influence the fishery's maximal effort. We tested our approach on eight Pacific tuna and billfish populations, four of which have been identified recently as in decline and threatened with overfishing. The severe depletion of all four populations could have been predicted in the 1950s, using our approach. Our results demonstrate that species threatened by human harvesting can be identified much earlier, providing time for adjustments in harvesting practices before consequences become severe and fishery closures or other socioeconomically disruptive interventions are required to protect species.

early warning | preventative management | overharvesting | mechanistic | assessment

Marine fisheries are an important global source of food and livelihoods (1–4), but there are concerns that current fishing practices threaten some marine species with severe depletion or eventual extinction (2–5). Many of the largest commercial fishing methods, such as trawling, longlining, and seining, unavoidably catch multiple species simultaneously (6–9). Multispecies fisheries pose a particular threat of extinction or severe depletion because fishing can remain profitable as long as some valuable species remain abundant, even while others collapse (6–11). In contrast, in a single-species fishery profits tend to fall as the target population declines, thereby removing the incentive to fish before extinction occurs (10). Multispecies fisheries pose a threat to two types of species or stocks (populations): (*i*) commercially valued species, called "weak stocks", which are more vulnerable to overharvesting than are other commercially valuable species (6), and (*ii*) by-catch species, which are caught accidentally and create little economic incentive to cease fishing as their populations collapse because they have little or no commercial value (7–9).

Failure to prevent collapse of weak stocks and by-catch species can impose substantial long-term environmental and economic costs. Slow-growing populations are most likely to collapse, but can take several decades to recover (5). Recovery often requires long-term fishery closures or reductions in effort, having substantial economic and social consequences (3, 5). Moreover, population declines caused by one fishery can diminish yields and profits in other commercial or artisanal fisheries that depend on the same species (e.g., ref. 12).

Despite these costs, species threatened by fishing have rarely been identified until after their populations have declined substantially (2–5, 7, 8). Assessments of fishery impacts on species mostly focus on estimating current exploitation rates or past population trends (13–15), which identifies already declining species rather than predicting future declines. Data limitations have made empirical prediction of future threats from fishing challenging, particularly for weak stocks and by-catch species. Oceans are difficult to sample extensively, and few economic incentives exist to gather data on species other than the most commercially valued species (7, 8). Some predictive models (e.g., ref. 16) have been developed to forecast the impacts of some fisheries, but these are often data intensive. Some of the characteristics that make a population susceptible to overfishing are well known—for example, low population growth rates (3–11, 17, 18), high value and/or low fishing costs (10, 11, 17–19), and schooling behavior (18). Recently, some correlative approaches based on these characteristics have been developed for assessing likely relative threats to data-poor species (4, 20–22). However, predicting the severity of future threats in absolute terms with this type of approach can be challenging.

Here, we present a mechanistic approach that uses readily available data to predict the potential of current fishing practices, if maintained, to eventually cause a population to be driven extinct or "overfished", here defined as depletion below its maximum sustainable yield (MSY) abundance (N_{MSY}) (3). Our approach identifies combinations of biological and socioeconomic conditions that are likely to eventually lead to high mortality rates and population declines. As we show, these conditions can be identified long before either occurs.

We test the predictive power of our approach on eight tuna and billfish populations of the Western and Central Pacific

Significance

Threats to species from commercial fishing are rarely identified until species have suffered large population declines, by which time recovery can require costly remedial actions, such as fishery closures. We present a mechanistic approach to predicting the threats of future extinction or severe depletion posed by current multispecies fishing practices to a given population. We show that severe depletions recently experienced by four Pacific tuna and billfish populations could have been predicted in the 1950s, using our approach. Our results demonstrate that threatened species can be identified long before they experience severe population declines, providing time for preventative adjustments in fishing practices before consequences become severe and fishery closures or other socioeconomically disruptive interventions are required to protect species.

Author contributions: M.G.B. designed research; M.G.B., S.P., and D.T. performed research; and M.G.B., S.P., and D.T. wrote the paper.

The authors declare no conflict of interest.

See Commentary on page 15859.

[1]To whom correspondence may be addressed. E-mail: polasky@umn.edu or mgburgess@umn.edu.

This article contains supporting information online at www.pnas.org/lookup/suppl/doi:10.1073/pnas.1314472110/-/DCSupplemental.

Ocean fisheries. High-seas tuna and billfish have elicited recent conservation concern due to significant population declines and range contractions found in many species (17, 23, 24). Three of the populations in our study, bigeye tuna (*Thunnus obesus*) and both the northern and the southern striped marlin (*Tetrapturus audax*) populations, have been recently identified as experiencing overfishing—meaning their exploitation rates have exceeded the MSY exploitation rate (F_{MSY}) (24–27). A fourth, blue marlin (*Makaira nigricans*), whose overfishing status has been subject to considerable uncertainty (28), has undergone a significant population decline and range contraction (13, 23, 28). We determine whether our approach could have predicted threats to these four populations, using data from as early as the 1950s, and assess the threats predicted by the latest available data to all populations.

The Eventual Threat Index (*T*)

The central premise of our approach is that the shared threat of effort in a given multispecies fishery links the fates of species in a way that allows the fates of all species to be predicted if the fate of any one species can be predicted. The fates of some "key" species can be predicted based on their influence on the economic or regulatory factors that determine maximum fishing effort in the fishery. Other species' fates can be predicted by measuring their vulnerabilities to long-term depletion by the fishery relative to the key species. For the purposes of our approach, we define a "species" at the population level and a "fishery" as a group of fishermen using a particular type of gear to target a particular group of species in a particular region, with roughly uniform relative catch rates of the species (29).

