APPLIED ECOLOGY

# Global ecosystem overfishing: Clear delineation within real limits to production

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**The well-documented value of marine fisheries is threatened by overfishing. Management typically focuses on target populations but lacks effective tools to document or restrain overexploitation of marine ecosystems. Here, we present three indices and accompanying thresholds to detect and delineate ecosystem overfishing (EOF): the Fogarty, Friedland, and Ryther indices. These are based on widely available and readily interpreted catch and satellite data that link fisheries landings to primary production using known limits of trophic transfer efficiency. We propose theoretically and empirically based thresholds for each of those indices; with these criteria, several ecosystems are fished sustainably, but nearly 40 to 50% of tropical and temperate ecosystems exceed even extreme thresholds. Applying these criteria to global fisheries data results in strong evidence for two specific instances of EOF, increases in both pressure on tropical fish and a climate-mediated polar shift. Here, we show that these two patterns represent evidence for global EOF.**

## INTRODUCTION

Fisheries are an important part of the global economy. The fisheries sector represents >15% of the blue economy sector, exports are valued at >150 US$ Billion, and contributes 57 million jobs globally (*1*). In addition to trade and jobs, fish provide the primary, consistent source of protein to more than 35% of the world's population and more than 50% in least developed countries and account for one-fifth of all global protein sources, 6.7% of all protein consumed, a daily per capita of 34 calories, and an annual average of 20 kg of food (*1*). Approximately 30 to 35% of fish populations are fished unsustainably, with an additional 60% fully fished (*1*). The implications of unsustainable fisheries extend beyond simple status of fish populations and economic viability of fisheries to global food security, cultural survival, and even national security (*2*, *3*). Not only are fish populations, fleets, and fishery systems affected by unstainable fishing (*4*, *5*) but this also results in much broader impacts on marine ecosystems (*5*–*8*). To address many of these challenges simultaneously, a broader, more systematic means of detecting and delineating overfishing, before it sequentially affects fish population after fish population, fishery after fishery, and marine ecosystem functioning, is warranted (*5*).

Marine fishes and ecosystems experience overfishing. Most measures of overfishing address individual fish populations (Fig. 1A); however, governance systems also need to address the wider aspect of ecosystem overfishing (EOF; Fig. 1B). Clear definitions and demarcations of single stock (i.e., population) overfishing are well developed (Fig. 1B and fig. S1) (*9*, *10*). Although there are attempts to quantitatively characterize the impacts of EOF (*10*–*12*), few have clear thresholds and delineation of EOF (Fig. 1B) (*12*–*14*), and no definitions are widely used. In the less-developed world, the capacity to conduct monitoring, management, and enforcement of fisheries is notably lacking, thus some easily estimable EOF measures would be valuable. For developed countries, the question is whether emphasis on excessive population detail has resulted in eroding overall population and ecosystem condition, as well as missed opportunities (i.e., we miss the forest for the trees; e.g., even reasonable single species Total Allowable Catches can exceed system-level carrying capacity and lead to overfishing) (*5*, *15*). It would be valuable to have a means whereby a nation or sector could assess whether it is experiencing EOF, in a way that other nations could also evaluate to readily determine whether there is compliance. A solid international definition of EOF, one that is not based on stock assessment models, assumptions of steady-state maximum sustainable yield (MSY), copious data, nor excessive monitoring requirements would be extremely valuable, especially as global ocean conditions continue to change. Here, we define EOF as an instance where the sum of all catches is flat or declining, total catch per unit effort (CPUE) is declining, and total landings relative to ecosystem production exceeds suitable limits.

Here, we propose three novel indicators to ascertain the occurrence of EOF, the Ryther index, Fogarty index, and Friedland index. These are based on the ecological principle of trophic transfer, with specific thresholds developed for each index to delineate whether EOF is actually occurring. The Ryther index is composed of total catch presented on a unit area basis for an ecosystem. The Fogarty index is the ratio of total catches to total primary productivity in an ecosystem. The Friedland index is the ratio of total catches to chlorophyll in an ecosystem. The proposed thresholds are based on facets of carrying capacity limits to production of communities of fish populations, limited by trophic transfer efficiencies (TEs) (*12*, *14*). In essence, we are espousing the basic tenet of renewable natural resource management, such that any harvest meets the condition of $R_{\text{removal}} \leq R_{\text{renewal}}$ for each rate ($R$). Using known limits to ecosystem production (*16*–*18*), we posit estimated limits to global and regional fishery production.

## RESULTS

### Indicator thresholds and geographically specific responses

Current observations coupled with simple, theoretical estimates of catches imply that the Ryther index should probably be on the order of 0.3 to 1.1 t km$^{-2}$ year$^{-1}$ or practically not to exceed (NTE) ~1 t km$^{-2}$ year$^{-1}$, with an extreme limit NTE 3 t km$^{-2}$ year$^{-1}$. Previously empirically derived tipping points typically occur in fished ecosystems with total catches greater than 3 to 5 t km$^{-2}$ year$^{-1}$ (*15*, *18*, *21*), with expected system-wide MSYs on the order of 1 to 3 t km$^{-2}$ year$^{-1}$ (*15*, *21*). For now, we propose a Ryther index threshold of ~1 t km$^{-2}$ year$^{-1}$ to delineate EOF, consistent with this range of reported and derived results (Fig. 2A).

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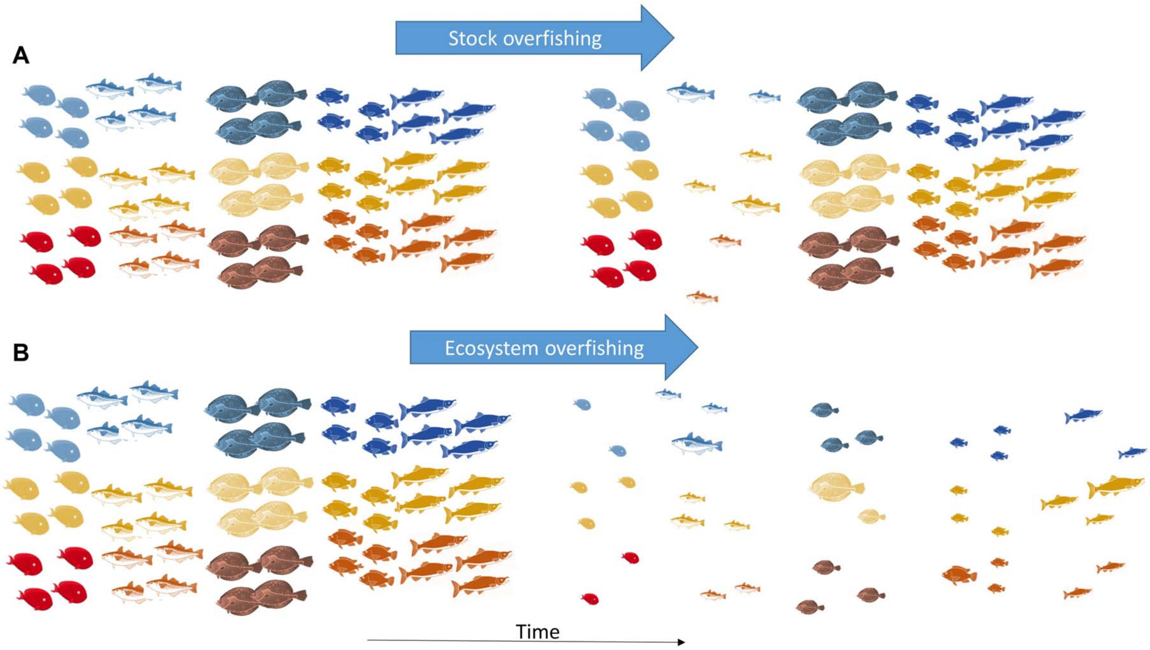


