



Extinction Risk and Overfishing: Reconciling Conservation and Fisheries Perspectives on the Status of Marine Fishes

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Anthropogenic disturbances are ubiquitous in the ocean, but their impacts on marine species are hotly debated. We evaluated marine fish statuses using conservation (Red List threatened or not) and fisheries (above or below reference points) metrics, compared their alignment, and diagnosed why discrepancies arise. Whereas only 13.5% of Red Listed marine fishes ($n=2952$) are threatened, 40% and 21% of populations with stock assessments ($n=166$) currently are below their more conservative and riskier reference points, respectively. Conservation and fisheries metrics aligned well (70.5% to 80.7%), despite their mathematical disconnect. Red Listings were not biased towards exaggerating threat status, and egregious errors, where populations were categorized at opposite extremes of fisheries and conservation metrics, were rare. Our analyses suggest conservation and fisheries scientists will agree on the statuses of exploited marine fishes in most cases, leaving only the question of appropriate management responses for populations of mutual concern still unresolved.

Human impacts on natural ecosystems are diverse and accelerating^{1,2}. On land, where the primary threat to wildlife is habitat loss, recent comprehensive assessments of birds, mammals, and amphibians have revealed 13%, 21%, and 30% of these species to be threatened with a heightened risk of extinction, respectively³. But whereas there is a general consensus in the scientific community about the status of terrestrial species^{3,4}, the state of marine species, and in particular marine fishes, remains deeply controversial^{5–10}.

Much of the controversy over the status of marine fishes can be traced to divergent beliefs about how these species should be regarded - as commodities to be managed for maximum productivity, or as wildlife, and integral components of diverse ecosystems^{11,12}. Within fisheries contexts, the most valuable populations are evaluated using complex population dynamics models, termed stock assessments, that estimate biomass trajectories as well as reference points against which to benchmark population status¹³. In contrast, conservation evaluations typically focus on extinction risk; for exploited marine species this is most commonly evaluated against the rate of change in abundance¹⁴. Under the most widely used conservation framework, the International Union for Conservation of Nature's (IUCN) Red List of Threatened Species, species that have declined $\geq 50\%$ within the most recent ten year or three generation period (whichever is longer) are considered to be threatened with extinction¹⁵.

A longstanding and unresolved aspect of the debate is the relevance of Red List evaluations to marine fishes. Critics have argued that these conservation evaluations exaggerate threat status for marine fishes, positing these species have low extinction risk relative to other vertebrates, may still number in the millions of individuals when listed as threatened, and that declines in abundance are usually the result of managed exploitation^{16–22}. Embedded in these criticisms is the question of whether Red List and fisheries assessments disagree as to which populations are in trouble, which is our focus herein, or whether they agree but still differ as to what the appropriate management response should be for populations deemed to be in trouble. Disagreement about the latter stems from the fact that there are significant biological differences between falling below a fishery reference point, which might signal impaired productivity or recruitment, and being threatened with extinction. While populations threatened with extinction require bold management action, such as mandatory prohibitions on all forms of human-induced mortality, overfished ones may require only a moderate management response, such as catch

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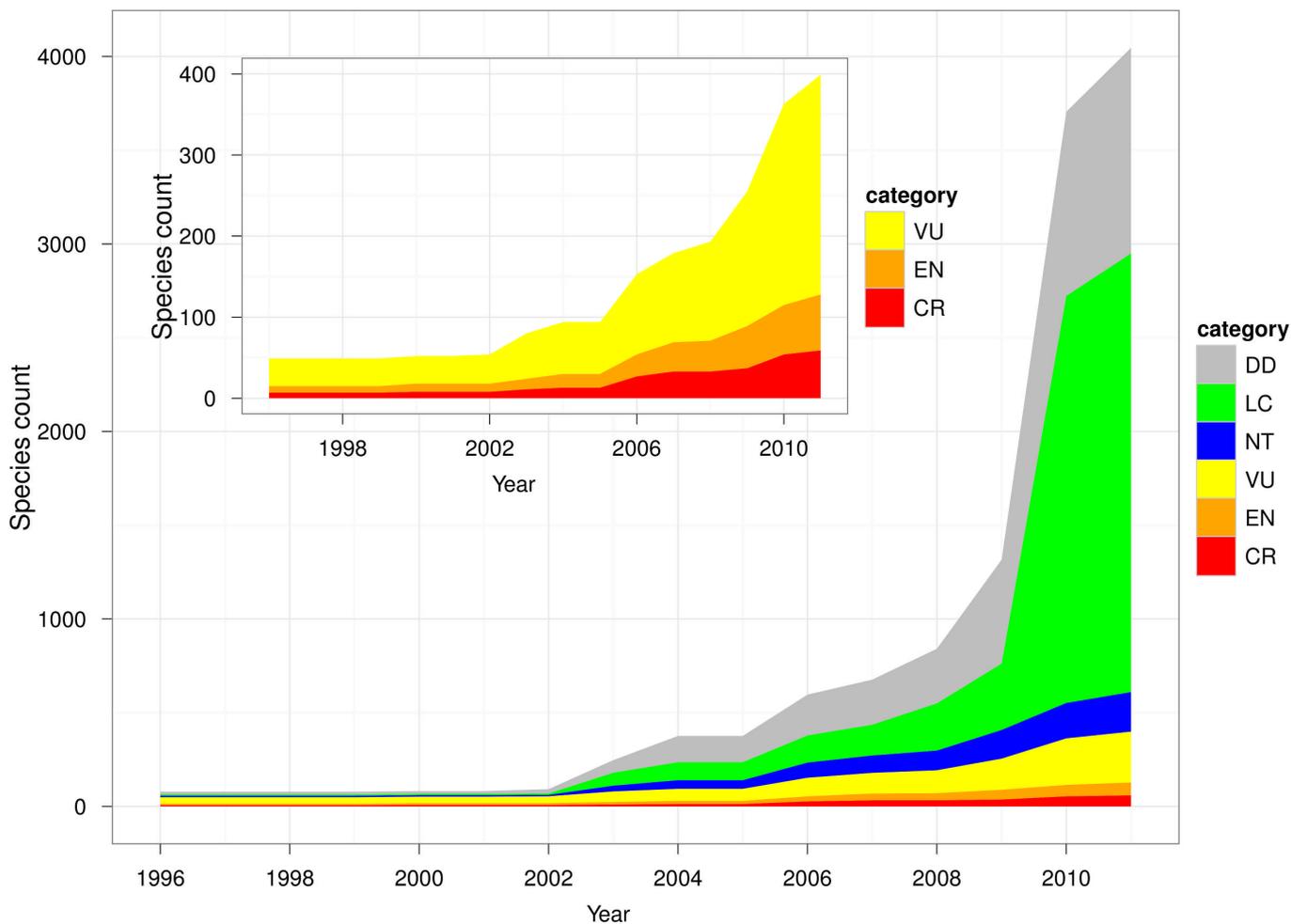