For each fishery, *j*, we measure the "vulnerability" to long-term depletion of species *i* at time *t* [denoted $V_{ij}(t)$], using three population-specific pieces of data that are readily available for many fisheries: population size [$N(t)$] (e.g., ref. 30), average catch-per-unit effort [$CPUE(t)$] (e.g., ref. 31), and maximum per-capita growth rate (r) (e.g., refs. 30, 32):

$$V_{ij}(t) = \frac{CPUE_{ij}(t)}{r_i N_i(t)}. \quad [1]$$

Vulnerability measures the fraction of species *i*'s maximum population growth rate [$r_i N_i(t)$] lost on average to each unit of fishing effort (e.g., hooks, days fished, etc.) (10, 11). Because fishing effort is shared by all species, the fishery's relative long-term impacts on different species can be predicted by measuring their relative vulnerabilities as defined in Eq. **1** (Fig. 1*A*). We derive the mathematical properties of relative vulnerabilities in a general theoretical model in *SI Materials and Methods*. In general, effort levels greater than $1/V$ put a species on a path to extinction, as this implies the total catch rate ($CPUE*Effort$) is larger than the maximum population growth rate (rN).

If a fishery is profitable, effort increases until either profit declines to zero because commercially valued species become depleted (10, 11) or regulations prevent further increase because species protected by management become depleted (Fig. 1 *B* and *C*). Profitability or regulations thus impose an upper bound on fishing effort in the fishery that determines which species will likely experience a severe decline or extinction.

Except in rare cases (19, 33), a fishery would be expected to cease operation before all of its commercially valued species are driven extinct, due to a lack of profitability, regulatory intervention, or both (e.g., ref. 34). Thus, there is at least one species in most fisheries whose importance to the fishery's profits or regulations ensures that the fishery will close before this species is driven extinct. Because high profits and nonbinding limits on the exploitation of managed species in a fishery tend to lead to increases in effort (10, 11), most fisheries also have one or more commercially valued or managed species that are likely to be exploited at least at a minimum rate. Species having both of these properties are key species because their long-term fates are most easily predicted or bounded. We predict the long-term threat of current fishing practices to a given species by calculating its vulnerability relative to a key species in each fishery in which it is caught.

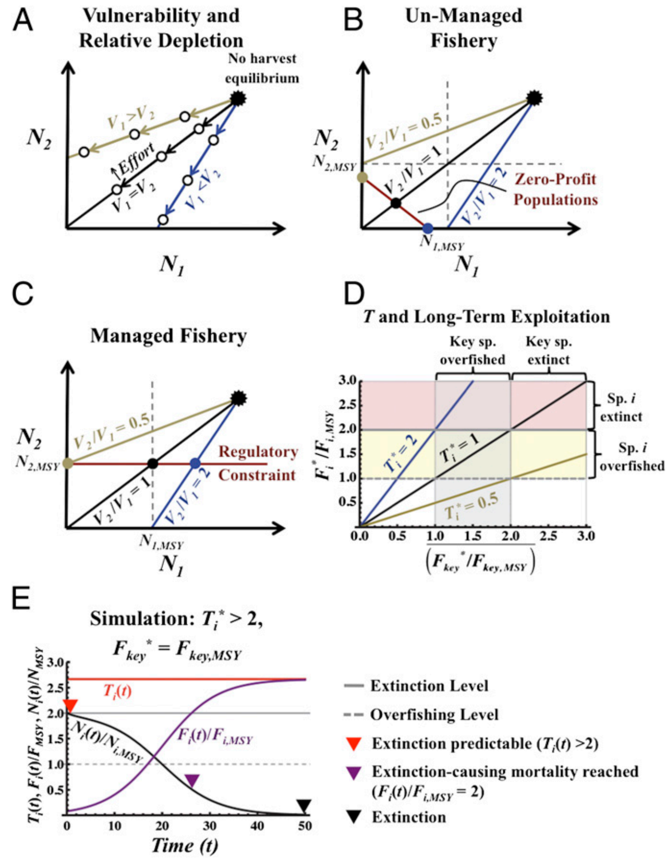

Fig. 1. General theory and simulated example. *A–D* illustrate the theoretical framework and *E* provides an illustrated example. Each panel assumes $r = 2F_{MSY}$ for all species, and all but *D* assume constant vulnerabilities (V). *A* illustrates how species' relative vulnerabilities determine relative depletion, which combined with effort determines long-term abundances for populations (open circles). Higher effort pushes the outcome farther down the set of possible abundances determined by species' relative vulnerabilities (blue, black, and yellow lines). *B* and *C* illustrate how relative vulnerabilities and profitability (*B*) or regulatory constraints (*C*) (dark red lines) jointly determine long-term species abundances (solid circles). *C* assumes that the fishery is managed to harvest species 2 at MSY. *D* illustrates the theoretical relationship between the long-term exploitation rate of species *i* (F_i^*/F_{MSY}) and the average long-term exploitation rate of the key species ($\overline{F_{key}^*/F_{Key,MSY}}$), as determined by the long-term T_i value (T_i^*), shown for $T_i = 2$ (blue), $T_i = 1$ (black), and $T_i = 0.5$ (yellow). For $T_i = 2$, species *i* will be harvested to extinction when the key species is harvested at MSY or overfished. In contrast, for $T_i = 0.5$, the key species would be harvested to extinction before species *i* would be overfished. *E* shows time trends of the eventual threat index ($T_i(t)$), mortality ($F_i(t)/F_{i,MSY}$), and abundance ($N_i(t)/N_{MSY}$) for the case of a bycatch species (*i*) caught in two fisheries whose technologies and relative fleet sizes do not change and where the key species in each fishery is harvested at MSY. Extinction of species *i* is predictable in year 0 whereas extinction causing mortality does not occur until year 26. Growth equations and parameter values for *E* are provided in *Materials and Methods*.

In a managed fishery, the most vulnerable species targeted by management is a likely key species, as fishing effort is likely to increase only until this species reaches the minimum population size or maximum exploitation rate allowed by management (Fig. 1*C*). In an unmanaged fishery, the species generating the most revenue is a likely key species, as its importance to the fishery's profits will likely prevent it from being either driven extinct or underexploited (10, 11). In the analysis presented here, we identify key species in this manner. However, our approach to threat prediction is robust to many other approaches to identifying key species (*SI Materials and Methods*). For instance, if a key species could be profitably driven extinct due to the presence of another valued species that is more robust, the other valued species would become the key long before the first was near extinction.