**Fig. 1. Schematic of stock and EOF.** (**A**) Schematic of population overfishing. While a population is experiencing overfishing, the abundance and biomass (here as the number of fish icons) and fish size declines over time, along with many other facets related to population and fleet dynamics. (**B**) Schematic of EOF. Analogous to population overfishing, EOF is the result of continued fishing pressure on multiple populations, leading to sequential depletion across populations in an ecosystem over time.

As expected, Fogarty ratio of 0.22 to 0.92 per mil (‰), or practically NTE ~1‰, with an extreme limit NTE of ~2.5‰ emerges from theoretically based limits coupled with estimates of global catches. Previously modeled and empirical estimates suggested that catches relative to primary production (PP) exceeding 1 to 2‰ resulted in a tipping point (*11*, *13*, *21*). For now, we propose a Fogarty index threshold of ~1‰ to delineate EOF, consistent with this range of reported and derived results (Fig. 2B). Using logic similar to the Fogarty ratio, we propose a threshold for the Friedland index NTE ~1 to delineate EOF (Fig. 2C).

Examining these indices by latitudinal band (Fig. 2A) reveals that no latitudes exceed the Ryther index threshold, although the Arctic and north temperate regions are within the range of what could possibly be considered fully fished or overfished if a lower threshold were used (i.e., >0.3 t km$^{-2}$ year$^{-1}$). Increasingly, the tropical band is approaching that level. Similar to the Ryther index, the Fogarty ratio indicates that no region is above the threshold (Fig. 2B), with both the Arctic and north temperate regions well within the range of what could be considered fully fished (i.e., >0.25‰). The Friedland ratio indicates that the north temperate and tropical bands are above the threshold (Fig. 2C) potentially experiencing EOF. The Friedland ratio for the Arctic and south temperate regions are around 0.3 to 0.5, indicating that they are not likely experiencing EOF. The Antarctic region exhibits low values for all three indices, likely reflective of both limited data availability and difficult-to-access fisheries. From all three indices (Fig. 2), the general picture for major latitudinal bands is that most places are not experiencing EOF, but the tropics and north temperate regions may be close to an EOF threshold depending upon the index examined (e.g., Friedland ratio) or level of threshold one uses.

Recognizing the absolute scale of global ocean areas, all portions of which may not be entirely fished (*19*, *22*), it is important to examine these three indicators at the more resolved large marine ecosystem (LME) scale. Presenting representative examples from each region (Fig. 3, A to C), it is clear that many tropical and temperate LMEs are experiencing EOF according to the Ryther index, with many ecosystems experiencing catch rates of >5 t km$^{-2}$ year$^{-1}$, and many (especially in the tropics) are experiencing over 8 t km$^{-2}$ year$^{-1}$. Those are well above even the extreme threshold of 3 t km$^{-2}$ year$^{-1}$. The polar regions also have some LMEs potentially experiencing EOF; many have a Ryther index between 1 and 3 t km$^{-2}$ year$^{-1}$. The Ryther index threshold of 1 t km$^{-2}$ year$^{-1}$ may be a low value for delineating EOF, and even 3 to 5 t km$^{-2}$ year$^{-1}$ would indicate a high degree of EOF, nearing theoretically extreme values. Of the 65 LMEs, using the threshold of 1 t km$^{-2}$ year$^{-1}$ for the Ryther index, 12 of 20 tropical regions (60.0%), 14 of 26 temperate regions (53.8%), and 5 of 17 polar regions (29.4%) are experiencing EOF.

The Fogarty index (Fig. 3, D to F) exhibits similar patterns to the Ryther index. Here, the number of ecosystems experiencing EOF is not as high as the Friedland ratio (Fig. 3, G to I) or even the Ryther index (Fig. 3, A to C) relative to their proposed thresholds. Yet, several LMEs exhibit Fogarty ratios of 2 to 3‰, an indication of probable EOF and approaching the extreme threshold. Of the 65 LMEs, using the threshold of 1‰ for the Fogarty index, 6 of 20 tropical regions (30.0%), 10 of 26 temperate regions (38.5%), and 5 of 17 polar regions (29.4%) are experiencing EOF. The Friedland index confirms the results of the other indices, yet all example tropical and most temperate regions exhibit EOF according to this index (Fig. 3, G to I ). Many polar regions also exhibit EOF according to the Friedland ratio. It may be because the Friedland threshold of 1 is too low, the index is too sensitive, or the catches overshadow chlorophyll values; however, even given these caveats, the potential for EOF appears much greater in the tropics, given the magnitude of this index there (~10 to 20) compared to the temperate (*5*–*10*) and polar (*2*–*5*) regions. Of the 65 LMEs, using a


**Fig. 2. The three novel indicators of ecosystem overfishing for major latitudinal bands.** Values of the potential measures to delineate EOF; the Ryther index (**A**), the Fogarty ratio index (**B**), and the Friedland ratio index (**C**) for all of the five latitudinal bands. The solid black line represents the proposed threshold (for the Friedland ratio; data are below the threshold for Ryther and Fogarty indices and thus is not shown). N Temp, northern temperate zone; S Temp, southern temperate zone.

**Fig. 3. The three novel indicators of ecosystem overfishing, for example large marine ecosystems in the tropical, temperate, and polar regions.** Values of the potential measures to delineate EOF; the Ryther index (**A** to **C**), the Fogarty ratio index (**D** to **F**), and the Friedland ratio index (**G** to **H**) for representative examples of the 65 LMEs that had an index above one of the noted threshold values (black lines) at some point during the time series. Not all of the 65 LMEs are shown. The solid black line represents the proposed threshold.

threshold of ~1 for the Friedland index, 15 of 20 in tropical regions (75.0%), 19 of 26 temperate regions (73.1%), and 4 of 17 polar regions (23.5%) are experiencing EOF.