Figure 1 | Total number of marine fish species on the IUCN Red List each year by category. Red List categories are Data Deficient (DD), Least Concern (LC), Near Threatened (NT), or one of the three threatened categories, Vulnerable (VU), Endangered (EN), Critically Endangered (CR). Inset is expanded view of the species listed in threatened categories: VU, EN, or CR.

restrictions to stop or reverse their declines. Critics argue that, in the worst cases, threat listings could lead to unnecessary fisheries closures with high associated socioeconomic costs²³. Despite these concerns, momentum for marine fish conservation listings is growing (Figure 1^{24,25}). In light of this trend, and because the relevance of extinction risk criteria to marine fishes and the state of marine fisheries are both still hotly debated^{15,7,8,26–29}, there is an urgent need to understand why fisheries scientists’ and conservation biologists’ perceptions about the status of marine fishes differ.

Here, we take a critical step toward resolving this debate by systematically evaluating two of its central questions: 1) What is the status of marine fishes according to fisheries (above or below reference points) and conservation (Red List threatened or not) metrics? and 2) How well do these metrics align? We hypothesize that if the Red List is an accurate measure of extinction risk then comparing a population’s Red List status with its fishery status should result in poor alignment, since falling below a fishery reference point is not generally considered equivalent to heightened extinction risk. In contrast, if alignment between these metrics is high, it suggests that the Red List exaggerates extinction risk but shows that the two metrics do provide consistent measures of when a population is considered to be in trouble and requiring improved management measures. We used the IUCN Red List (Version 2011.2²⁴) and a new compilation of fisheries stock assessments from around the world (updated from Ricard et al.³⁰), to first summarize the extinction risk categorizations of the 4048 marine fish species on the Red List, and the fisheries statuses of 166 assessed marine fish populations relative to

their reference points. Direct comparison of conservation and fishery statuses are challenging because Red List evaluations typically are conducted at the species, not population, level and because few populations with stock assessments also have recent Red Listings ($n=31$)^{15,30}. To facilitate such a comparison, we assigned each assessed marine fish population to a Red List Category using the most common IUCN Criteria (A1), which measures the proportional change in the mature component of populations over the longer of ten years or three generations¹⁵. We then quantified the alignment of these two metrics using a hits, misses, false alarms framework³¹ (Table 1), and diagnosed why discrepancies occur.

Table 1 | Framework for assessing the performance of the IUCN Red List (Criterion A1) in relation to fisheries reference points. The fishery status categories of “OK” or “In trouble” correspond to whether the biomass of the population was above or below its fishery reference point (e.g. B_{msy} or B_{pa}), respectively. The IUCN Red List status of threatened includes populations fitting the Red List Critically Endangered, Endangered, and Vulnerable categories

Fishery Status	IUCN Red List status (%)	
	Threatened	Not threatened
OK	False Alarm	Hit (True negative)
In trouble	Hit (True positive)	Miss



Results

Status of marine fishes. We first evaluated the fishery status of each assessed population by comparing its current adult biomass to the upper and lower reference points from its stock assessment. Because there is no consensus amongst fisheries scientists as to which reference point is most robust, different management agencies use different types of reference points. Many fisheries management agencies, including the U.S. and Canada, use reference points related to the concept of maximum sustainable yield (MSY): B_{msy} , the population biomass that should provide the MSY is often considered by jurisdictions as a fisheries target. Increasingly, however, it is recognized both from economic^{40,41} and ecosystem^{53,54} perspectives that it is beneficial to maintain populations above B_{msy} , and thus it would be better regarded as a limit. Still, in at least the U.S. and Australia, $0.5B_{msy}$ is used as the lower limit^{33,52}. Thus we used B_{msy} as an upper, and $0.5B_{msy}$ as a lower, reference point in our analyses of populations with MSY based reference

points. Populations in Europe are benchmarked against a lower reference point B_{lim} (B_{lim}), the biomass below which recruitment is likely to be impaired, and an upper one $B_{precautionary}$ (B_{pa}), meant to provide a buffer above B_{lim} .³² We note that because MSY is a measure of population productivity, there is no fixed proportion of B_{msy} for all populations below which recruitment is impaired, nor is there a direct translation between B_{msy} and B_{pa} . We included both types of reference points in our analyses because they are the benchmarks used by the fisheries management agencies themselves to flag populations they consider to be in trouble.

Forty percent ($n=67$) of assessed marine fish populations currently are below their upper (more conservative) reference point (B_{pa} or B_{msy}), and over half of these populations ($n=35$, 21% of total) also are below their lower (riskier) reference point (B_{lim} or $0.5B_{msy}$; Figure 2A and B). Of these overfished populations, five U.S. ones (Georges Bank Atlantic cod (*Gadus morhua*, Figure 3A), southern New England-Mid Atlantic winter flounder (*Pseudopleuronectes*

