LETTER

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The trophic fingerprint of marine fisheries

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Biodiversity indicators provide a vital window on the state of the planet, guiding policy development and management[1,2]. The most widely adopted marine indicator is mean trophic level (MTL) from catches, intended to detect shifts from high-trophic-level predators to low-trophic-level invertebrates and plankton-feeders[3–5]. This indicator underpins reported trends in human impacts, declining when predators collapse ("fishing down marine food webs")[3] and when low-trophic-level fisheries expand ("fishing through marine food webs")[6]. The assumption is that catch MTL measures changes in ecosystem MTL and biodiversity[2,5]. Here we combine model predictions with global assessments of MTL from catches, trawl surveys and fisheries stock assessments[7] and find that catch MTL does not reliably predict changes in marine ecosystems. Instead, catch MTL trends often diverge from ecosystem MTL trends obtained from surveys and assessments. In contrast to previous findings of rapid declines in catch MTL[3], we observe recent increases in catch, survey and assessment MTL. However, catches from most trophic levels are rising, which can intensify fishery collapses even when MTL trends are stable or increasing. To detect fishing impacts on marine biodiversity, we recommend greater efforts to measure true abundance trends for marine species, especially those most vulnerable to fishing.

Adoption of an ecosystem approach to fisheries requires managers to conserve marine biodiversity, not just focus on fished stocks[8]. Biodiversity indicators are used to assess the impacts of fishing and the effectiveness of management, and thus guide the development of future policies[9–12]. The most widely used indicator, catch MTL, measures shifts in reported catches from high-trophic-level predators such as cod to low-trophic-level species such as filter-feeding oysters and small herbivorous fish[3,13]. In 1998, catch MTL was reported to be declining at an alarming 0.1 units per decade ("fishing down marine food webs"[3]), and was interpreted to result from broad reductions in top predator biomass[3–5]. Catch MTL was the primary marine index chosen by the Convention on Biological Diversity to measure global biodiversity, and has been applied widely to report on the state of the marine environment[1–5,9–12].

Catch MTL is interpreted to track changes in the underlying ecosystem[3–5,14], but its usefulness as an indicator has been questioned because catches are influenced by changes in economics, management, fishing technology and targeting patterns[6,15–20]. Here we conducted the first large-scale test of whether catch MTL is a good indicator of ecosystem MTL, marine biodiversity and ecosystem status. We identified four main patterns of fisheries development and modelled their influence on MTL, and then compared these theoretical predictions with estimates of MTL from global compilations of catches, long-term trawl surveys, and fisheries stock assessments[7], addressing three key questions: (1) whether catch MTL is positively correlated with ecosystem MTL, (2) what is the global MTL trend based on data from different sources, and (3) whether trends in MTL are informative about trends in marine ecosystem status.

We compiled ecosystem models[21] from 25 different ecosystems around the world, and simulated four main scenarios to examine the theoretical relation between catch MTL and ecosystem MTL (Fig. 1). The four scenarios were 'fishing down'[3], as already outlined, 'fishing through'[6], in which sequential expansion of low-trophic-level fisheries rather than collapses of top predators drives MTL, 'based on availability'[19], in which easily accessible species with high biomass are targeted first before expanding to less-accessible stocks with lower yields, and 'increase to overfishing', in which all species are fished with growing intensity over time until depleted. The simulations show that 'fishing down' and 'fishing through' both produce declining trends in catch MTL, but that 'fishing down' results in greater initial declines in ecosystem MTL, and more collapsed species than does 'fishing through'. These scenarios predict that, at the end of the