The occurrence of EOF in LMEs is consistently detected across all indicators. Of particular note are some Southeast Asian LMEs, with values much higher than even the most extreme proposals for thresholds, aligning with what we know about these ecosystems (see the Supplementary Materials). Like all the data herein, these results are subject to the vagaries of misreporting, Illegal, Unreported, and Unregulated (IUU) catches, and the usual challenges of global databases (*1*, *23*, *53*). Those LMEs and broader regions noted here as likely experiencing EOF are generally the same ones identified as being susceptible to higher fishing pressure in global studies using other proxies for fishing-induced ecosystem-level perturbation, including PP required (*11*), the L index and probability of sustainability (*12*), size spectra parameters (*24*) or cumulative biomass, and trophic level (TL) and cumulative production curves (*14*). They also correspond to those ecosystems with well-documented histories of sequential population overfishing (cf. Eq. 3). Here, we have an independent, readily estimable threshold to determine whether these LMEs are experiencing EOF.

The polar regions have experienced the least number of LMEs with EOF, but even then still exhibit several LMEs with indications of EOF occurring. The tropics consistently have the highest proportion of LMEs with EOF across these indices. More so, the tropics have seen the number of LME experiencing EOF increase over time (Fig. 3, A, D, and G). The temperate regions also have a high number of LMEs experiencing EOF, with ~40 to 50% exhibiting such a pattern. Hence, the temperate regions have limited capability to absorb shifting fishing pressure from the tropics (*20*, *25*).

### Evidence for global Ecosystem Overfishing: Two specific instances

Given the definitions of EOF, coupled with the three indicator thresholds for both latitudinal and LME-parsed catches, we examined the collective evidence to determine to what extent EOF may be occurring at a global level. First, we see that tropical pressure on fisheries is increasing. Unlike the polar regions (Fig. 4B) and temperate regions (Fig. 4C), total catches in the tropics have increased over time (Fig. 4D) (*1*, *26*, *27*). The continual expansion of tropical fishing is such that fishing signatures are seen at every longitude (Fig. 5). The longitudinal spread of catches in the tropics has and continues to expand (Fig. 4E). The area fished is now greatest in the tropics (*1*, *20*, *28*), although this region's fleets are composed primarily of smaller vessels (i.e., <20 m) (*1*, *29*). The effort in the tropics is expanding (Fig. 4F) (*20*, *28*), such that the highest

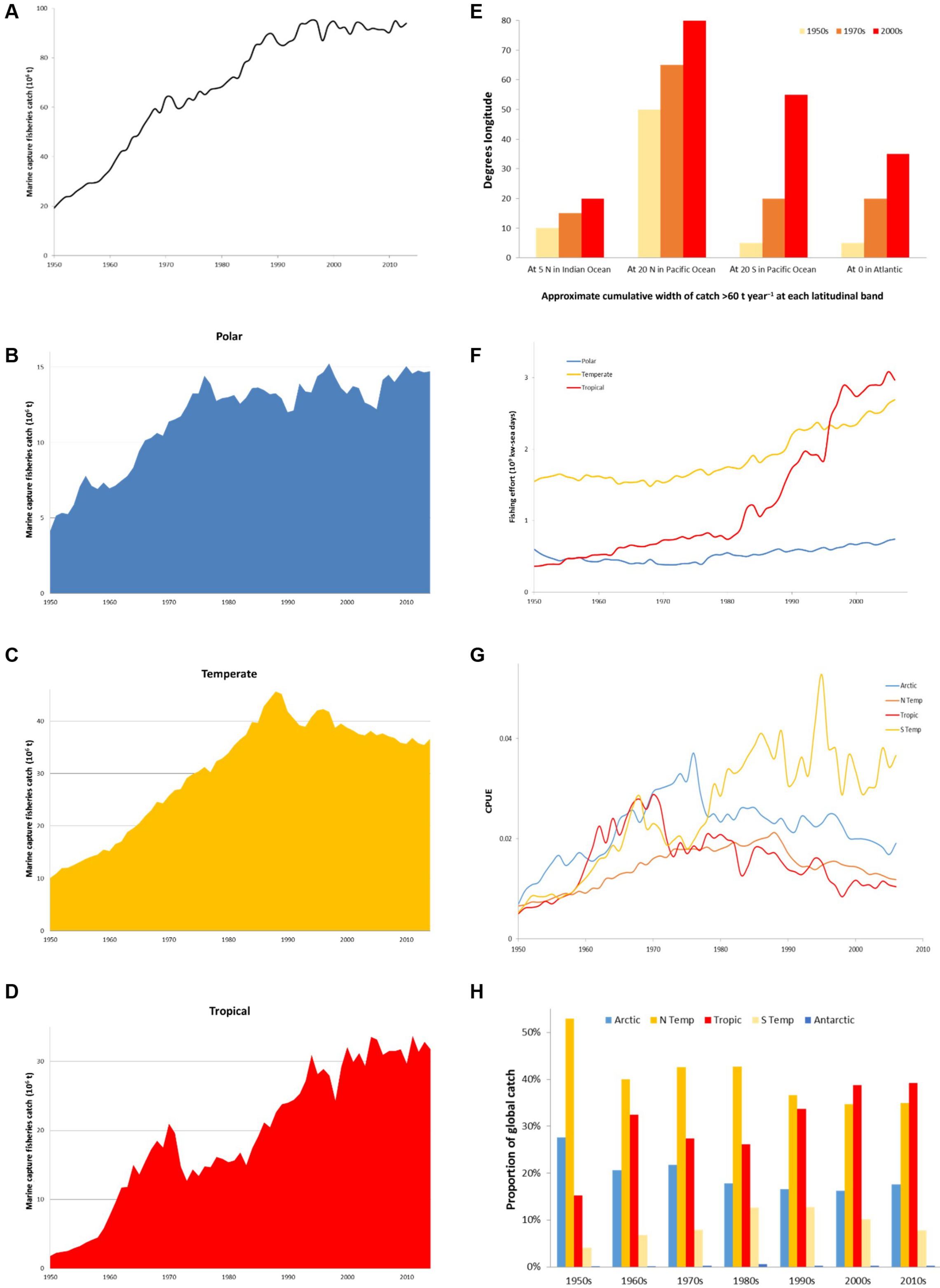


**Fig. 4. Multiple characterizations of global fishing and fisheries catch demonstrating core criteria of EOF for different regions, with a particular demonstration of polar fishery stasis and increases in tropical fishing.** (**A**) Total, global marine capture fisheries catch of all taxa over time. Total marine capture fisheries catch of all taxa over time, as integrated into major latitudinal bands; polar (**B**), temperate (**C**), and tropical (**D**). All latitudinal bands have data from both northern and southern hemispheres. (**E**) The width at each latitudinal band (four examples given) at which total average annual marine capture fisheries catch exceeded 60 t km$^{-1}$. (**F**) Total fishing effort for exemplary latitudinal bands over time. (**G**) Total CPUE by latitudinal band over time. (**H**) The proportion of global fish catch in latitudinal bands over time. These are presented in approximate widths as degrees of longitude.