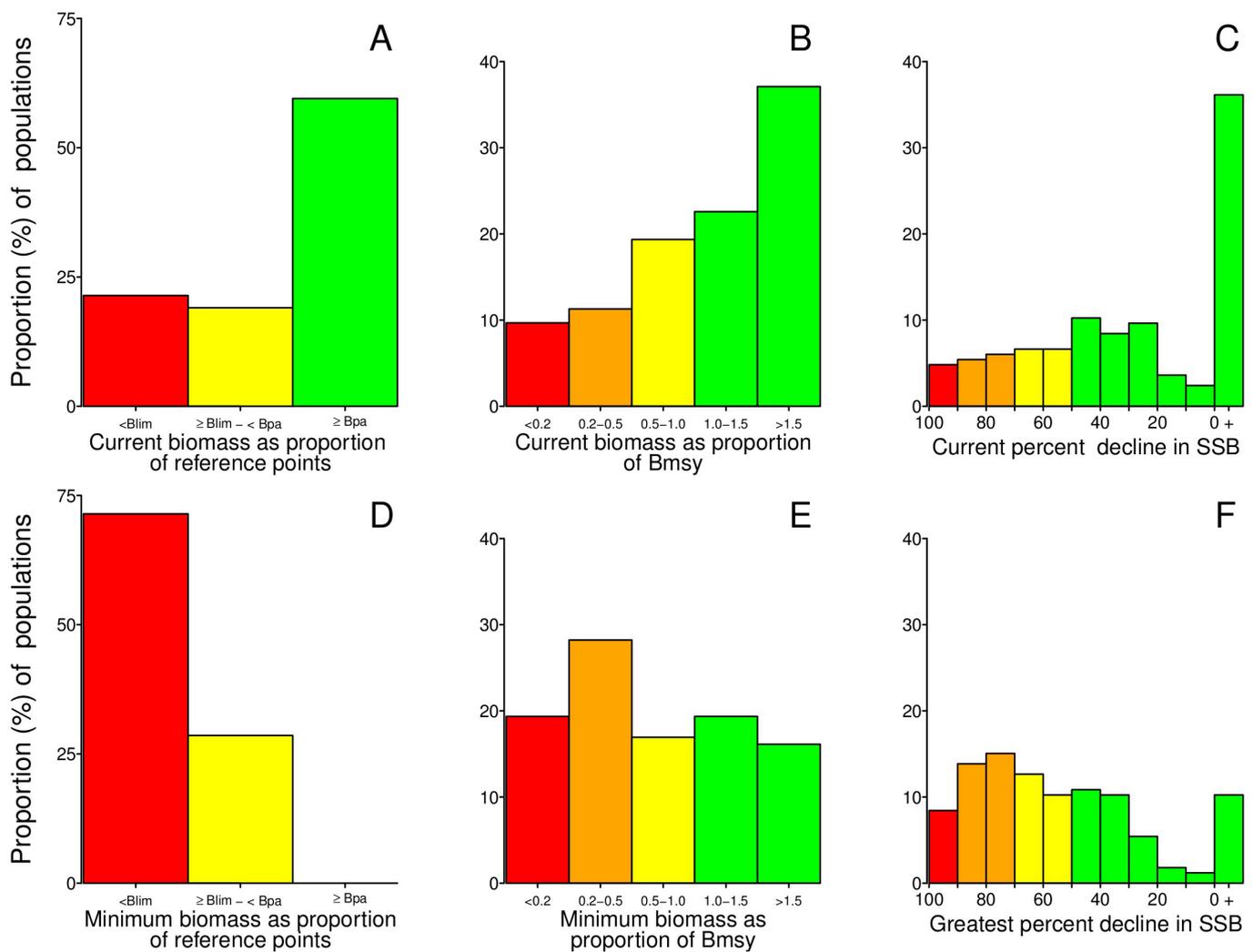


Figure 2 | Proportion (%) of assessed marine fish populations that currently meet (A–C), or have ever met (D–F), fisheries or conservation criteria for concern. (A) Current adult biomass of European populations ($n=42$) as a proportion of their B_{pa} and B_{lim} reference points, and (D) the minimum adult biomass ever experienced by those same populations as a proportion of their reference points. Colors correspond to fisheries threat level: above upper ICES reference point B_{pa} (green), between upper and lower ICES reference points (yellow), and below B_{lim} (red); (B) Current adult biomass of all other assessed populations ($n=124$) as a proportion of their B_{msy} reference point, and (E) the minimum adult biomass ever experienced by those same populations as a proportion of their B_{msy} reference point. Colors correspond to increasing threat, from not overfished (green) through to overfished (orange and red). (C) Estimated percent change in adult biomass for each population ($n=166$) from the most recent year back over the longer of ten years or three generations, and the corresponding IUCN Red List category: CR (red), EN (orange), VU (yellow), or not threatened (green), under Criterion A1. (F) Estimated greatest percent decline in adult biomass for the same populations ($n=166$) over the longer of ten years or three generations, and the corresponding IUCN Red List category, as above.