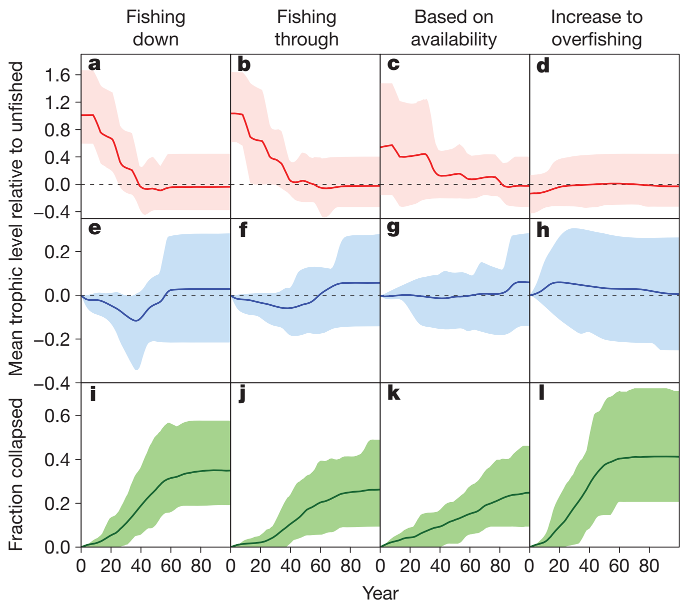

Figure 1 | Changes in MTL relative to unfished ecosystem MTL. Red, catches; blue, ecosystem biomass; green, the corresponding fraction of groups that are collapsed. Each panel shows the mean (solid line) and confidence intervals (10th and 90th, shading) of models from 25 ecosystems, for 100 years since the modelled start of fishery development. The scenarios are as follows. **a**, **e**, **i**, 'Fishing down': fishing top predators to depletion before sequentially switching to and depleting lower and lower trophic level groups. **b**, **f**, **j**, 'Fishing through': maintaining high catches of top predators while sequentially adding species at lower and lower trophic levels. **c**, **g**, **k**, 'Based on availability': targeting the most abundant and accessible taxa first before shifting to less-abundant and harder-to-access taxa. **d**, **h**, **l**, 'Increase to overfishing': expanding fishing mortality on all fished groups over time to twice the sustainable level for each group.

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simulations, most species are depleted (and many are collapsed to less than 10% of unexploited biomass), but MTL has returned to values observed in unexploited systems, because species across all trophic levels are equally depleted. More variability is observed in outcomes from the 'based on availability' scenario, which generally predicted declines in catch MTL, but less change in ecosystem MTL. Finally, the 'increase to overfishing' scenario hardly influenced catch and ecosystem MTL, but resulted in many collapsed species. These results (Fig. 1) are averaged over all models, and obscure substantial differences observed in particular models (Supplementary Figs 1–4). Overall, catch and ecosystem MTL were negatively correlated in many ecosystem models (35–38% of all models) in the 'fishing down', 'fishing through', and 'based on availability' scenarios, but usually positively correlated for the 'increase to overfishing' scenario and for additional scenarios in which fishing was applied evenly across all species (Supplementary Figs 5–10). Importantly, this shows that when fishing disproportionately affects one part of the food web, the relation between catch MTL and ecosystem MTL often breaks down, but when fishing similarly affects all species, catches act as a representative sample of ecosystem changes.

We calculated catch MTL from global fishery landings, finding substantially different values and trends to those reported in ref. 3 (Fig. 2a). In particular, catch MTL has not declined steeply since the 1970s, but initially declined and then increased from the mid-1980s. Other recent publications reporting similar trends[2,22,23] have not explained why their results differ from those in ref. 3. We discovered that these differences arose from updates to the main source of trophic level estimates, FishBase[24], and not from changes in relative catches