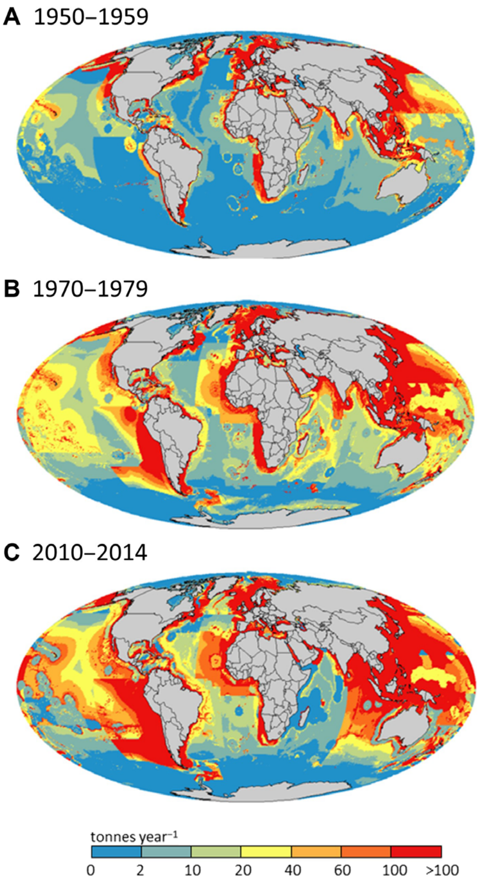


**Fig. 5. Global patterns in total fisheries catches from over more than 50 years as seen in three example stanzas.** Total average annual marine capture fisheries catch (including estimates of illegal unreported and discards) of all taxa for 1950–1959 (**A**), 1970–1979 (**B**), and 2010–2014 (**C**).

rate of increase in effort is seen in the tropics (Fig. 4F) (*28*). The collective CPUE in the tropics has decreased over time, declining by 50 to 80% from the 1950–1960s to 2010s (Fig. 4G) (*20*, *28*). In addition, the mean size of individual fishes remains small in the tropics and is actually declining (*30*, *31*). The valuation of fish caught in the tropics has slightly declined (*1*, *32*). In addition, fish food security has notably declined in the tropics (*2*, *3*). In tropical latitudes, this evidence collectively fits the pattern one would observe for EOF in any given ecosystem. Certainly, not all tropical ecosystems are experiencing EOF, but many are based on the three indices and ancillary information noted, consistent with EOF (Fig. 1B and fig. S1). The fraction of LMEs thought to be experiencing EOF is high in temperate regions but is highest in tropical regions (Figs. 2 and 3, A, D, and G).

Second, we see a polar shift occurring in fish populations, yet without an, as yet, concurrent shift in their associated fisheries. It is well documented that fish populations are shifting poleward (*29*, *33*), consistent with expectations from climate change impacts. Contrary to this well-documented shift in fish distribution, fisheries catches are not similarly shifting poleward (Figs. 4, B, C, and H; and 5) (*1*, *27*, *34*). The total polar (and temperate) catch is flat (Fig. 4, B and C), and the proportion of the total catch is shifting from the poles to the tropics (Figs. 4H and 5). The effort in polar regions is also predominantly flat (Fig. 4F) (*28*) . Thus, CPUE in polar regions is decreasing by a factor of 20 to 40% from the 1960s–1970s to 2010s (Fig. 4G) (*34*, *35*). The point is not that polar catches and effort are necessarily declining or projected to decline but rather that the tropical fleets that target tropical populations are not latitudinally following the generally poleward shift in tropical or temperate fish population distributions. Some LMEs in the polar regions are experiencing EOF (Fig. 3, C, F, and I), but the fraction of LMEs thought to be experiencing EOF is lowest in polar regions.

Combining both the polar shift and expanded tropical pressure, we can infer a global occurrence of EOF, with particular impact on the tropics. Fish populations (and productivity) are shifting out of the tropics at a time when effort there is increasing (Fig. 4F). The proportion of catch in the tropics is increasing (Fig. 4H). Total CPUE is still notably lower there than in temperate or polar regions (Fig. 4G) (*35*). Although the total catch in the tropics is increasing (Fig. 4D), it is still not at the level as in temperate regions (Fig. 4C). The expansion of the amount (Fig. 4F) and extent (Fig. 4E) of effort are greatest in the tropics (and may continue to grow) (*25*, *28*). This implies a notable increase in fishing pressure in the tropics that is not ameliorated via shifting fishing effort into other latitudinal bands. Thus, CPUE is declining both the most and the fastest in the tropics (Fig. 4G); the decline in CPUE in the polar and temperate regions over the past 60+ years has ranged from 20 to 40%, whereas in the tropics, it is 50 to 80% (Fig. 4G) (*34*, *35*). Even if tropically oriented fleets were able to shift latitudes (crossing marine exclusive economic zone claims), it remains unclear whether temperate regions could absorb shifts from the tropics, given that many temperate regions are also experiencing EOF, and catches there have been flat for >30 years (Fig. 4C), with many of the fleets generating much of the fishing effort originating in those regions (*20*, *25*). Both the latitudinal bands and LME examinations of EOF imply that the tropics are increasingly experiencing EOF.

## DISCUSSION

Collectively, the three indices proposed here attempt to define and delineate thresholds of EOF. Hence, they are a potential international standard for tracking fisheries ecosystem status. Being able to clearly and consistently identify EOF is not insignificant. We assert that the approach proposed here would help in even (extremely) data poor situations. These indices are easily estimable, are based on widely repeated and available data, are readily interpretable, and are a pragmatic attempt to identify when an ecosystem would be experiencing EOF based on well-understood and well-accepted PP and food web limitations. These indices are able to accommodate a dynamic ocean, particularly as two of these indices link directly to measures of primary productivity. Detecting overfishing at an ecosystem level would also help to avoid many of the corollary impacts we have seen when managing fished taxa on a population-by-population basis (*5*) and holds promise for detecting major signals more rapidly (*12*, *14*) by establishing shifts in ecosystem and fisheries productivity much more quickly than piecing together any such shifts together in a meta-analysis from a population-by-population basis.