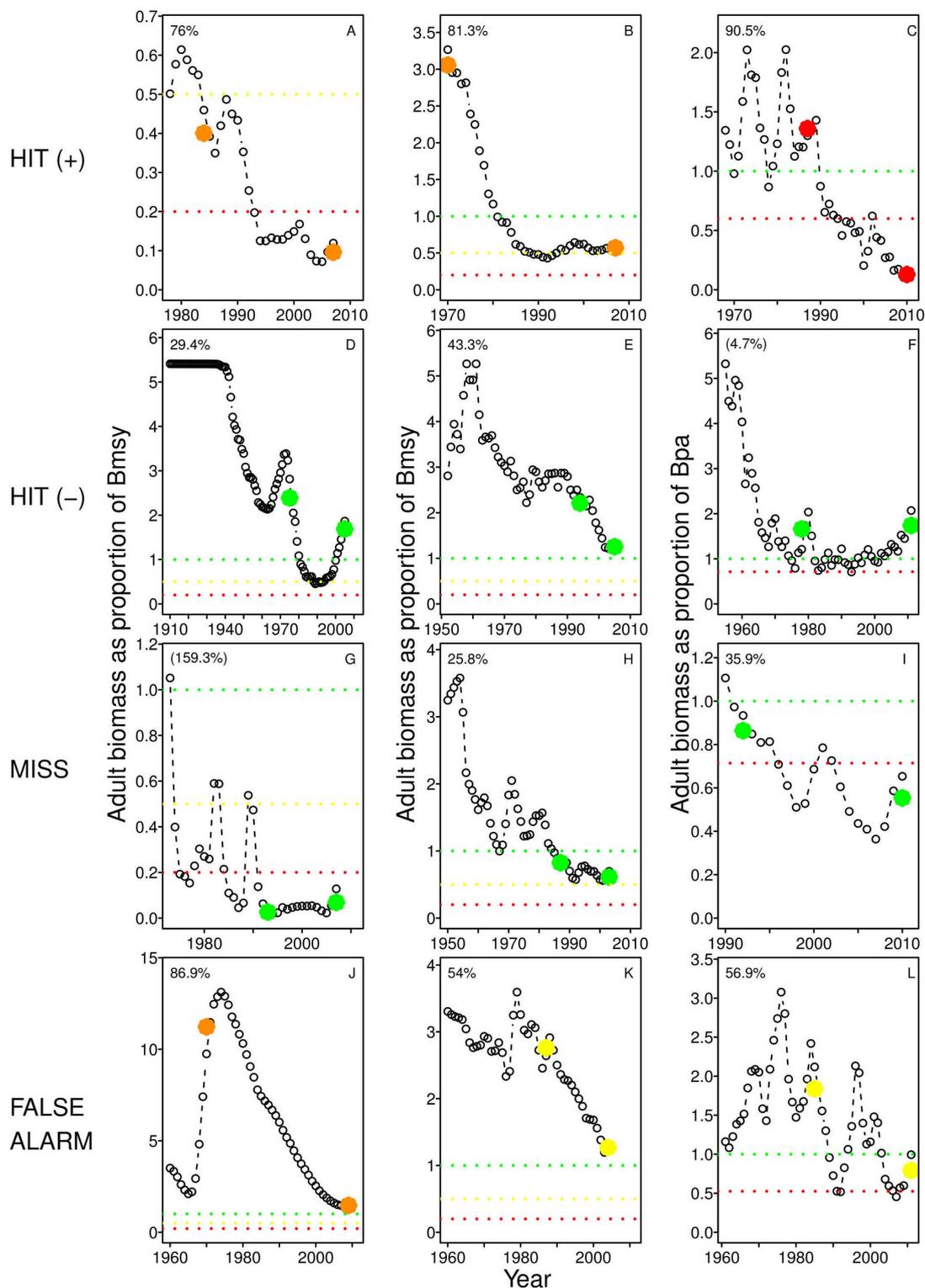


Figure 3 | Time series of adult biomass illustrating cases of alignment and misalignment. Populations are organized by management region: US (left column), non-US (middle column), or Europe (right column), and illustrate cases where the current fisheries reference points and estimated IUCN Red List status (Criterion A1) align (positive hits (top row) or negative hits (2nd row)), where the Red List would miss listing an overfished population as threatened (3rd row), or would list a population that is not considered overfished as threatened, producing a false alarm (bottom row): (A) Georges Bank Atlantic cod (*Gadus morhua*), (B) Atlantic bluefin tuna (*Thunnus thynnus*), (C) Irish Sea Atlantic cod (*G. morhua*), (D) U.S. northern Pacific Coast petrale sole (*Eopsetta jordani*), (E) Central western Pacific yellowfin tuna (*Thunnus albacares*), (F) Iceland cod (*G. morhua*), (G) Southern New England-Mid Atlantic yellowtail flounder (*Limanda ferruginea*), (H) Western Pacific Ocean striped marlin (*Kajikia audax*), (I) North Sea and eastern Channel whiting (*Merlangius merlangus*), (J) Bering Sea and Aleutian Islands Greenland turbot (*Reinhardtius hippoglossoides*), (K) Indian Ocean bigeye tuna (*T. obesus*), and (L) Faroe Plateau Atlantic cod (*G. morhua*). Note (L) is only a false alarm from the perspective of its lower fisheries reference point. Colored circles correspond to IUCN Red List categories: Critically Endangered (red), Endangered (orange), Vulnerable (yellow), or not threatened (green); associated estimated decline is located in the upper left of each plot. Colored dotted lines correspond to fisheries reference points: B_{msy} or B_{pa} (green), $0.5B_{msy}$ (yellow), $0.2B_{msy}$ or B_{lim} (red).



Table 2 | The proportion (%) of populations meeting each of four possible alignment outcomes (positive hit, negative hit, miss or false alarm) under four different scenarios. A) Current estimated Red List status or B) Estimated Red List status following the population's greatest decline, each compared to upper (more conservative; B_{msy} or B_{pa}) or lower (riskier; $0.5B_{msy}$ or B_{lim}) reference points

	Ref. point	Hit (+ve)	Hit (-ve)	Miss	False Alarm	# of populations
A) Current Status	Upper	22.9	53.0	17.5	6.6	166
	Lower	15.7	65.1	5.4	13.9	166
B) Greatest Decline	Upper	47.0	33.1	6.6	13.3	166
	Lower	32.5	38.0	1.8	27.7	166

americanus) and yellowtail flounder (*Limanda ferruginea*, Figure 3G), southern Atlantic coast red snapper (*Lutjanus campechanus*), and southern California cowcod (*Sebastes levis*) appear to be in the worst shape, having each declined to less than 10% of their upper reference points (Table S2).

In comparison, 29.5% ($n=49$) of assessed populations currently would be classified as threatened on the Red List (Criterion A1; Figure 2C), almost midway between the numbers considered to be in trouble from conservative and risky fisheries perspectives. Of these threatened populations, eight (4.8% of total) have declined by a sufficient amount ($\geq 90\%$) to be classified as Critically Endangered (CR): U.S. populations of snowy grouper (*Epinephelus niveatus*), southern California cowcod (*S. levis*), and red snapper (*L. campechanus*) on the southern Atlantic coast and Gulf of Mexico; blue warehou (*Seriola lalandi*) and orange roughy (*Hoplostethus atlanticus*) in Australia; southern bluefin tuna (*Thunnus maccoyii*); and Irish Sea cod (Figure 3C, Table S2). Nineteen populations (11.4% of total), including Georges Bank Atlantic cod (*G. morhua*, Figure 3A) and Atlantic bluefin tuna (*Thunnus thynnus*, Figure 3B), would qualify as Endangered (EN, declines $\geq 70\%$ but $< 90\%$), and the remaining twenty-two threatened populations (13.3% of total), including two rockfish (*Sebastes spp.*), Bering Sea and Aleutian Islands Greenland turbot (*Reinhardtius hippoglossoides*, Figure 3J), Indian Ocean bigeye tuna (*Thunnus obesus*, Figure 3K), and four Atlantic cod populations (*G. morhua*, including the Faroe Plateau population, Figure 3L) would qualify as Vulnerable (VU, declines $\geq 50\%$ but $< 70\%$) (Table S2).

In contrast, only 13.5% ($n=399$) of the 2952 marine fish species listed on the IUCN Red List (in categories other than Data Deficient) are considered to be threatened, and very few of these are considered to be at a high risk of extinction ($n=59$ CR, 2.0% of total and $n=69$ EN, 2.3% of total; Figure 1). The vast majority are classified as Least Concern ($n=2350$; 79.6%). When only those marine fishes subject to large scale intentional use (Threat 5.4.2²⁴; total $n=282$) were considered, however, the proportion of threatened ones more than doubled, to 29.1% ($n=82$), almost exactly the same as in our estimated Red List.