Fish species are typically caught in multiple fisheries so to be practical the threat measure must capture the vulnerability to harvest of each species across all of the fisheries in which it is caught. For each fishery, we measure its impact on species i relative to that fishery's key species at time t, using the ratio, $V_{ij}(t)/V_{key,j}(t)$. This ratio can also be measured by replacing measures of *CPUE* in Eq. **1** with total catch in the fishery, if this is easier to measure, as effort will cancel out ($Catch = CPUE*Effort$). We measure the combined threat of all fisheries to species i at time t by calculating the "eventual threat index", $T_i(t)$,

$$T_i(t) = \sum_j \left[\left(\frac{V_{ij}(t)}{V_{key,j}(t)} \right) \left(\frac{Catch_{key,jj}(t)}{\sum_k Catch_{key,jk}(t)} \right) \right]. \quad [2]$$

$T_i(t)$ sums the $V_{ij}(t)/V_{key,j}(t)$ ratios for all fisheries catching species i, including where species i is a key species, and weights the $V_{ij}(t)/V_{key,j}(t)$ for each fishery j by the catch of its key species in year t ($Catch_{key,jj}(t)$) as a fraction of its key species' total catch from all fisheries in year t ($\sum_k Catch_{key,jk}(t)$).

If fishing practices and relative efforts in different fisheries do not change, then $T_i(t)$ becomes a constant through time, denoted T_i*, even as total effort changes (*SI Materials and Methods*). Fishery managers commonly evaluate threats to populations by comparing their estimated abundances (N) and mortality rates (F, where $F = Catch/N$) to those producing MSY (N_{MSY} and F_{MSY}) (e.g., refs. 3, 4, 24–28, 30). With the common assumption in fisheries that the fishing mortality rate, F at MSY for a species, F_{MSY}, is half of its maximum growth rate, r (35), T_i* can be shown (*SI Materials and Methods*) to have the useful property

$$\frac{F_i^*}{F_{i,MSY}} = T_i^* \overline{\left(\frac{F_{key}^*}{F_{key,MSY}} \right)}, \quad [3a]$$

where F_i* is species i's long-term fishing mortality rate, and $\overline{\left(\frac{F_{key}^*}{F_{key,MSY}} \right)}$ is a weighted average of the long-term fishing mortality rates of the key species of fisheries catching species i. Thus, $T_i(t)$ predicts the long-term mortality rate (F) that current fishing practices at time t would eventually impose on species i relative to the key species of the fisheries in which it is caught, were these fishing practices to continue indefinitely (Fig. 1*D*).

Managed fisheries often aim to maintain their target species at their MSY populations (2–4). This would mean that $\overline{\left(\frac{F_{key}^*}{F_{key,MSY}} \right)} = 1$ if all fisheries were well managed, and consequently the fishing mortality rate of species i (F_i/F_{MSY}) would approach T_i* in the long term (i.e., $F_i^*/F_{i,MSY} = T_i^*$). Fig. 1*E* illustrates this property in a simulation model (*Materials and Methods*). Unmanaged fisheries tend to overfish their target species (10, 11) [i.e., $\overline{\left(\frac{F_{key}^*}{F_{key,MSY}} \right)} > 1$]. Because key species are unlikely to be driven extinct by their fisheries (10, 11, 34), it can be assumed that an upper bound on fishing effort is set by $F_{key}^* \leq r$ (i.e., harvest rate ≤ maximum growth rate) for all key species. Because we are assuming $F_{MSY} = r/2$, this implies $\overline{\left(\frac{F_{key}^*}{F_{key,MSY}} \right)} < 2$. Thus, it is reasonable to assume that

$$T_i^* \leq \frac{F_i^*}{F_{i,MSY}} < 2T_i^*. \quad [3b]$$

Under these assumptions, measured $T_i(t)$ values should be interpreted as implying that current fishing practices at time t pose a high threat of species i's eventual extinction if $T_i(t) \geq 2$ (because this implies $F_i^* \geq r_i$), a high threat of eventual overfishing and a possible threat of extinction with poor management if $1 < T_i(t) < 2$, a possible threat of overfishing with poor management if $0.5 < T_i(t) \leq 1$, and a very low threat of overfishing if $T_i(t) \leq 0.5$ (Fig. 1*D*). Fishing gear, targeting behaviors, and management often change in response to evolving technology (e.g., ref. 36), markets (e.g., ref. 37), or political climate. Thus, $T_i(t)$ should be remeasured on a regular basis.

If assuming that $r = 2F_{MSY}$ or that MSY is a measurable and desired target for management is inappropriate (e.g., ref. 38), our index, $T_i(t)$, can still be used to predict threats, but the threshold values for interpretation ($T_i(t)$ = 2, 1, 0.5) would need to be adjusted (*SI Materials and Methods*). Our approach can also be adapted to incorporate age structure, by altering the procedure for measuring vulnerabilities (*SI Materials and Methods*).

Case Study: Western and Central Pacific Tuna and Billfish

To test our approach, we use historical data for eight tuna and billfish populations of the Western and Central Pacific (39) to estimate yearly T values from the 1950s to the present time, using Eqs. **1** and **2**. We compare each population's earliest possible T and V estimates (1953–1967, depending on the population) to their observed abundance and exploitation trends from these early years up until the most recent year for which data are available (1997–2009, depending on the population) (Figs. 2–4) (24–28, 30, 40–44) (*SI Materials and Methods*). These populations are the northern and southern populations of Pacific albacore tuna (*Thunnus alalunga*), bigeye tuna (*T. obesus*), blue marlin (*M. nigricans*), the northern and southern Pacific striped marlin (*T. audax*), North Pacific swordfish (*Xiphias gladius*), and yellowfin tuna (*Thunnus albacares*). Northern and southern populations of some species are treated separately because they are considered ecologically distinct (25, 26, 40, 42, 43). We use international catch data from longline, purse-seine, and pole-and-line fisheries (31) (Fig. 3), together accounting for 92% of all reported tuna and swordfish catch in this region in 2010 (45). For the purposes of estimating T, we define "fisheries" spatially by dividing the Western and Central Pacific Fisheries Commission (WCPFC) Convention area (39) into 15 regions (Fig. S1) (~30° × 30°), having roughly uniform relative catch rates within fisheries (45). We also distinguish between shallow- and deep-set longline catch and between purse-seine catch from schools associated and unassociated with floating objects, as these are known to have different catch rates (46, 47). We also tried other ways of distinguishing fisheries for our analysis and found our predictions were robust to these alternatives (*SI Materials and Methods* and Fig. S2). We estimate historical T values, assuming open access, as there was little international management of these fisheries before the 1980s (48). For all populations, we find our T estimates robust to considerations of older data limitations (*SI Materials and Methods*). We use 3-y moving geometric averages of T to reduce noise. We compare T values to average annual fishing mortality rates (denoted U) (30) from the fisheries studied ($U_{Combined}$ = combined catch/average population biomass) (Fig. 2 and *SI Materials and Methods*) instead of instantaneous fishing mortality (F), as the latter is difficult to estimate without seasonal and size- or age-structured catch and population data, which are not publicly available for these fisheries (31). For the same reason, we also use average annual measures of *CPUE* and maximum per-capita growth rate in estimating V and T (*SI Materials and Methods*).