One could easily envision that if these catch values exceed the thresholds proposed here, or certainly the theoretically extreme thresholds, then the appropriate action to minimize EOF could be enacted in an ecosystem. There would obviously need to be a local policy choice regarding the level of EOF threshold (as proposed here, the theoretical maximum, something more precautionary, etc.) established in a given jurisdiction, but the estimates thereof would be relatively straightforward to delineate EOF. However, if an ecosystem is determined to be overfished, what specific action/s could be taken? At one level, the solution is simple—that is, lower fishing pressure. Yet, at another level, the solution is complicated, with many social, economic, ecological, and even existence considerations. Enacting management to ultimately lower fishing pressure has many potential avenues (*4*), and all should be explored given a local or regional context. The salient point here is that the value of having international standards would be that any party could obtain and calculate these estimates from readily available sources, and if the ratios exceeded the commonly noted threshold, then a clear agreement and obvious consensus on whether overfishing was occurring, or not, would then not be debatable. Rather, what appropriate actions to best mitigate EOF would be (specifically via particular management measures, beyond generally a lowering of fishing pressure) open for discussion and that would shift the burden of proof to one that would better emphasize sustainability.

Does this evidence for EOF have a solid theoretical underpinning? From the trophic transfer relationship (Eq. 5), catches increase when fish are targeted at lower TLs, TE is higher, or primary productivity (PP) is higher. What we see is that, in tropical regions, although TL of catches is declining (leading to ↑*C*) (*1*, *36*), the TE is declining (i.e., ↓*C*) (*12*, *27*, *35*) and PP is shifting (i.e., ↓*C*) (*24*, *37*, *38*). Thus, the theoretical net effect is less potential catch in tropical regions, confirming the trends observed. Conversely, in polar regions, we see that, although TL of catches is increasing (i.e., ↓*C*) (*1*), both TE is increasing (i.e., ↑*C*) (*12*, *27*) and PP is shifting to that region (i.e., ↑*C*) (*14*, *24*, *39*). Certainly, some taxa could obtain much of their energetic requirements in other ecosystems and migrate into a different ecosystem whereupon they would be caught; however, in these instances (e.g., straddling stocks and highly migratory species), it would be advisable to consult these indices in adjacent ecosystems. As a percentage of LMEs or taxa, and given the large areas of most LMEs, these would be exceptions to the general patterns of EOF detected herein. Given this caveat, the theoretical net effect is more potential catch in polar regions, again confirming observed trends. Furthermore, other potential measures of EOF using similar theoretical underpinnings (*11*, *12*, *14*) and other criteria (*15*, *19*, *24*) all generally confirm the results shown here, particularly in the tropical latitudinal band, even without the clear thresholds presented here. Thus, EOF is not expected to occur everywhere, but is expected to increase in prevalence at lower latitudes, and likely to exceed the proposed thresholds.

EOF is not occurring in every marine ecosystem, but it is widespread. Any instance of EOF has implications that collectively, and by definition, are not positive. In some instances, the ramifications of EOF are likely to be severe, potentially even leading to crisis. These instances are particularly acute in the tropics. The potential for strong impacts from EOF in the tropics, in terms of degraded economies, loss of stability and capacity of governance, food security, cultural identity, national security, and, in some instances, existence (*1*–*3*) are clearly heightened by our results and clarified by the indices we propose. Conversely, this approach could perhaps identify specific regions with further potential fisheries production to ameliorate these tropical concerns.

The extent of EOF in many ecosystems and over a large proportion of the world's oceans is highly consequential and not trivial. Our proposed delineations provide an opportunity to establish international standards of what constitutes EOF and hence thresholds for action exceeded. Only when we can define and identify EOF can we begin to address it.

## MATERIALS AND METHODS

### Defining (ecosystem) overfishing

The dynamics of single population overfishing are well chronicled; as catch (*C*) declines, effort (*E*) increases, which is then repeated

$$C\downarrow, E\uparrow, \mathrm{CPUE}\downarrow \ldots \tag{1}$$

This is Graham's "Law of Overfishing" (*40*, *41*) implying that as CPUE declines, an increasing amount of time is spent fishing in an increasingly larger area. For an individual population, as the fishing rate (*F*) increases mortality up to an unknown maxima, while numbers of fish (*N*), biomass of the population (*B* or *B* at MSY), mean size (usually length), mean weight at age, mean size and age at maturity, fecundity, recruitment (*r*), somatic and population growth (*g*), productivity, and ultimately yield (*Y*) all decrease (Fig. 1A)

$$F_{\rightarrow\max} \overset{\text{yields}}{\longrightarrow} \downarrow \left\{ \begin{array}{c} N, B, Y, B/B_{\mathrm{MSY}} \\ r, \mathrm{size}_{\mathrm{mat}}, \mathrm{age}_{\mathrm{mat}} \\ wt_a, len, g \end{array} \right. , \uparrow \left\{ \begin{array}{c} E \\ \mathrm{Area}_{\mathrm{fished}} \\ F/F_{\mathrm{MSY}} \end{array} \right. \tag{2}$$

As this occurs, the area fished and effort to catch fish increase, resulting in a fishing rate that exceeds that for MSY ($F/F_{\mathrm{MSY}} > 1$). There are various caveats to this regarding growth or recruitment overfishing (*4*, *10*), but the general patterns hold based on population dynamic theory. This theory and practice of population overfishing have well-demarcated features (*4*, *9*, *10*), which lead to relatively clear thresholds of overfishing and overfished population status, important decision criteria for fisheries management.

The typical yield curve (fig. S1) demonstrates that fishing effort has an optimal level of catches, with anything exceeding that resulting in overfishing. Several properties of this curve, or proxies thereof, are used to set fishing thresholds. Translating fishing effort into fishing rates has led to the relationship whereby $F/F_{\mathrm{MSY}} > 1$ (or proxies of $F_{\mathrm{MSY}}$; e.g., $F_{0.1}$, $F_{35\%}$, etc.) is defined as overfishing, often used as a threshold in conjunction with estimates of biomass or productivity [biological reference point (*4*, *9*, *10*)]. This implies a sustainable level of harvesting with biomass at ~50% of carrying capacity, with associated thresholds for *B*. In other words, the fishing effort should be at a rate that is less than the rate of fish production to maintain the population.

Most measures of overfishing have focused on individual fish populations (Fig. 1A and fig. S1), yet governance systems need to address the wider aspects of EOF (Fig. 1B). There have been several attempts to quantitatively characterize the impacts of EOF (*10*–*13*). However, there are few, if any, with clear thresholds and delineation of EOF (*12*, *14*) and no definitions that are widely used. By extending definitions of single-species overfishing, we posit that there is an analogous suite of overfishing dynamics for ecosystems (Fig. 1B) (*10*, *14*). As individual population *C* declines and *E* increases, such that CPUE ultimately declines beyond what is economically viable for a given population, *C* shifts toward a second, less preferred species, and the cycle then repeats itself ad infinitum

$$\begin{gathered} C_1\downarrow, E_1\uparrow, \ldots \mathrm{CPUE}_1 \rightarrow \min; \rightarrow \\ E_2\uparrow, C_2\uparrow, \mathrm{CPUE}_2\uparrow, C_2\downarrow, E_2\downarrow, \ldots \mathrm{CPUE}_2 \rightarrow \min; \rightarrow \sum_{i=1}^{n} C_i, E_i \end{gathered} \tag{3}$$