To set the current status of marine fishes in context, we asked what proportion of assessed populations would ever have been considered to be in trouble from fisheries and conservation perspectives? Almost three-quarters (73%) of populations have fallen below their upper fisheries benchmark at some point in the past, and just over half (54%) have ever fallen below their lower one. The extent of over-exploitation varied significantly by region: whereas all populations under European management ($n=42$) have been below their upper benchmark (B_{pa}) and 71% have been below their lower one (B_{lim}) (Figure 2D), only 77% and 58% of U.S. populations ($n=77$), and 45% and 30% of non-U.S. populations ($n=47$) have been below their upper (B_{msy}) or lower ($0.5B_{msy}$) benchmarks, respectively (Figure 2E). From a conservation perspective, 60% ($n=100$) of assessed marine fish populations could have been classified as threatened at some point in their past, according to Criterion A1, which is almost midway between the number of populations that have ever been considered to be in trouble from conservative or risky fisheries perspectives, and over twice as many as would be listed currently

(Figure 2F). Under this “worst case” scenario, 14 populations would have been classified as Critically Endangered, 48 as Endangered, and 38 as Vulnerable.

Alignment of conservation and fisheries metrics. Overall, the current fishery and conservation statuses of individual marine fish populations are well-aligned: 75.9% alignment (sum of positive and negative hits) when estimated Red Listings were compared to the populations benchmarked against their upper (more conservative) fisheries reference points, and 80.7% when populations were compared to their lower (riskier) ones (Table 2). In both cases, negative hits, where populations were not considered to be in trouble from either a fishery or conservation standpoint, made up the majority of alignments (Figure 3D–F). Misalignments were dominated by misses, where the Red List criterion failed to classify a population below its fishery reference point as threatened, when Red Listings were compared to the upper fisheries reference points (17.5%, Figure 3G–I). False alarms, where the Red List classified a population as threatened but the population was above its fishery reference point, dominated when Red Listings were compared to the lower reference points (13.9%; Figure 3J–L; Table 2). Different outcomes can occur only for populations whose biomass is between its two reference points. Western Pacific striped marlin (*Kajikia audax*), for example, is categorized as a miss when compared to its upper reference point (B_{msy}) but a negative hit when compared to its lower one ($0.5B_{msy}$; Figure 3H). Alignment was greater for European populations, benchmarked against B_{pa} (81.0%) and B_{lim} (90.5%), than for U.S. and other populations, benchmarked against B_{msy} (74.2%) and $0.5B_{msy}$ (77.4%). Relative to those other populations, European ones had a greater proportion of negative hits, and almost no false alarms (none for B_{pa} and two (4.8%) for B_{lim}). A related analysis based upon Red List Criterion A4, which identifies populations as threatened for declines $\geq 30\%$, showed a much higher proportion of false alarms and lower overall alignment than analyses using Criterion A1 (Table S3).

To gain further insight into the extent of the alignment, and severity of misalignments, we compared the alignment of each population's individual estimated Red List category (Criterion A1: CR, EN, VU or not threatened) with its upper and lower fisheries reference points, as well as two additional MSY-based ones ($1.5B_{msy}$ and

Table 3 | The proportion (%) alignment between the estimated Red List Status and the actual (upper (B_{pa}) and lower (B_{lim})) fishery reference points of European marine fish populations (managed by ICES). Red List threatened categories are Critically Endangered (CR), Endangered (EN), Vulnerable (VU)

Reference point	IUCN Red List status (%)				Total populations
	CR	EN	VU	not threatened	
$\geq B_{pa}$	0.0	0.0	0.0	59.5	25
$< B_{pa} - \geq B_{lim}$	0.0	0.0	4.8	14.3	8
$< B_{lim}$	2.4	9.5	4.8	4.8	9
Total	2.4	9.5	9.5	78.6	42



$0.2B_{msy}$). Five populations were considered to be of greatest concern from both conservation and fisheries perspectives, being classified as Critically Endangered and below their lowest fisheries reference point (B_{lim} or $0.2B_{msy}$): Irish Sea cod (*G. morhua*, Figure 3C), southern Atlantic coast red snapper (*L. campechanus*) and snowy grouper (*E. niveatus*), southern California cowcod (*S. levis*), and southern bluefin tuna (*T. maccoyii*). We found few egregious errors, where populations were categorized at opposite extremes of the fisheries and conservation metrics: only nine populations (4.8% of European, Table 3; and 3.2% of other populations, Table 4) that were below their lowest fisheries reference point were classified as not threatened, and only six populations (all B_{msy} -based ones) that were above their highest fisheries reference point ($>1.5 B_{msy}$) were classified as threatened (0.8% EN and 4.0% VU; Table 4). Encouragingly, there were no cases where a population above its upper reference point was classified as Critically Endangered. In fact, most misalignments occurred when populations either were near the threshold of where they would be classified as threatened or near their fisheries reference points (e.g. Figure 3K–L).

Finally, the overall level of alignment between populations' theoretical "worst case" conservation status, according to Criterion A1, and their fishery status at the corresponding point in time was similar to that of the current statuses: 80.1% for the upper fisheries reference points, and 70.5% for the lower ones (Table 2). The relative proportion of positive and negative hits, however, was substantially different, with over twice as many positive hits under this worst case scenario than currently. Moreover, the number of false alarms doubled, occurring in 13.3% and 27.7% of populations when compared to upper and lower reference points respectively, while misses became rare (Table 2).

Discussion

Extinction risk criteria and fisheries reference points provided consistent signals for most assessed marine fishes. Total alignment was high both for populations' current statuses (75.9% and 80.7% for upper and lower reference points, respectively) and their "worst case" scenarios (80.1% and 70.5%), although the composition of hits differed markedly (Table 2). Negative hits dominated the alignment of populations' current statuses, indicating populations that are considered to be both well-managed and at a low risk of extinction. Still, almost 23% of populations currently are considered to be in trouble from both conservation and fisheries perspectives, and a further 24.1% are considered to be in trouble from either conservation (6.6%) or (the more conservative) fisheries perspectives (17.5%). In contrast, the "worst case" analysis was dominated by positive hits, revealing that almost half of populations would have been considered both threatened and overfished (by more conservative standards) at some point in their past (Table 2). Although we focus our discussion solely on the analyses involving Criterion A1, we note that our

general discussion points relating to the causes and consequences of misalignment between conservation and fisheries reference points, also holds for Criterion A4 (Table S3).

Despite high overall alignment, the concern that the Red List exaggerates the threat status of marine fishes^{16,19} is warranted under some circumstances. We found the proportion of false alarms varied substantially depending on the time period and reference points, with the greatest proportion (27.7%) occurring when "worst case" Red Listings were compared to lower reference points (Table 2). False alarms arise under this scenario because the reference points are so low that despite substantial declines, the populations remain above them. Notably, fewer than half of these same Red List evaluations were flagged as false alarms when the populations were benchmarked against upper reference points (13.3%, Table 2).