Longline fishing effort began to expand rapidly in the 1950s and 1960s, using predominantly shallow sets targeting bigeye and yellowfin tuna in northern and equatorial regions and albacore tuna in southern regions (31, 49) (Fig. 3 and Table S1). There was little effort in the purse-seine and pole-and-line fisheries (31). At this time, T estimates (Fig. 2) predicted that North Pacific swordfish and all three marlin populations were on paths

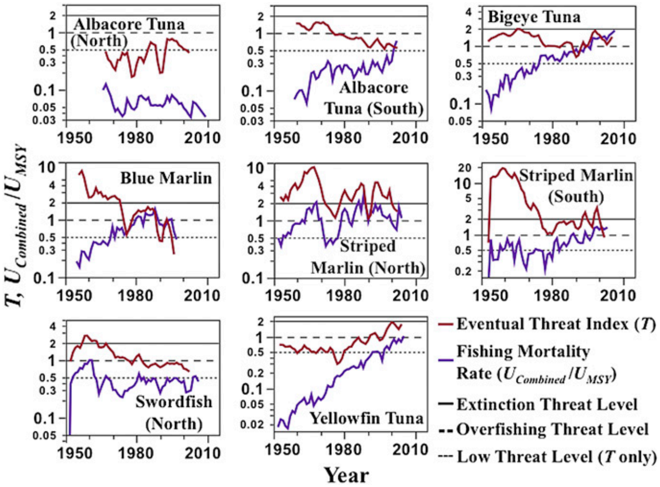

Fig. 2. Exploitation histories and estimable T values. A comparison of eventual threat index values [T (3-y geometric mean), red] to the combined fishing mortality rates ($U_{Combined}$) from longline, purse-seine, and pole-and-line fisheries as a fraction of the mortality rate producing MSY (U_{MSY}), ($U_{Combined}/U_{MSY}$, purple), for each population. Levels indicating high extinction threats (T, $U_{Combined}/U_{MSY}$ = 2) (solid black lines), high overfishing threats (T, $U_{Combined}/U_{MSY}$ = 1) (dashed black lines), and low overfishing threats (T = 0.5) (dotted black lines) are shown.

toward extinction ($T > 2$), South Pacific albacore and bigeye tuna were on paths toward overfishing ($1 < T < 2$), and there were low threats to yellowfin and North Pacific albacore tuna ($T \leq 0.5$). In the mid-1970s, the tuna-targeting longline fishery largely shifted toward using deeper sets, with many of the remaining shallow sets targeting swordfish (49) (Fig. 3 and Table S1). This shift in fishing technology led to reductions in the threat level predicted by T for most species (Figs. 2 and 3) because the profits from the shallow-set longline fishery were now heavily dependent in many places on swordfish, which has high vulnerability relative to other species (Table S1). This limited the capacity of the shallow-set swordfish fishery to threaten other species. Additionally, the catch rates of swordfish and albacore tuna were lower in the deep-set longline fisheries that were targeting bigeye and yellowfin. As a result of this technological shift, T estimates for North Pacific swordfish, South Pacific albacore tuna, and blue marlin no longer indicated a threat beginning in the late 1970s and continuing to the early 1990s (Figs. 2–4). Also in the 1970s, the purse-seine and pole-and-line fisheries began to expand, targeting primarily skipjack tuna (*Katsuwonus pelamis*), with yellowfin and bigeye tuna as significant by-catch (31, 47), particularly in purse-seine sets targeting schools associated with floating objects (47). This led to increases in T values for yellowfin and bigeye tuna. An eventual threat to yellowfin is predicted beginning in the early 1990s ($T > 1$) (Figs. 2 and 4) as an increasing fraction of purse-seine landings came from purse-seine sets targeting associated schools (Fig. 3).

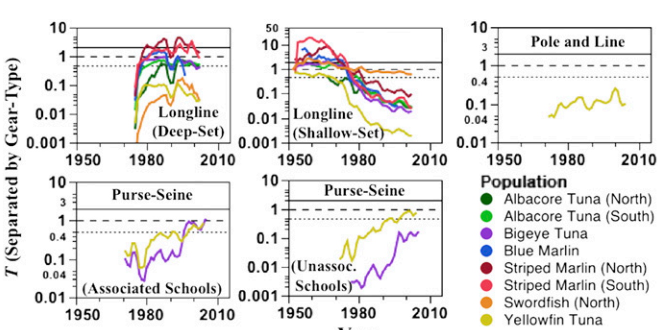

Fig. 3. Gear-specific threats. Fishing gear-specific estimates of threats (3-y geometric mean T values summed only over fisheries within each gear type) are shown. T values of 2 (solid line) (high extinction threat), 1 (dashed line) (high overfishing threat), and 0.5 (dotted line) (low overfishing threat) are highlighted. The shift in longline fishing toward deeper sets beginning in the 1970s led to a reduction in the threat caused by the shallow-set longline fishery to all populations and introduced a threat from the deep-set fishery to striped marlin populations. Purse-seine fisheries have recently begun to pose a threat to bigeye and yellowfin tuna.