Overall, *C* in the ecosystem increases until CPUE declines, escalating to the point of systemic degradation. This is the Law of Sequential

Depletion (*10*, *41*, *42*), a corollary to Graham's Law of Overfishing (*40*, *41*). The cycle of CPUE implies an expansion of both geographic and taxonomic scopes as fleets pursue more and more distinct types of biomass in more and more distinct and distant habitats to maintain economically viable levels of CPUE (Fig. 1B) (*19*, *20*, *22*). For the system of populations, as total $C$ (or $E$) increases as integrated across all species, the mean size (usually some measure of length), total $B$, and total yield decline, whereas the size spectrum slope ($\beta$) increases (*19*, *24*). Besides the facets noted above (Eq. 2), occurring across all species, other composite impacts are also observed. The species composition changes, and thus biodiversity may change, but not always in a predictable manner as, by definition, any particular diversity estimate can result from multiple responses to a range of changes in multiple configurations of species composition. These caveats aside, the principles of sequential depletion generally hold as based on theories from community ecology in a perturbation context (*14*). For energy flow and food webs affected by fisheries, as overall $C$ (or $E$, or $F$) increases, the L index, total system throughput, system ascendancy ($A$), $B$ of apex predators of conservation significance, cumulative $B$ inflection points, cumulative $P$, mean TL, and system redundancy ($R$) all decline (*12*, *14*). Disruption in trophic linkages also typically occurs [e.g., forage fishes (*42*)]

$$F_{\text{system}\rightarrow\max} \xrightarrow{\text{yields}} \downarrow \left\{ \begin{array}{c} \Sigma N, \Sigma B, \Sigma Y, B_{\text{apex}} \\ \bar{l}, cumB_{\text{infl}}, cumP \\ L_{\text{index}}, TST, A, R, TL_{\mu} \end{array} \right., \uparrow \left\{ \begin{array}{c} E, \beta \\ \text{Area}_{\text{fished}} \\ F_{\text{system}}/F_{\text{system MSY}} \end{array} \right. \tag{4}$$

Similar to the single population instance, as this occurs, the area fished and effort to catch all fish increase, resulting in a system-level fishing rate that exceeds that for MSY of the system ($F_{\text{system}}/F_{\text{systemMSY}} > 1$). In essence, one can extend the typical yield curve from an individual population to an entire system of fishes (fig. S1), with the same general properties and relationships. Doing so, links all fisheries removals to the nominal carrying capacity of the ecosystem. In other words, fishing effort should be at a rate that is less than the rate of ecosystem production required to maintain the aggregate of all fished taxa. Several example calculations have estimated these multispecies, aggregate, or system-wide MSYs (*15*, *27*), but although extant, their use as thresholds has been quite limited in practice. We propose analogous thresholds but ones that are based on a more direct relationship to ecosystem productivity.

We acknowledge that there are many other potential facets of EOF relating to habitat, bycatch, biodiversity, apex predators, ecosystem functioning, etc. (Fig 1B) (*4*–*8*, *42*). Yet, we emphasized trophic transfer as a basis for determining the limits of fisheries production as that is intuitive, has had copious background studies establishing and describing these relationships (*16*, *17*, *24*), and most population-oriented definitions of overfishing similarly focus on production of the population while acknowledging that other facets of population productivity do not typically use those other features (i.e., links to habitat, predation, etc.) to delineate population overfishing (*4*, *9*).

To summarize, we define EOF as an instance where the sum of all catches are flat or declining, total CPUE is declining, and total landings relative to ecosystem production is excessive. The question is: At what point are landings deemed excessive?

### Real limits to global fisheries production

The productivity of the World Ocean is large but finite. The PP of the World Ocean is 40 to 50 Gt C year$^{-1}$, given mass-balance constraints of PP and nutrient recycling pathways (which converts to ~400 to 500 Gt year$^{-1}$ wet weight) (*43*, *44*). Climate change considerations predict that where that PP both occurs and is transferred to upper TL organisms of commercial importance will shift, vary in timing of major blooms, and change in species composition (*17*, *24*, *37*, *38*), with tropical regions generally projected to be less productive (*37*, *38*). Yet, no projections have PP globally increasing (*24*, *37*–*39*). Thus, theoretically, there exists an overall, global cap on fish production as determined by lower TL production [sensu (*45*, *46*)].

The limitations to fishery production by PP have been recognized for some time (*45*, *47*–*49*). The PP required to support fishing ultimately limits the total amount of fish that can be caught in any given part of the world's ocean (*11*, *17*, *18*). It is increasingly recognized that different pathways of production are important in increasing fisheries potential production (*16*, *27*), but ultimately, PP can limit the dynamics and options of fishing fleets (*50*).

Previous estimates of global marine capture fisheries production tend to be on the order of 0.1 Gt year$^{-1}$ (i.e., ~100 × 10$^6$ t year$^{-1}$). Estimates of total, global fisheries yield ranges from 200 × 10$^6$ t year$^{-1}$ (*49*), 140 to 180 × 10$^6$ t year$^{-1}$ (*27*), 150 × 10$^6$ t year$^{-1}$ (*48*), 130 × 10$^6$ t year$^{-1}$ (*34*), 115 × 10$^6$ t year$^{-1}$ (*47*), and 100 × 10$^6$ t year$^{-1}$ (*11*, *45*) to 68 × 10$^6$ t year$^{-1}$ [although this was just mean annual catch from 54 of 66 LMEs (*17*)]. A few more recent estimates are closer to 1000 × 10$^6$ t year$^{-1}$ (i.e., 1 Gt year$^{-1}$), ranging from 790 × 10$^6$ t year$^{-1}$ (*20*) and 1.1 Gt year$^{-1}$ (*35*, *51*) to 2 Gt year$^{-1}$ (*52*), but those are recognized as being at the higher end of the estimates when considered relative to total, global net primary production (NPP).

Recent official estimates of the total marine capture fishery yield remain on the order of 0.1 Gt year$^{-1}$ (*1*). Debates as to the exact magnitude of total marine capture fisheries yield persist (*23*, *34*, *46*, *50*, *53*). These debates center around the actual magnitude of fishery production potential, whether the estimates are carrying capacity ($K$) or biomass at MSY ($K/2$), whether the estimates adequately capture IUU fishing, the methods for extrapolating data are appropriate, and other concerns over missing or misrepresented data. Regardless of these debated caveats as to the magnitude and source of the estimates, the total catch of global marine capture fisheries has been essentially flat for nearly 30 years (cf. Fig. 4A). Thus, the world is likely at some level of global fishery yield stasis.