False alarms reflect conflicting signals between conservation and fisheries metrics, and a concern is that threat listings in these cases may undermine successful fishery management, giving the impression that populations are not being properly managed even when, according to fishery metrics, they are. Additionally, legislation in Australia (Environmental Protection and Biodiversity Conservation Act), Canada (Species at Risk Act), and the U.S. (Endangered Species Act) requires mandatory conservation measures be implemented if a population is deemed threatened with extinction^{23,34}, potentially resulting in catch restrictions and lost income to communities depending on the resource. Critics of the Red List argue such conservation measures can be overly aggressive because rapid declines in managed fish populations typically result from the "fishing-down" phase of developing fisheries, in which biomass is reduced to a target level (e.g. B_{msy}) after which the exploitation rate is set to maintain the population at that level¹⁹. Our analysis partially supports this contention: ten of eleven populations classified as false alarms in our "worst case" scenario analysis (whose decline ended at least ten years prior to the end of its time series, to allow investigation of subsequent population changes), subsequently stabilized above their upper fishery reference points, such that their current statuses aligned as negative hits. Recognizing this may occur, the IUCN guidelines provide flexibility in extinction risk evaluation for populations whose declines are being actively managed¹⁵. In fisheries lacking effective management controls, however, it seems unlikely that population declines would be curtailed in this manner. For these populations, false alarms may in fact be useful warning signals of impending overfishing. Indeed, even in our analysis of the most data-rich, and presumably best managed marine fishes effective curtailment of declining populations was not the norm: the majority of populations meeting the Red List A1 criterion for threatened also had fallen below their fisheries reference points and thus were positive hits, not false alarms (Table 2).

Encouragingly, false alarms were rare when the current statuses of marine fishes were compared, especially when populations were benchmarked against their upper reference points ($n=14$, 6.6%, Table 2; Figures 3J–L and S1). Few of these false alarms were egregious: none of the populations was listed as Critically Endangered, which would have indicated an enormous mismatch between the two metrics, and only three were listed as Endangered (Figure 3J, Tables 3 and 4). What's more, two of the false alarms, smooth oreo (*Pseudocyttus maculatus*) on the west end of New Zealand's Chatham Rise and orange roughy (*H. atlanticus*) along the mid-east coast of New Zealand, were very close to their fishery reference point thresholds (the latter had recently been below it) and thus were on the verge of being classified as positive hits (Figure S1). Legitimate concern remains, however, for the other nine false alarms. Threat status was exaggerated for many of these populations because they started at very high biomass (mean = $4.9 B_{msy}$, range = 2.8 to $11.2 B_{msy}$; Figure S1). For populations exhibiting high long-term variability, such as these, establishing relevant population baselines is a challenge³⁵. Greenland turbot (*R. hippoglossoides*) in the Bering Sea

Table 4 | The proportion (%) alignment between the estimated Red List Status and the actual B_{msy} fishery reference points of US and other non-European marine fish populations. Red List threatened categories are Critically Endangered (CR), Endangered (EN), Vulnerable (VU)

Reference point	IUCN Red List status				Total populations
	CR	EN	VU	NT	
$> 1.5 B_{msy}$	0.0	0.8	4.0	32.3	46
$1.0-1.5 B_{msy}$	0.0	1.6	2.4	18.5	28
$0.5-1.0 B_{msy}$	0.0	3.2	4.8	11.3	24
$0.2-0.5 B_{msy}$	2.4	4.8	1.6	2.4	14
$<0.2 B_{msy}$	3.2	1.6	1.6	3.2	12
Total	5.6	12.1	14.5	67.7	124



and Aleutian Islands, for example, plummeted only after peaking at an estimated 13 times B_{msy} during the 1970s North Pacific regime shift, and thus we evaluated it as Endangered when it was still at $1.5B_{msy}$ (Figure 3J). Notably, where extreme fluctuations or repeated natural population cycles are shown to be the drivers of declines, they are not to invoke threatened listings (Red List Guidelines Section 4.7: Extreme fluctuations) to avoid triggering false alarms.

Although false alarms are a real concern, the perception that the Red List is systematically biased towards exaggerating threat status in marine fishes is unfounded - misses also occur, and were in fact the main source of misalignment in our analysis of current status and upper reference points (17.5%; Table 2, Figures 3G–I and S1). Four of these cases were egregious misalignments: Southern New England winter flounder (*P. americanus*) and three of yellowtail flounder (*L. ferruginea*) populations on the U.S. east coast were each below $0.2B_{msy}$ yet evaluated as not threatened (Tables 3 and 4). Yet, we caution that such misses should not necessarily be regarded as a failure of the Red List criterion. Exploited populations may stabilize at low biomass following substantial declines (as occurs in their initial fishing down phase), and if they persist in that state for multiple generations it suggests they do not face imminent extinction and the Red List criterion is working appropriately. Such populations would still require increased management and conservation attention to maintain current biomass levels or restore them to former levels. Misses are, however, of concern for those populations below their fishery reference points that have not stabilized, but instead continue to decline at a rate insufficient to trigger an IUCN threat listing and subsequent conservation action. In such cases, the Red List would only be effective if a population declined to the extent that it triggered one of the other threat criteria¹⁵. This could have serious implications for data-poor populations in which the fishery status is unknown and the Red List is the only means of assessing population status, as it implies that populations requiring conservation attention will be overlooked.

The propensity for misses to occur appears greater for populations with shorter generation times and those for which artificially short generation times are used in Red List calculations^{23,36}. Such populations must decline at a faster annual rate to trigger a threatened designation¹⁴ and the three-generation period can be too short to capture the full extent of their declines, as illustrated by striped marlin (Figures 3H). Indeed, 39.1% of populations in our analysis for which the three generation period was ≤ 20 years were misses (when benchmarked against upper reference points), compared to only 9.2% for those with longer generation times. Similarly, when we fixed the three generation period for all populations to be 15 years (as in^{23,37}), the number of populations classified as Endangered or Critically Endangered dropped from twenty-seven to six, while the number of misses increased substantially (69% when benchmarked against upper reference points, 135% against lower ones; Tables 2 and S4). This may explain why an earlier comparison of fishery statuses and Red List statuses estimated using shorter generation times had a much higher proportion of misses (48% overall³⁶) than our analysis. Longer exploitation times also may increase the likelihood of misses because these populations are more likely to have already undergone their most substantial declines (during their initial fishing down phase) and have stabilized (e.g. Figure 3H).