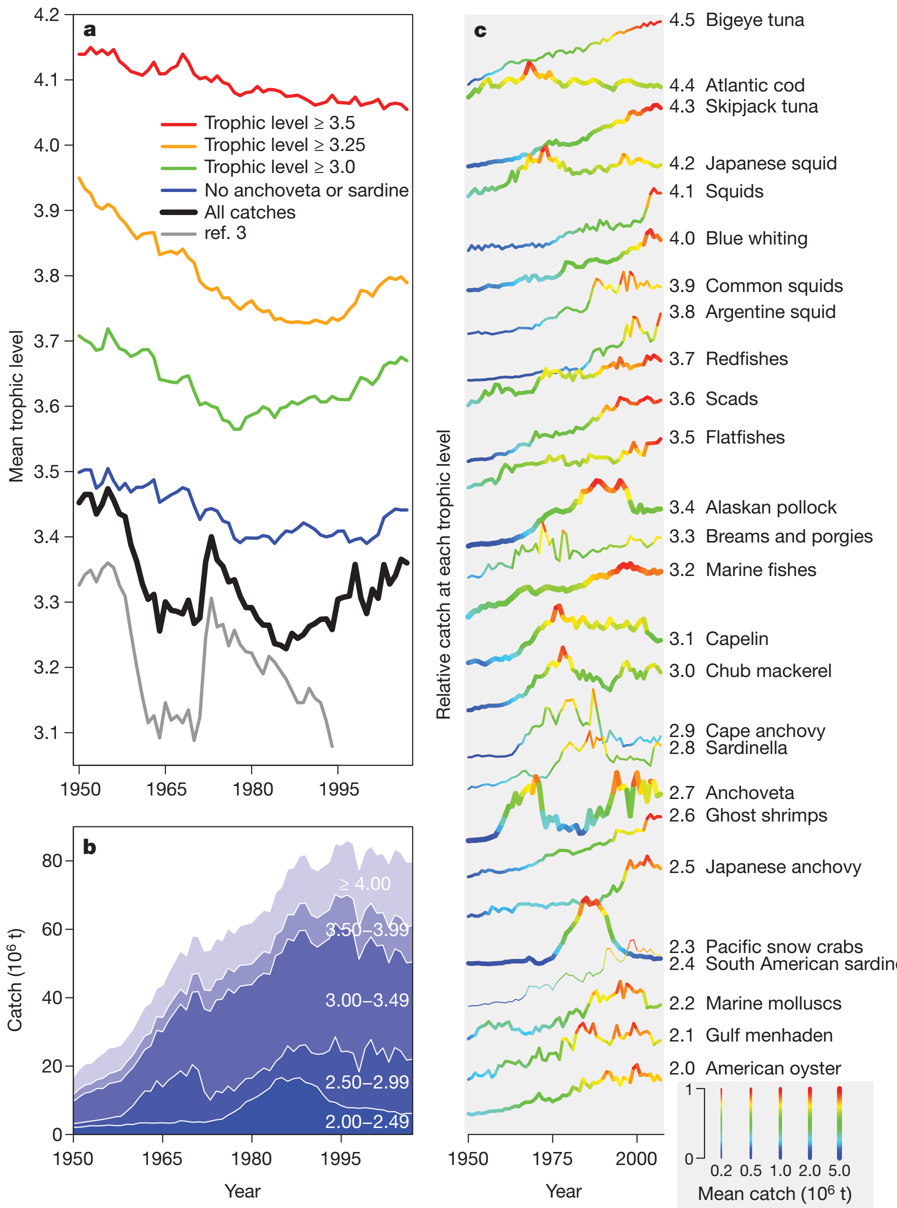

Figure 2 | Trends in MTL from global marine catches. a, Catch MTL in ref. 3 (grey), compared with catch MTL calculated from the most recent data (black), calculated after excluding anchoveta and South American sardine (blue), and calculated after excluding all species below trophic level 3.0 (green), 3.25 (orange), and 3.5 (red). **b**, Total catches divided into 0.5 trophic level bins. **c**, Relative catch trends divided into 0.1 trophic level bins, with the most dominant taxon in each bin listed on the right (when summed, these taxa account for 50% of global catches). The legend for **c** at the bottom right explains that line colours are graded from zero (deep blue) to maximum relative catch (red) within each bin, while line width is proportional to average annual catch. t, metric tonnes.

among species. One key change was increasing the trophic level estimate of anchoveta from 2.2 to 2.7, which markedly altered the global catch MTL trend, and highlights the sensitivity of catch MTL trends to uncertainty in trophic level estimates (for more details see Supplementary Materials and Supplementary Figs 12–14).