The estimates and observed values of total, global catch are within expected ranges given assumptions of TE from PP of 40 to 50 Gt C year$^{-1}$. Essentially, all one needs to estimate fish production is to simply convert PP to biomass and scale up three to four TLs where most caught species function (*11*, *27*). Given the first law of thermodynamics and constraints due to TEs up the food web (*12*, *14*, *54*), there are limits to how much fish any ecosystem can produce and, hence, can be (potentially) caught (*45*, *47*–*49*). Biomass transfers up TLs with a notable inefficiency of energy transfer

$$C_{\text{tot}} = \sum_{1=1}^{\text{TL}} \alpha \cdot \text{PP} \cdot \text{TE}_i^{\text{TL}-1} \tag{5}$$

where PP is often expressed NPP, $\alpha$ is a scalar for local conditions (set to ~15 to 20% for average availability of the TL in estimating total catch, a value that emerges when estimated from maintaining a global average catch that has been stable for the past 30 years) (*12*, *16*, *27*), TE is usually between 10 and 16% (*27*), and the relationship essentially bend or curve downward biomass by about two to three orders of magnitude at TLs 3 at 4, the TL at which most fish are captured (global averages at TL ~3.4) (*35*, *36*).

A sensitivity analysis was conducted on the trophic transfer relationship shown in Eq. 5. A surface of responses with PP ranging from 35 to 55 Gt C year$^{-1}$, TLs ranging from 2.8 to 4.2, and TE ranging from 6 to 16% was examined. Outputs were used to explore the range of probable thresholds for the indices noted below. The results of the sensitivity analysis reveal that catch decreases with an increase in TL, a decline in PP, and/or a decline in TE

$$\downarrow C \begin{cases} \uparrow \text{TL} \\ \downarrow \text{TE} \\ \downarrow \text{NPP} \end{cases} \tag{6}$$

Estimates of global catch are most sensitive to changes in TE, with order-of-magnitude effects transmuted through the exponential TL values. Assuming a NPP of ~45 ± 5 Gt C year$^{-1}$ (i.e., 450 ± 50 Gt year$^{-1}$ wet weight), TE of 10 to 14%, α = 15 ± 5%, and TL ~3.2 to 3.6, when used in these simple trophic transfer calculations results in an estimate of total fishery yield ranging from ~0.1 to 1 Gt year$^{-1}$, consistent with other predictions and slightly higher than current observations.

To obtain higher catches from these calculations one would necessarily have to assume higher PP, which is not projected to occur (*16*, *24*, *39*), or higher TEs at the extremely high end of observed ranges, which, although feasible, are not widely observed (*27*, *35*). Thus, on average, it is likely in practice, given the relatively fixed primary production and observed flat fisheries catches, that the world's marine capture fisheries may only have limited potential to become more productive. Using centroid values of NPP of ~45 Gt C year$^{-1}$ (i.e., ~450 Gt wet weight year$^{-1}$), TE of 12%, α = 15%, and TL ~3.4 results in estimates of marine capture fisheries yield of ~416 × 10$^{6}$ t year$^{-1}$, or potentially double or triple that of total catches typically observed, estimated, and reported. Thus, depending upon assumptions of TE (*27*, *35*), and certainly in specific regions, the potential does exist for increased fisheries yield. A reasonable range of fisheries yield is thus, based on current estimates and this scoping exercise, likely on the order of 0.1 to 0.42 Gt year$^{-1}$. Collectively, the global limits on PP, and hence fish production, imply that global fisheries yield may not yet be at a global carrying capacity but may be approaching these limits. The global consistency of catches for the past 30 years coupled with catches relative to PP of 0.1 to 3‰ again implies some level of global fishery yield stasis.

### Derivation of novel indices and delineation of EOF

Given the limits to fishery production in any given ecosystem forms a reasonable basis for delineating EOF. This can be expressed via three new indices proposed here. Using the centroid values of PP of ~45 Gt C year$^{-1}$, trophic TE of 12%, α = 15%, and TL ~3.4 again results in estimates of fisheries yield of ~0.42 Gt year$^{-1}$, with a reasonable range—based on theory and observation—of fisheries yield thus likely on the order of 0.1 to 0.42 Gt year$^{-1}$. This range of likely fishery yields can bracket the limits of fisheries production, can be used to bracket relationships of fisheries landings to other variables, and can provide an empirical basis for potential thresholds.

Scaling these production estimates by an area allows the calculation of the maximum sustainable yield for any part of the ocean. Given that the surface area of the world's ocean is approximately 363 M km$^{2}$, one can estimate the areal values of catch, which can be reasonably expected. We call this the Ryther index (*45*). Ryther's original work (*45*) not only related landings to PP but also provided a global thinking and evaluation of fisheries catch. Thus, catches of 0.1 to 0.42 Gt year$^{-1}$ would result in a yield of 0.27 to 1.14 t km$^{-2}$ year$^{-1}$, suggestive of a possible threshold NTE (~1). Even extreme estimates of global total catch around 1 Gt year$^{-1}$ would result in a value of 2.7 t km$^{-2}$ year$^{-1}$ (~3 t km$^{-2}$ year$^{-1}$).

Another potential measure of EOF would be to contrast the ratio of fisheries catches to PP in an ecosystem. We call this the Fogarty ratio index (presented as per mil) (*27*). Fogarty *et al.* (*27*) have been estimating these values for some time and have proposed the use of this ratio as a means to manage fisheries. Simple calculations based on trophic transfer theory and an order of magnitude bracketing by a TL between 3 and 4 (based on Eq. 5) suggest a range of possible catches relative to PP that would be feasible. That is

$$\begin{aligned} &\text{For a} \sim 10\%\ (\text{TE})\ \hat{}\sim 3\ (\text{TL}) = 0.1^3 \rightarrow 0.001 = 1‰; \\ &\sim 10\%\ (\text{TE})\ \hat{}\sim 3.5\ (\text{TL}) \rightarrow 0.0003 = 0.3‰; \\ &\sim 15\%\ (\text{TE})\ \hat{}\sim 3\ (\text{TL}) \rightarrow 0.003 = 3‰; \\ &\sim 10\%\ (\text{TE})\ \hat{}\sim 4\ (\text{TL}) = 0.1^4 \rightarrow 0.0001 = 0.1‰ \end{aligned} \tag{7}$$

Thus, on the basis of simple trophic transfer calculations, the Fogarty ratio of catches relative to PP ranges from 0.1 to 3‰. This again is suggestive of reasonable limits to catch potential and hence a possible threshold. Thus, given catches of 0.1 to 0.42 Gt year$^{-1}$ would imply an expected ratio of catch to PP of 0.22 to 0.92‰, suggesting a possible threshold NTE (~1). Even an extreme estimate of catches near 1 Gt year$^{-1}$ would result in a value of 2.2‰ (~2.5‰).