T values from as early as the 1950s have consistently predicted threats of eventual extinction ($T \geq 2$) or overfishing ($T > 1$) from then-current fishing technologies for both northern and southern striped marlin populations (extinction), for blue marlin (extinction, pre-1975, and overfishing until the 1990s), and for bigeye tuna (overfishing) (Figs. 2 and 4). As predicted, all four of these populations eventually did experience mortality rates from these fisheries ($U_{Combined}$) exceeding U_{MSY}, but not until decades after T values predicted this (Fig. 2). Our predictions provided a warning beginning 40 y before this occurred for bigeye tuna and South Pacific striped marlin. These four populations also suffered significant population declines and have abundances currently either at (bigeye tuna) or below (striped marlin) N_{MSY} (25–27) (Fig. 4). Blue marlin's N_{MSY} is unknown (28). These depletions were only recognized three or more decades after they could have been predicted by measuring T (Fig. 4). Blue marlin has also experienced a significant range contraction in this region (23). The first stock assessments identifying these populations as overfished ($N < N_{MSY}$) or experiencing overfishing ($F > F_{MSY}$ or $U > U_{MSY}$) came out in the 1980s or later (25–28, 50, 51) (Fig. 4).

T values from the last two decades predict a threat of eventual overfishing to yellowfin tuna (Fig. 2). Although it has not yet become overfished ($N > N_{MSY}$, $U_{Combined} < U_{MSY}$) (Figs. 2 and 4) (41), its mortality rate is steadily increasing (Fig. 2), and it has undergone a marked population decline since T predicted a threat (Fig. 4). Early T values (1950–1970) indicated a threat to South Pacific albacore tuna (Fig. 2), and it suffered a significant decline during that period, leading to concern for an overfishing threat in an early stock assessment (52) (Fig. 4). More recent T values (post-1970s) have not indicated a threat (Fig. 2), and it is not currently considered to be overfished or experiencing overfishing (24, 40). Its population has been relatively stable (Fig. 4). Similarly, more recent T values for North Pacific swordfish and albacore tuna do not indicate a threat and neither population appears to be on a trajectory toward overfishing (42, 43) (Figs. 2 and 4).

Our most recent estimates of T, under the assumption of open access, suggest that the northern and southern striped marlin population and yellowfin and bigeye tuna face severe overfishing, and the striped marlin populations may face extinction (Figs. 2 and 4), if these fisheries are poorly managed and current technologies remain the same. The striped marlin populations are particularly threatened by deep-set longline fisheries; and yellowfin and bigeye tuna are particularly threatened by purse-seine fisheries targeting schools associated with floating objects (Fig. 3). Purse-seine fisheries targeting associated schools have received recent conservation attention (47). However, shallow-set longline fisheries have received far more conservation attention than deep-set fisheries, as shallow sets tend to have higher by-catch rates (46). Because of the key species' (bigeye and yellowfin tuna) relatively lower vulnerabilities in the deep-set fishery, our results suggest that effort in the deep-set fishery has a greater potential to profitably increase in the future. If this occurs, striped marlin would be highly impacted. Although a continued expansion of purse-seine fishing might mitigate some of the threat to the striped marlin by depleting yellowfin and bigeye tuna, the possible threat of deep-set longline fisheries merits further study.

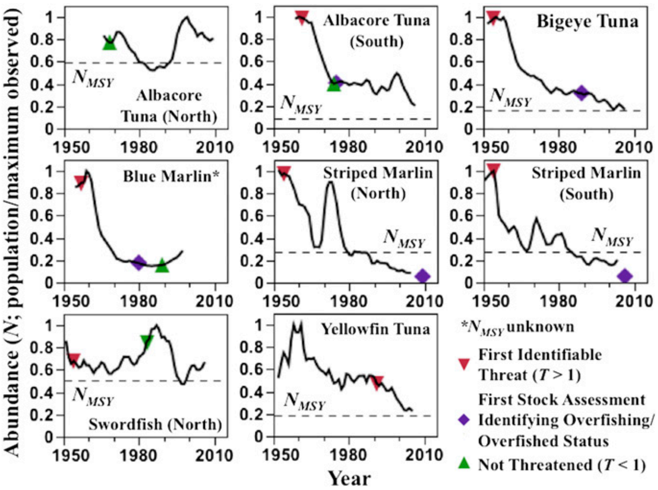

Fig. 4. Assessment histories and earliest identifiable threats. Shown is a comparison of when threats could have been identified by estimating T ($T > 1$: red triangles) vs. when populations were first assessed as overfished ($N < N_{MSY}$) or subject to overfishing ($F > F_{MSY}$) in stock assessments (purple diamonds). The populations' abundance trends are shown (black curves), each scaled to its maximum value in the series. Estimates of N_{MSY} (dashed lines) and dates when the eventual threat index no longer would have predicted an overfishing threat ($T < 1$) (green triangles) are also shown.

Discussion

For each of the four populations currently believed to be experiencing or to have recently experienced overfishing ($F > F_{MSY}$ or $U > U_{MSY}$) (24–28), our approach was able to predict a threat of eventual overfishing or extinction starting from as early as the 1950s (Figs. 2 and 4), before each began its dramatic population decline (Fig. 4). Moreover, for all populations except North Pacific albacore tuna, which has a very low mortality rate, estimates of T and $U_{Combined}/U_{MSY}$ appear to be converging (Fig. 2), consistent with the theory underlying the use of T as an eventual threat predictor (*SI Materials and Methods*). Because these results suggest that our approach can predict threats well in advance of high mortality rates and declines in abundance (Figs. 2 and 4), its use in these and other fisheries may provide time to adopt preventative management before fishery closures or other highly disruptive interventions are needed. Of the four populations predicted by our approach to be currently threatened, only the striped marlins are already severely overfished ($N < N_{MSY}$) (25–27, 41). Thus, it could be possible to avoid severe depletion of yellowfin and bigeye tuna in this region.