In addition to anchoveta, global catch MTL trends are affected by other highly fluctuating stocks of small pelagic fishes. Dips and recoveries in catch MTL in the 1960s and 1980s were caused by the respective rapid development and collapse of anchoveta and sardine fisheries, which fluctuate in response to climate and fishing and are often out of phase with each other[25]. Catch MTL is much smoother over time when recalculated without these two species (Fig. 2a). Examining species grouped by 0.1 trophic level bins (Fig. 2c) reveals that catches of small pelagic species peaked at various times from the 1960s to the present[25]. Consequently, trends differ considerably when small pelagics are excluded by re-estimating catch MTL from groups with trophic levels above 3.0, 3.25 or 3.5 (ref. 5) (Fig. 2a). Declining trends in catch MTL within the remaining higher-trophic-level groups are driven by the collapse in Atlantic cod catches since the 1960s; removing Atlantic cod results in increasing catch MTL trends for groups above trophic levels 3.0, 3.25 and 3.5 (Supplementary Fig. 14). However, although Atlantic cod catches declined, catches of most other high-trophic-level predators expanded over time (Fig. 2c), while global catches increased until the mid-1980s and then levelled off[23,26,27] (Fig. 2b). Overall, fishing pressure has expanded at all levels of marine food webs, similar to our model scenario "increase to overfishing".

Ecosystem MTL estimates were calculated in two ways: survey MTL from biomass estimates from 29 long-term trawl surveys, and assessment MTL from biomass estimates of 242 fisheries stock assessments. Trawl surveys offer consistent time series of ecosystem biomass, whereas assessments combine information from multiple sources to estimate biomass trends, focusing on important commercial stocks. Survey MTL is affected by catchability differences among species, and both survey MTL and assessment MTL are dependent on the selection of species that are surveyed or assessed, but both sources provide MTL estimates that can be used to measure ecosystem changes directly. We found that survey MTL and assessment MTL were higher than catch MTL (Fig. 3), reflecting the greater focus of surveys and stock assessments on bottom-dwelling high-trophic-level fish species that account for only a moderate proportion of total catch weight. Survey MTL initially declined, but is now higher than in the 1970s, whereas assessment MTL declined until the 1990s before recovering to within 0.05 units of the start value. Catch MTL was not positively correlated with ecosystem MTL. When all data are combined, catch MTL was negatively correlated with both survey MTL (Pearson correlation $r = -0.55$) and assessment MTL ($r = -0.31$) (Fig. 3); when restricted to a common set of stocks, catch MTL was also negatively correlated with assessment MTL ($r = -0.41$) (Supplementary Fig. 18). These results indicate that catch MTL does not track changes in ecosystem MTL.

We also compared catch, survey and assessment MTL in individual ecosystems, finding that catch MTL is negatively correlated with survey MTL for 13 of 29 surveys, and negatively correlated with assessment MTL in 4 of 9 ecosystems. Three examples demonstrate these differences. In the Gulf of Alaska, catch and assessment MTL are dominated by Alaskan pollock and failed to capture the well-documented regime shift from low-trophic-level shrimp and crabs to high-trophic-level fish in the late 1970s[28,29], but the Gulf of Alaska small-mesh shrimp survey did detect this shift, increasing 0.8 units (Fig. 4b, survey 3 in red). Conversely, the early-1980s collapse of cod and shift to invertebrates in eastern Canada (Fig. 4g, h) is captured by dramatic declines in catch MTL, but hardly visible in trawl surveys in the region, which lacked invertebrate data. Finally, in the Gulf of Thailand, where almost all fished species collapsed and survey MTL declined[30], catch MTL increased continuously (Fig. 4m). The Gulf of Thailand pattern resulted