Misalignment between Red Listings (A1) and fisheries reference points is heavily influenced by the fundamental difference in how these two metrics evaluate if populations are in trouble. The former is a rate based approach, while the latter is based upon relative biomass levels without reference to the time period over which the changes occurred. Perfect alignment would occur if, for example, all populations started at unfished biomass, B_0 , their maximum sustainable yields occurred at 50% of this level (i.e. the simplistic assumption of the Schaefer model³⁸), and they declined by at least this amount. In reality, the proportion of B_0 at which B_{msy} occurs is strongly linked to

compensatory population dynamics, and often occurs at much lower levels³⁹. Species with high maximum population growth rates, such as herring (*Clupea harengus*), can have $B_{msy}:B_0$ ratios between 0.20 and 0.30¹³. Reference points also may be set at a fixed ratio of B_0 when data to estimate B_{msy} are lacking (e.g. Australia uses a default B_{msy} of $0.4 B_0$ in such cases¹³). This mathematical disconnect is a major source of misalignment between these conservation and fishery metrics: whereas a $\geq 50\%$ decline would trigger a threatened listing under the Red List, a 70% or 85% decline would be needed for a productive population (assuming a $B_{msy}:B_0$ ratio of 0.3) to fall below its upper or lower fishery reference points, respectively (e.g. Figure 3J–L). Such populations will be prone to false alarms early in the development of their fisheries if their populations start at high biomass.

Several caveats must be borne in mind when interpreting our findings. First, although the Red List is primarily a species level assessment tool, we conducted our evaluations at the population level. Apart from the pragmatic reason that this facilitated direct comparisons with population-level fisheries assessments, for widely distributed species such as many marine fishes the population is the most relevant level when considering ecological roles and contributions to individual ecosystems. Populations can be highly adapted to local conditions, such that specific morphological and behavioral adaptations may limit the potential for recolonization by populations from other regions⁴². Moreover, loss of individual populations typically precedes species level extinctions^{43,44}. As such, regional Red List assessments have been conducted for many marine fish species^{15,24}. Second, only the most data rich populations, which have stock assessments and reference points, could be included in our analysis. These populations all are actively managed, which could limit the transferability of our findings to fisheries lacking the management control necessary to effectively curtail exploitation rates. For relatively data-poor fisheries (i.e. those without a stock assessment or reference points, but with some index of abundance), however, our results suggest threat listings could serve as accurate flags for ones that are in trouble.

Additionally, we assumed fishery reference points are true measures of marine fish population status. Clearly, however, there is great variation in the types of reference points used which can strongly influence alignment of fishery and conservation metrics (Tables 2–4). Reference points used in Europe are, for example, set at a much lower proportion of B_0 than MSY-based ones^{32,41}, and we therefore had expected to find low levels of alignment for these populations. Instead, European populations had very high alignment (90.5%) compared to B_{msy} managed ones (77.4%), and alignments comprised mainly of negative hits (Table 3) despite these populations generally being in poor shape⁴¹. This seemingly contradictory finding arises from the extremely low reference points and the long exploitation history of European populations, such that for these populations the majority of declines occurred prior to the most recent three-generation period and did not trigger the Red List threat criteria. If European fisheries management moves to more conservative B_{msy} -based reference points, as is proposed for 2015⁴⁵, many of these depleted but stable populations would likely become misses. A general move by fisheries management agencies around the world towards B_{msy} based reference points^{40,46}, would help alleviate the problem of a lack of consistent reference points that has hindered recent global fisheries analyses^{30,47,48}.

Perhaps the most critical assumption of our analysis is that we equated falling below a fishery reference point with a Red List threatened status, and hence an increased extinction risk. This assumption embodies a central component of the debate about the relevance of the Red List to marine fishes: few fisheries scientists would consider overfished populations to be at risk of extinction. Thus, while the mix of false alarms and misses in our results provides empirical support that Red List is not systematically biased towards exaggerating when populations are in trouble, the overall high degree of alignment suggests that the Red List does exaggerate extinction risk for many



populations since those just below their reference points are unlikely to face a heightened risk of extinction. This conclusion is supported by simulation models that suggest marine fishes with threatened listings have low probabilities of going extinct in the near future^{16,19}, and by the discrepancy between the number of marine fishes listed on the Red List as being threatened with extinction ($n=399$, Fig. 1) and the number listed as having gone extinct ($n=1$, New Zealand Grayling (*Prototroctes oxyrhynchus*)²⁴). Still, we acknowledge that the process of extinction is poorly understood^{11,14,42}, and that while global extinctions of marine fishes appear to be exceedingly rare, local extirpations are not⁴⁹. Thus, while it appears marine fishes listed as threatened are not necessarily imminently at risk of biological extinction, substantial declines in their abundance still are likely to have significant consequences for biodiversity, ecosystem functioning, and human welfare⁵⁰, especially if such depletions are not easily reversed. Others have therefore suggested the Red List categories should be renamed as conservation priorities I–IV⁴² to better reflect its intent of serving as a method of conservation prioritization. We believe such a renaming is unlikely, but would advocate consideration of the Red List threat categories in this manner as a useful heuristic solution for helping to move the debate between the fisheries and conservation communities forward.

Despite fundamental differences in methodology, Red List and fisheries assessments for marine fishes align well. Thus, while debate about the relevance of the Red List to marine fishes continues^{26,27}, the empirical evidence indicates conservation and fisheries scientists will, in most cases, agree on which exploited marine fishes are in trouble and require improved management measures. We hope this research will encourage similar scrutiny of other conservation evaluation frameworks, which have been developed for marine fishes to “improve upon” the Red List^{17,20,34}. Those who argue that the Red List exaggerates threat status for marine fishes also may be surprised to learn the proportion of marine fishes listed as threatened on the Red List is very low (13.5%; Figure 1²⁴). Although this contention was borne out for some of the marine fish populations in our analysis (typically those assessed against riskier reference points or in the “fishing down” phase of fishery development¹⁹), more populations were considered to be in trouble from both perspectives (positive hits) than by the Red List alone (false alarms). Moreover, for fisheries lacking stock assessments and management controls to curtail fishing mortality, such threat listings might serve as useful warnings signals of (impending) overfishing. Indeed, while stock assessments are a financial impossibility in most fisheries ($n \cong 350$ assessments globally³⁰), the Red List provides a relatively easy and transparent means of flagging populations in trouble ($n=2952$ marine fish assessments to date²⁴). Our results suggest it also is an accurate means of doing so. Thus, with momentum for conservation evaluations of marine fishes growing, we urge fisheries scientists to recognize the Red List as a useful, complementary approach to evaluating the global impacts of marine fisheries, and for the fisheries and conservation communities to work together to determine mutually acceptable management responses for population which they both deem to be of concern.