Multispecies tuna fisheries are also known to significantly impact sharks, sea turtles, and other by-catch species in the Pacific and elsewhere (7, 53–55). The slow population growth and high recent catch rates of these species suggest they likely have high vulnerabilities, and many could be threatened with extinction (7, 53–55). Our approach, along with recent advances in by-catch monitoring and data-poor abundance estimation methods (53–55), could be used to rapidly assess future extinction threats posed by current fishing practices to by-catch species worldwide.

Internationally cooperative management of large high-seas fisheries can be challenging (2, 3), but will be critical to protecting weak stocks and by-catch species in tuna and billfish fisheries (7, 17, 23, 24, 53–55). Managing each fishery to protect its most vulnerable species is one possible solution (56). However, such "weak-stock management" can cause faster-growing populations to be underexploited, which lowers profits and decreases food supplies (56). Trade-offs between conservation and yield could be mitigated by improving the species selectivity of fishing technologies (7, 36). Measurements of T and V/V_{key} can be used to set selectivity goals and monitor progress. Marine protected areas or other spatial fishing restrictions, which can provide refuges or reduce impacts on species' spawning grounds, are also useful management tools that have been implemented in some fisheries, including some Pacific tuna fisheries (57). Another option is to manage the relative sizes of different fisheries with different catch rates, for example the deep-set longline and purse-seine fisheries. This type of management could mitigate both over- and underharvesting without requiring technological advances by equalizing species' aggregate catch rates. Recent studies suggest that some spatial management strategies, such as maritime zoning (57) or setting regional catch quotas for fishery-wide goals (58), could accomplish this in Pacific tuna (57) and groundfish (58) fisheries.

Our approach, like all other approaches to threat assessment, is subject to uncertainties associated with measurement of populations' sizes, growth rates, and catch rates (30) and should be interpreted accordingly. Moreover, we strongly encourage the incorporation of size- or age-structure data when using our approach, whenever possible, and describe a possible method for incorporating age structure in *SI Materials and Methods*.

Our approach is designed to identify direct threats to populations from fisheries in which the populations of interest are not the key species. It is not relevant to a species that is the key species in most or all of the fisheries in which it is caught. It is for this reason that we do not present T values for skipjack tuna. Although many species severely threatened by fishing are weak stocks or by-catch species in multispecies fisheries (6–9), a few target species, such as southern bluefin tuna (17) and caviar-producing sturgeons (19), are threatened by their high and increasing rarity value (19). Our approach is also not designed to predict indirect threats from fishing mediated by species interactions. If $T_i > 2$, current practices are likely to lead to a harvest rate of species i that exceeds its maximum growth rate, guaranteeing extinction. However, extinction or severe depletion can be caused indirectly by fishing at a much lower level. For example, a recent sea otter decline in Alaska may be linked to a trophic cascade caused by offshore fisheries (59)—a threat our approach would not have detected. Further research is needed to develop preventative approaches for threats from species interactions and rarity value.

Growing human populations and rising food demands are putting increasing pressure on marine ecosystems (2–4). Long-term costs and societal impacts of conservation could be substantially reduced by shifting resources toward preventative measures, instead of rescuing already threatened species (60). Developing cost-effective approaches that can predict future threats to species is a valuable tool for conservation. Our results illustrate that a simple mechanistic theory has the potential to effectively predict species threats well into the future, thus allowing time for preventative management actions.

Materials and Methods

Mathematical derivations of the properties and generalizations of the eventual threat index, T, can be found in *SI Materials and Methods*. A detailed description of our data sources and methods for the case study can also be found in *SI Materials and Methods* (Figs. S1–S4). This includes population, catch, effort, and price data; estimates of population growth rates; estimates of populations' vulnerabilities; methods for determining the key species in each fishery; and an analysis exploring the sensitivity of our case-study results to older data limitations and different means of defining key species and fisheries.

Simulation Model: Fig. 1*E*. Fig. 1*E* shows the results of a simulated model designed to illustrate the properties of T in fisheries managed to exploit their target species at MSY. The model simulates two fisheries each catching three species. Fishery 1 targets species 1 and fishery 2 targets species 2, but both fisheries catch both species 1 and 2, as well as a by-catch species, *i*. All three species are assumed to have logistic growth and linear catch rates, such that the instantaneous rate of population change of species x (where $x = 1, 2, i$) at time t is given by

$$\frac{dN_x(t)}{dt} = r_x N_x(t)\left(1 - \frac{N_x(t)}{2N_{x,MSY}}\right) - q_{x1}N_x(t)E_1(t) - q_{x2}N_x(t)E_2(t). \quad [4]$$

Here, $E_j(t)$ is the level of effort in fishery j at time t, and q_{xj} is the per-capita per-unit-effort catch rate of species x in fishery j, which we assume is constant in this model. Vulnerability, $V_{xj}(t) = q_{xj}/r_x$ is constant. Fishing effort in both fisheries (j, k = 1, 2; $k \neq j$) grows according to Eq. **5**:

$$\frac{dE_j(t)}{dt} = aE_j(t)\left(0.5r_j - q_{jj}E_j(t) - q_{jk}E_k(t)\right). \qquad [5]$$

Here, a is a constant determining the adjustment rate of effort to the target species exploitation rate relative to its target rate (F_{MSY}). We use the following parameter values: $\{N_{x,MSY} = 1, N_x(0) = 2$ for all x; $E_1(0) = E_2(0) = 0.1$; $r_1 = r_2 = 1$; $r_i = 0.5$; $q_{11} = q_{22} = q_{i1} = q_{i2} = 0.1$; $q_{12} = q_{21} = 0.05$; $a = 0.35\}$. Species 1 is the key species in fishery 1, and species 2 is the key species in fishery 2 for the calculation of $T_i(t)$.

ACKNOWLEDGMENTS. We thank Steve Gaines, Paul Venturelli, Chris Costello, Belinda Befort, Keith Criddle, and two reviewers for their comments and Jon Brodziak, Daniel Ricard, and Pierre Kleiber for their assistance with stock assessment data. This work was supported by the University of Minnesota and by the Natural Sciences and Engineering Research Council of Canada (Postgraduate Scholarship D3-389196-2010 to M.G.B.).