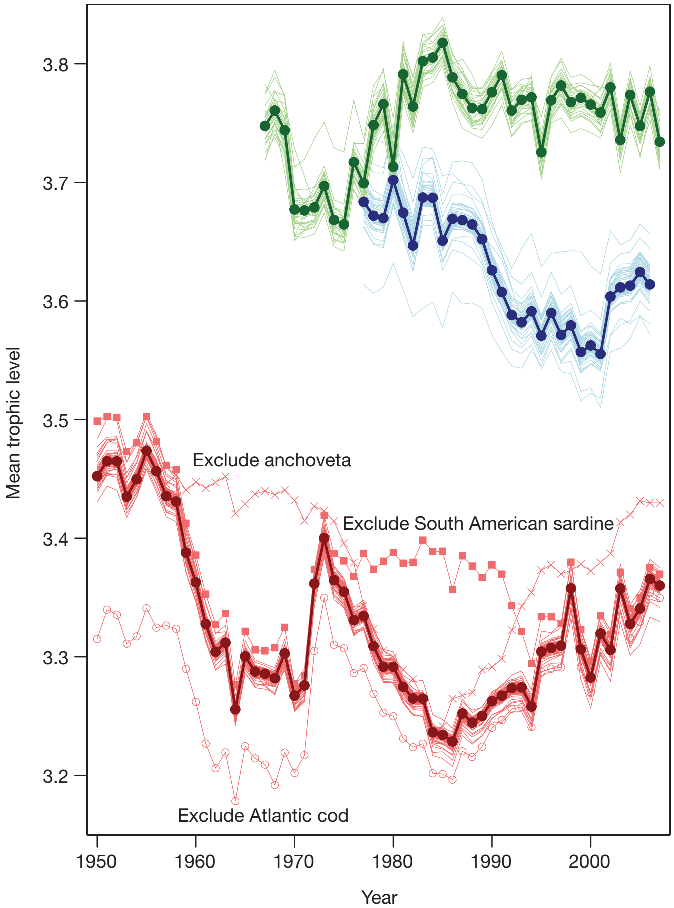

Figure 3 | Measured MTL. Thick lines show MTL from long-term trawl surveys (green), fisheries stock assessments (blue) and global catches (red). Faint lines show the effect of jack-knifing—excluding one unit at a time from the analysis and recalculating the respective trend. The exclusion of anchoveta (crosses), South American sardine (small squares), and Atlantic cod (open circles) substantially influenced the catch MTL time series.

from fishery development similar to the 'based on availability'[19] scenario: fisheries first targeted the most accessible species yielding the highest revenue—mussels, shrimps and small fish—before expanding to high-trophic-level fish.

Global fisheries are at a crucial turning point, with high fishing pressure throughout marine food webs being offset in some regions by rebuilding efforts[7]. To measure the successes and failures of management, it is important for biodiversity indicators to track fishing impacts. Indicators such as catch MTL use readily available data and are quick and easy to calculate, but without improvement are ineffective measures of trends in biodiversity. Our theoretical models and empirical comparisons of catch MTL with ecosystem MTL suggest that catch MTL does not reliably measure the magnitude of fishing impacts or the rate at which marine ecosystems are being altered by fishing. Instead, we recommend a greater emphasis on measuring and reporting changes in marine biodiversity by tracking trends in abundance relative to reference points for conservation and sustainable use. To target limited resources in the best way, we should focus on assessing species vulnerable to fishing that are not currently assessed, and on developing and expanding trend-detection methods that can be applied more widely, particularly to countries with few resources for science and assessment. Through such efforts we can better detect and convey the true impact of fisheries on marine biodiversity.