Methods

Data. To assess the fishery status of marine populations, we used all available recent stock assessments with estimates of adult (spawning stock) biomass and biological reference points (referred to herein as assessed populations). All assessments, except those from Europe ($n=42$), are from Version 1.0 of the RAM Legacy Stock Assessment Database, a new global database of stock assessments for commercially exploited marine populations³⁰. For European populations, we obtained the 2011 assessments from the International Council for the Exploration of the Sea (ICES)⁵¹. Overall, populations in our analysis came from Argentina, Australia, Canada, Europe, New Zealand, South Africa, and the U.S., and their adult biomass time series averaged 46 years (range 15–132 years). We benchmarked the biomass of populations against the upper and lower biological reference points from their stock assessments¹³, rather than estimating a common set of reference points (as in^{30,48}). Assessments from the RAM Legacy Database used B_{msy} and $0.5B_{msy}$; European ones used B_{pa} and B_{lim} . Six of

the European populations had only B_{pa} calculated, and four had only B_{lim} . For these we used the relationship:

$$B_{lim} = B_{pa} e^{(-1.645\sigma)} \quad (1)$$

from⁵⁵ with $\sigma = 0.3$ to estimate these few missing reference points.

To assess the conservation status of marine fish populations, we first summarized the status of all marine fishes listed on the Red List (Version 2011.2²⁴). However, the limited number of marine fish populations with both a recent stock assessment and a recent IUCN Red List evaluation ($n=31$, with Red List evaluations coming from only twenty-four different fish species) precluded a broad direct comparison of these two metrics. Instead, we estimated the Red List status of all assessed marine fish populations according to Criterion A1, which requires an estimate of generation length. Generation length is defined as the average age of mature individuals in a population and thus reflects the turnover rate of breeding individuals¹⁵. We estimated generation length for all assessed marine fish populations as:

$$\text{Generation length} = A_{50} + 0.25 \times (\text{longevity} - A_{50}) \quad (2)$$

modified from the IUCN guidelines¹⁵, using population specific estimates for A_{50} (the age at 50% maturity), and longevity, the theoretical maximum age of each population prior to the commencement of exploitation, wherever possible. We extracted these estimates ($A_{50} n=93$, longevity $n=74$) from the RAM Legacy Database, and when absent, sought them from the populations’ respective assessments and/or the primary literature. Where population-specific longevity estimates were not available, we used species-level estimates, seeking these first from the primary literature and secondarily from FishBase⁵⁶ ($n=63$). In the six cases where these also were not available, we used the maximum age from the stock assessment model (typically a “plus group” in which all individuals greater than that age are combined, as in³⁶). The mean age at A_{50} of assessed populations was 5.7 years (range 0.3–38 years), and the mean generation length was 12.7 years (range 1.6–69 years) (Table S1). Thus, while some previous analyses have used 15 years as a coarse approximation for three generations in marine fishes^{23,37}, our analysis - in which three generations averages 38.1 years - reveals this to be a significant underestimate.

Analysis. We assigned each population to Red List Categories by calculating its proportional change in adult biomass over the longer of ten years or three generations (Criterion A1¹⁵), in each of two time periods: 1) the current Red List status by calculating the proportional change in biomass back from the most recently available biomass estimate, 2) the theoretical “worst case” Red Listing by identifying the time period of greatest proportional decline in biomass. According to the Red List Guidelines, Criterion A1 applies when declines are reversible, understood, and have ceased; when these conditions are not met, one of Criterion A2–A4, which have lower decline thresholds for threatened status (30%, as opposed to 50% for A1), is to be used¹⁵. We used Criterion A1 for each of our main analyses because all of the populations included have stock assessments and are managed to some degree, suggesting declines are potentially reversible, and the cause is understood to be primarily fishing in each case. Criterion A1 also has been most commonly applied to marine fishes³⁶. An additional analysis, based upon the A2–A4 decline threshold is presented in Table S3. In all of our Red List assignments, we calculated the proportional change in biomass between the mean of the last three years and the mean of the first three years of the time period under consideration, so as to reduce the influence of single year fluctuations in population biomass on threat designation. Although we initially considered estimating the proportional change in biomass by fitting generalized linear models, we found they occasionally fit the data poorly. Where three generations was longer than a population’s time series ($n=45$), the entire time series was used.

We then quantified the alignment between populations’ estimated current Red List status and their current fisheries status using a hits, misses and false alarms framework (Table 1^{31,36,57}). We assigned the fisheries status of each population first by benchmarking it against its upper biomass reference point, and second against its lower biomass reference point (described in Data), in each case designating the population as being above or below the reference point by comparing its mean biomass in the most recent three years to the reference point. There are four possible outcomes under the hits, misses, false alarms framework: i) a positive hit occurs when a population is below its reference point and the Red List criterion for a threatened listing is met; ii) a negative hit occurs when a population is above its reference point and the threat criterion is not met; iii) a miss occurs when a population is below its reference point but did not meet the criterion for a threatened listing; and iv) a false alarm occurs when a population is above its reference point but the threat criterion is (erroneously) met. Thus, positive and negative hits are indicative of alignment between the conservation and fisheries metrics, while misses and false alarms indicate inconsistent signals.

We examined the extent of the alignment or misalignment by comparing individual Red List threat categories (CR, EN, VU) with the upper and lower reference points, and two additional ones, $1.5B_{msy}$ and $0.2B_{msy}$. $1.5B_{msy}$ is an arbitrary level used to identify populations well above their upper reference points, while $0.2B_{msy}$ has been used as a metric of “collapsed” populations^{48,58}. Listing a population as Critically Endangered when its biomass is well above its upper reference point (e.g. $>1.5B_{msy}$) would be indicative of an egregious false alarm, whereas a Vulnerable listing when the biomass is just slightly above the upper reference point would be a minor one. At the other extreme, listing a population as not threatened when its biomass is well below its lower reference point (e.g. $<0.2B_{msy}$) would be an egregious miss, whereas listing such a population as Critically Endangered would be a strong positive hit.



Finally, we repeated the application of the hits, misses, false alarms framework twice more, to gauge the alignment between the theoretical “worst case” Red Listing for each population and its fishery status at the end of this decline period, when benchmarked against i) its upper fisheries biomass reference point or ii) its lower one.

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Author contributions

Both authors contributed to the content of this paper. TDD and JKB designed the study and wrote the manuscript. TDD performed the analyses and prepared figures and tables.

Additional information

Supplementary information accompanies this paper at <http://www.nature.com/scientificreports>

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