1. Godfray HC, et al. (2010) Food security: The challenge of feeding 9 billion people. *Science* 327(5967):812–818.
2. Beddington JR, Agnew DJ, Clark CW (2007) Current problems in the management of marine fisheries. *Science* 316(5832):1713–1716.
3. Worm B, et al. (2009) Rebuilding global fisheries. *Science* 325(5940):578–585.
4. Costello C, et al. (2012) Status and solutions for the world's unassessed fisheries. *Science* 338(6106):517–520.
5. Hutchings JA, Reynolds JD (2004) Marine fish population collapses: Consequences for recovery and extinction risk. *Bioscience* 54:298–309.
6. Hilborn R (1985) Apparent stock-recruitment relationships in mixed stock fisheries. *Can J Fish Aquat Sci* 42:718–723.
7. Lewison RL, Crowder LB, Read AJ, Freeman SA (2004) Understanding the impacts of fisheries bycatch on marine megafauna. *Trends Ecol Evol* 19:598–604.
8. Hall MA, Alverson DL, Metuzals KI (2000) By-catch: Problems and solutions. *Mar Pollut Bull* 41:204–219.
9. Boyce JR (1996) An economic analysis of the fisheries by-catch problem. *J Environ Econ Manage* 31:314–336.
10. Clark CW (1976) *Mathematical Bioeconomics: The Optimal Management of Renewable Resources* (Wiley, New York).
11. Clark CW (1985) *Bioeconomic Modelling and Fisheries Management* (Wiley, New York).
12. Whitmarsh D, Pipitone C, Badalamenti F, D'Anna G (2003) The economic sustainability of artisanal fisheries: The case of the trawl ban in the Gulf of Castellamare, NW Sicily. *Mar Policy* 27:489–497.
13. International Union for the Conservation of Nature (2011) *IUCN Red List of Threatened Species. Version 2011.2* (International Union for the Conservation of Nature, Gland, Switzerland). Available at www.iucnredlist.org. Accessed August 27, 2013.
14. Mace GM, et al. (2008) Quantification of extinction risk: IUCN's system for classifying threatened species. *Conserv Biol* 22(6):1424–1442.
15. Cadima EL (2003) *Fish Stock Assessment Manual*, FAO Fisheries Technical Paper 393 (Food and Agriculture Organization of the United Nations, Rome).
16. Christensen V, Walters CJ (2004) Ecopath with Ecosim: Methods, capabilities and limitations. *Ecol Modell* 172(2):109–139.
17. Collette BB, et al. (2011) Conservation. High value and long life—double jeopardy for tunas and billfishes. *Science* 333(6040):291–292.
18. Roberts CM, Hawkins JP (1999) Extinction risk in the sea. *Trends Ecol Evol* 14(6):241–246.
19. Courchamp F, et al. (2006) Rarity value and species extinction: The anthropogenic Allee effect. *PLoS Biol* 4(12):e415.
20. Dulvy NK, et al. (2004) Methods of assessing extinction risk in marine fishes. *Fish Fish* 5:255–276.
21. Cheung WWL, Pitcher TJ, Pauly D (2005) A fuzzy logic expert system to estimate intrinsic extinction vulnerabilities of marine fishes to fishing. *Biol Conserv* 124(1):97–111.
22. Le Quesne WJF, Jennings S (2012) Predicting species vulnerability with minimal data to support rapid risk assessment of fishing impacts on biodiversity. *J Appl Ecol* 49(1):20–28.
23. Worm B, Tittensor DP (2011) Range contraction in large pelagic predators. *Proc Natl Acad Sci USA* 108(29):11942–11947.
24. Juan-Jordá MJ, Mosqueira I, Cooper AB, Freire J, Dulvy NK (2011) Global population trajectories of tunas and their relatives. *Proc Natl Acad Sci USA* 108(51):20650–20655.
25. Langley A, et al. (2006) *Stock Assessment of the Striped Marlin (Tetrapturus audax) in the Southwest Pacific Ocean*, WCPFC-SC2-2006/SA WP-6 (Western and Central Pacific Fisheries Commission, Kolonia, Federated States of Micronesia).
26. Brodziak J, Piner K (2009) Model averaging and probable status of North Pacific striped marlin, *Tetrapturus audax*. *Can J Fish Aquat Sci* 67:793–805.
27. Harley S, Hoyle S, Williams P, Hampton J, Kiebler P (2010) *Stock Assessment of Bigeye Tuna in the Western and Central Pacific Ocean*, WCPFC-SC6-2010/SA-WP-04 (Western and Central Pacific Fisheries Commission, Kolonia, Federated States of Micronesia).
28. Kleiber P, Hinton MG, Uozumi Y (2003) Assessment of blue marlin (*Makaira nigricans*) in the Pacific using MULTIFAN-CL. *Mar Freshw Res* 54:349–360.
29. Branch TA, Hilborn R, Bogazzi E (2005) Escaping the tyranny of the grid: A more realistic way of defining fishing opportunities. *Can J Fish Aquat Sci* 56:2404–2419.
30. Ricard D, Minto D, Jensen OP, Baum JK (2012) Evaluating the knowledge base and status of commercially exploited marine species with the RAM Legacy Stock Assessment Database. *Fish Fish* 13:380–398.
31. Western and Central Pacific Fisheries Commission (2012) *WCPFC Public Domain Aggregated Catch/Effort Data* (Western and Central Pacific Fisheries Commission, Kolonia, Federated States of Micronesia). Available at www.wcpfc.int/wcpfc-public-domain-aggregated-catcheffort-data-download-page?sid=2618). Accessed March 1, 2012.
32. Myers RA, Bowen KG, Barrowman NJ (1999) Maximum reproductive rate of fish at low population sizes. *Can J Fish Aquat Sci* 56:2404–2419.
33. Clark CW (1973) Profit maximization and the extinction of animal species. *J Polit Econ* 81:950–961.
34. Hutchings JA, Myers RA (1996) What can be learned from the collapse of a renewable resource? Atlantic cod, *Gadus morhua*, of Newfoundland and Labrador. *Can J Fish Aquat Sci* 51:2126–2146.