Acknowledging that estimates of PP are not always available but that satellite imagery able to produce estimates of chlorophyll a may be more so, we propose a proxy index. Coupling catch statistics with chlorophyll a estimates, and acknowledging all the important nuances of chlorophyll a and different pathways of production (*16*, *27*), we propose a unitless ratio of catch: Chlorophyll a to evaluate relative fishery productivity in those instances where PP estimates are not readily available. We call this the Friedland ratio index. Using logic similar to the Fogarty ratio, an empirical threshold NTE ~1 emerges.

To evaluate these proposed overfishing thresholds, we examined ecosystems with known instances of both population and ecosystem deterioration (see the Supplementary Materials). We acknowledge that copious further simulation testing of these thresholds would be advisable, but as a first-order proposal, here, we present these thresholds as empirically and theoretically based limits to fishing relative to ecosystem productivity. The threshold value of approximately 1 (for each index and their respective units) may be conservative from the perspective of some locales that are more productive or trophically efficient, but we wanted to establish these to not be too sensitive to these nuances; the range of values could be lower (i.e., more precautionary), and the theoretically and empirically estimated extreme values would be ~3× higher. For ecosystems with documented levels of negative impacts, and in some instances, recovery, where a clear history of the trajectory of population and ecosystem dynamics is captured, these thresholds perform well (see the Supplementary Materials).

### Data sources and analysis

Marine capture fisheries data were obtained from Watson (*53*). This database represent a harmonized and mapped compilation of global catch from 1950 to 2014 sourced from the United Nations Food and Agriculture Organization's (FAO) Capture Production 1950–2014 dataset (release date: March 2016; www.fao.org), International Committee for the Exploration of the Sea 1950–2014 (www.ices.dk), Northwest Atlantic Fisheries Organisation Catch and Effort 1960–2014 (www.nafo.int), Southeast Atlantic Capture Production 1975–2014 (release date: June 2016) (www.seafo.org), General Fisheries Commission for the Mediterranean Capture production 1970–2014 (release date: April 2016) (www.gfcm.org), Fishery Committee for the Eastern Central Atlantic Capture production 1970–2014 (release date: May 2016) (www.fao.org/fishery/rfb/cecaf), Commission for the Conservation of Antarctic Marine Living Resources Statistical Bulletin 2016 Vol. 28 1970–2014 (www.ccamlr.org), and Sea Around Us project (SAUP) records for FAO area 18 (Arctic) v1 1950–2010 (extrapolated to 2014) (www.seaaroundus.org). See previous descriptions [and references therein (*19*, *28*, *53*)] for fuller details of data treatment.

For comparison, data were downloaded from FAO using the FishStatJ v2.12.2 software and database package. Data were also downloaded from the SAUP, by LME, using the online web interface to download CSV files. We explored these data across a range of taxa and taxa groups, across FAO statistical area, Regional Fisheries Management Organization, countries, exclusive economic zones (EEZs), and LME resolutions. Although there were differences among datasets in terms of magnitude, the same general trends and order of magnitude results were replicated (*23*, *34*, *46*, *50*, *53*). Thus, we used the compiled, composite set from Watson (*53*).

Upon examination of these data at multiple spatial scales, the clearest pattern in catches emerged from a half-degree by half-degree resolution of the data, as described previously (*19*, *28*, *53*). Effort data were similarly tallied and presented at this resolution (*28*). Catch data were analyzed using latitudinal assignments assigned to the various five (or three) broad latitudinal regions or LMEs (see below). As noted above, similar data were explored from FAO and SAU based on a country, an EEZ, LME, and statistical area assignation, but assignments to latitudinal cells were more resolved; hence, these other perspectives were not presented. We combined the Watson (*53*) data into latitudinal bands of 90°N to 55°N as Arctic, 55°N to 20°N as northern temperate, 20°N to 20°S as tropical, 20°S to 55°S as southern temperate, and 55°S to 90°S as Antarctic. The two temperate bands were combined into a global temperate band, as was the Arctic and Antarctic into a polar band. We also used the Watson (*19*, *53*) data for each of the 65 LMEs. We acknowledged that aggregation across spatial scales could obfuscate some patterns among fisheries, but is the scale at which most fisheries operate (i.e., LME scale), the main patterns should be emergent. Estimates of PP (see below) were chosen at resolutions consistent with these scales. We also acknowledged that aggregating across taxa could also obfuscate some patterns among fisheries, but since our primary purpose was to explore total catches by ecosystem and this is a relatively simple integration, the total catch patterns would also emerge.

We present the FAO total capture fisheries catch en bloc as that is a familiar graphic to the discipline, as well as by the three main latitudinal bands. Decadal averages of effort and CPUE were also provided [adapted from Anticamara *et al.* (*28*)], as well as proportions across latitudinal bands. Catch and CPUE were examined across example sequential stanzas (from 1950 to 1959, from 1970 to 1979, and from 2010 to 2014) and across longitudinal extent for several LMEs.

To highlight global shifts in distribution of catch across time, we present three stanzas spanning more than 50 years from the Watson data described above, one from 1950 to 1959, another from 1970 to 1979, and the most recent one from 2010 to 2014. Assignment of catches to 10° blocks was as described in Watson (*19*, *53*). These data were captured on a global projection, and the spatial density of catches was scaled to maximal catch across all eras. Catches assigned to LME areas and to latitudinal bands, expressed as t km$^{-2}$, are presented as the Ryther index.

Estimates of chlorophyll a and NPP were similarly estimated for all LMEs and latitudinal bands, from 1998 to 2014 using satellite imagery. These used a combined SeaWIFS and MODIS imagery set (https://oceancolor.gsfc.nasa.gov/). Chlorophyll a was adapted from the merged time series data (http://hermes.acri.fr/) at 25-km spatial resolution and annually integrated using monthly time steps. PP was estimated using the Behrenfeld method (*55*), was annually integrated using daily values, and then summed for each LME or latitudinal band.

The spatial catch data were compared to chlorophyll a values to calculate the Friedland ratio index. The same catch data were compared to estimates of NPP to calculate the Fogarty ratio index (*27*). Both LME and latitudinal bands were evaluated. We also acknowledge the difference in latitudinal bands and LMEs, such that LME areas tend to exclude open ocean ecosystems and, hence, are areas where fish catches and PP tend to concentrate. Thus, global phenomena need to be interpreted within regional and even local contexts. In addition, within an LME, other sources of production may be occurring at the sub-LME scale that might not be as readily detectable via satellite (upwelling, estuarine, etc. inputs) and thus sporadically and locally alter production estimates. Thus, we recommend that the indices proposed here be used cognizant of other potential sources of productivity and that are relevant to the scale at which fisheries management mostly occurs.

## SUPPLEMENTARY MATERIALS

Supplementary material for this article is available at http://advances.sciencemag.org/cgi/content/full/5/6/eaav0474/DC1

Fig. S1. The classical fishery yield curve showing catch and CPUE compared to effort.

Fig. S2. Fishery yield curves for all fish (total) catches for example LMEs.

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