35. Schaefer MB (1954) Some aspects of populations important to the management of the commercial marine fisheries. *Bull I-ATCC* 1(2):27–56.
36. Gilman E, et al. (2006) Reducing sea turtle by-catch in pelagic longline fisheries. *Fish Fish* 7(1):1–22.
37. Delgado CL, et al. (2003) *Fish to 2020: Supply and Demand in Changing Global Fish Markets* (International Food Policy Research Institute, Washington, DC, and World Fish Center, Penang, Malaysia).
38. Johannes RE (1998) The case for data-less marine resource management: Examples from tropical nearshore finfisheries. *Trends Ecol Evol* 13(6):243–246.
39. Western and Central Pacific Fisheries Commission (2013) *Convention Area Map* (Western and Central Pacific Fisheries Commission, Kolonia, Federated States of Micronesia). Available at www.wcpfc.int/convention-area-map. Accessed August 27, 2013.
40. Hoyle S (2011) *Stock Assessment of Albacore Tuna in the South Pacific Ocean*, WCPFC-SC&-2011/SA-WP-06 (Western and Central Pacific Fisheries Commission, Kolonia, Federated States of Micronesia).
41. Langley A, et al. (2009) *Stock Assessment of Yellowfin Tuna in the Western and Central Pacific Ocean*, WCPFC-SC5-2005/SA-WP-03 (Western and Central Pacific Fisheries Commission, Kolonia, Federated States of Micronesia).
42. International Scientific Committee for Tuna and Tuna-Like Species in the North-Pacific Ocean (2011) *Stock Assessment of Albacore Tuna in the North Pacific Ocean in 2011*, Report of the Albacore Working Group Stock Assessment Workshop, 424-8633 (ISC, Shizuoka, Japan).
43. Brodziak J, Ishimura G (2010) *Stock Assessment of North Pacific Swordfish (Xiphias gladius) in 2009*, NOAA Administrative Report H-10-01 (NOAA, Honolulu).
44. Langley A, Hampton J (2008) *Stock Assessment of Skipjack Tuna in the Western and Central Pacific Ocean*, WCPFC-SC4-2008/SA-WP-4 (Western and Central Pacific Fisheries Commission, Kolonia, Federated States of Micronesia).
45. Western and Central Pacific Fisheries Commission (2011) *Tuna Fishery Yearbook 2010* (Western and Central Pacific Fisheries Commission, Kolonia, Federated States of Micronesia). Available at www.wcpfc.int/statistical-bulletins. Accessed June 8, 2012.
46. Crowder LB, Myers RA (2001) *Report to Pew Charitable Trusts: A Comprehensive Study of the Ecological Impacts of the Worldwide Pelagic Longline Industry*. Available at http://moray.ml.duke.edu/faculty/crowder/research/crowder_and_myers_Mar_2002.pdf. Accessed August 4, 2011.
47. Secretariat of the Pacific Community (2001) *Report of the Fourteenth Meeting of the Standing Committee on Tuna and Billfish* (Secretariat of the Pacific Community, Noumea, New Caledonia). Available at http://www.spc.int/DigitalLibrary/Doc/FAME/Meetings/SCTB/14/RPT_SCTB14.pdf. Accessed August 27, 2013.
48. Secretariat of the Pacific Community (2012) *The Oceanic Fisheries Programme* (Secretariat of the Pacific Community, Noumea, New Caledonia). Available at www.spc.int/oceanfish/en/the-oceanic-fisheries-programme. Accessed August 27, 2013.
49. Kleiber P, et al. (2009) *North Pacific Blue Shark Assessment*, NOAA Technical Memorandum NMFS-PIFSC-17 (NOAA, Honolulu).
50. Miyabe N (1989) Preliminary stock assessment of Pacific bigeye tuna. *Report:* The 3rd *Southeast Asian Tuna Conference*, Indo-Pacific Tuna Development and Management Programme (Food and Agriculture Organization of the United Nations, Rome), pp 122–130.
51. Yuen HSH, Miyake PM (1980) Blue marlin, *Makaira nigricans. Summary Report of the Billfish Stock Assessment Workshop Pacific Resources*, NOAA-TM-NMFS-SWFC-5, ed Shomura RS (United States National Marine Fisheries Service, Washington, DC), pp 13–19.
52. Skillman RA (1975) An assessment of the south Pacific albacore, *Thunnus alalunga*, fishery, 1953-72. *Mar Fish Rev* 37(3):9–17.
53. Clarke SC, Harley SJ, Hoyle SD, Rice JS (2013) Population trends in Pacific Oceanic sharks and the utility of regulations on shark finning. *Conserv Biol* 27(1):197–209.
54. Worm B, et al. (2013) Global catches, exploitation rates, and rebuilding options for sharks. *Mar Policy* 40:194–204.
55. Lewison RL, Freeman SA, Crowder LB (2004) Quantifying the effects of fisheries on threatened species: The impact of pelagic longlines on loggerhead and leatherback sea turtles. *Ecol Lett* 7:221–231.
56. Hilborn R, Punt AE, Orensanz J (2004) Beyond band-aids in fisheries management: Fixing world fisheries. *Bull Mar Sci* 74:493–507.
57. Sibert J, Senina I, Lehodey P, Hampton J (2012) Shifting from marine reserves to maritime zoning for conservation of Pacific bigeye tuna (*Thunnus obesus*). *Proc Natl Acad Sci USA* 109(44):18221–18225.
58. Dougherty DT, Hilborn R, Punt AE, Stewart IJ (2013) Modeling co-occurring species: A simulation study on the effects of spatial scale for setting management strategies. *Can J Fish Aquat Sci* 70(1):49–56.
59. Estes JA, Tinker MT, Williams TM, Doak DF (1998) Killer whale predation on sea otters linking oceanic and nearshore ecosystems. *Science* 282(5388):473–476.
60. Wilson HB, Joseph LN, Moore AL, Possingham HP (2011) When should we save the most endangered species? *Ecol Lett* 14(9):886–890.