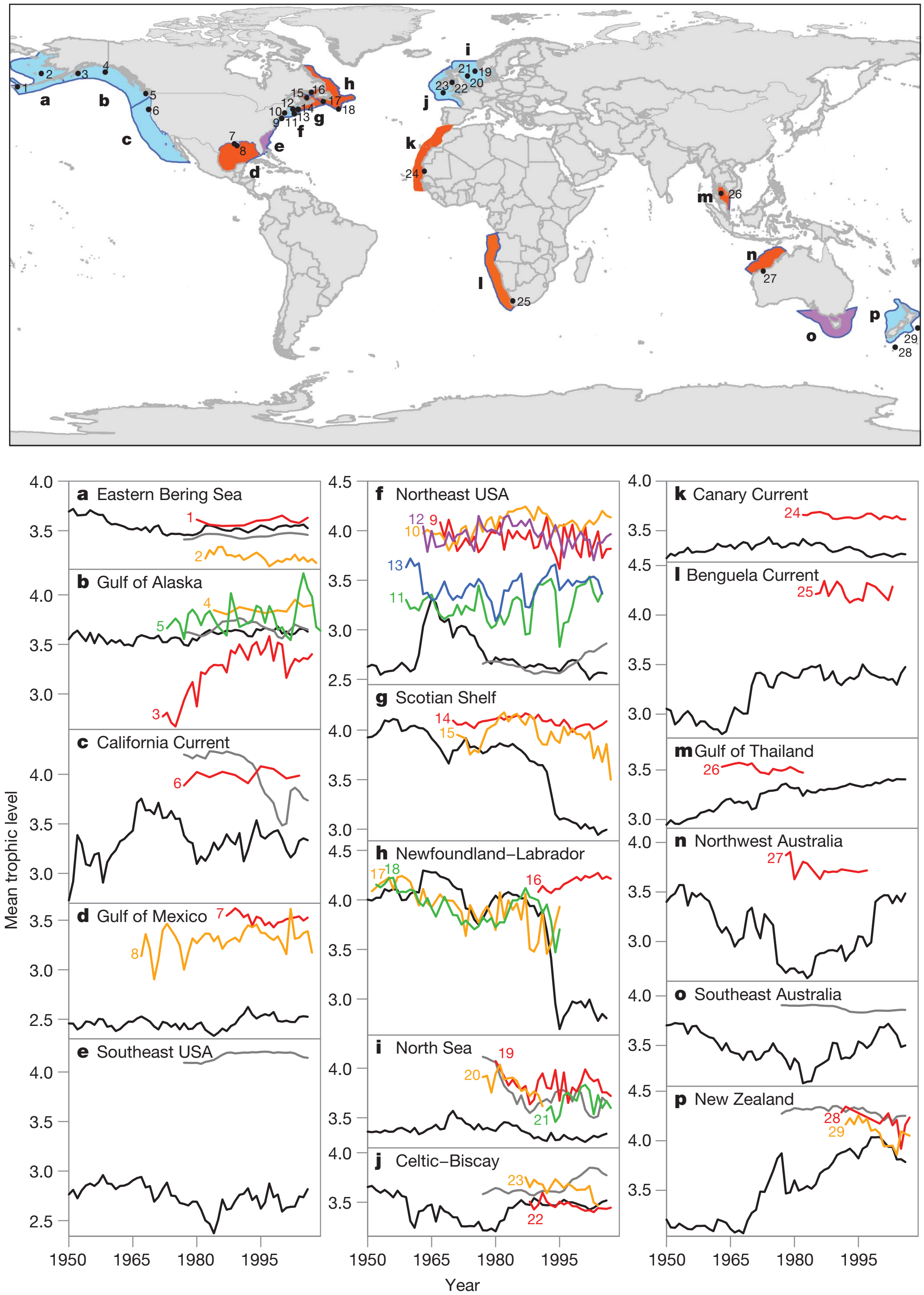

Figure 4 | MTL for each Large Marine Ecosystem. The MTL is shown for each Large Marine Ecosystem from catches (black lines), assessments (grey lines) and surveys (colours). The map shows the location of each Large Marine Ecosystem, highlighting those with data from all three sources (blue), from catches and surveys (red), and from catches and assessments (purple). Numbers on the map reflect the approximate centre of each survey.

METHODS SUMMARY

Each taxon in the analysis was assigned a diet-based fractional trophic level, mostly from the online database FishBase[24]. Primary producers are trophic level one by definition, and were not included in our analyses; herbivores and filter feeders are trophic level two; and omnivores and carnivores are at higher trophic levels. MTL is the catch- or biomass-weighted average of trophic levels of taxa recorded in a particular year. Ecopath with Ecosim models[21] were compiled from well-documented sources and run for 100 years with zero catch to reach unfished states, and then four main scenarios of fishery development (fishing down[3], fishing through[6], based on availability[19], and increase to overfishing) were applied during years 101 to 200. Global catch data were obtained from the United Nations Food and Agriculture Organization (FAO), while catch data for individual Large Marine Ecosystems came from the Sea Around Us Project of the University of British Columbia; trends in catch MTL from these two sources are nearly identical. Long-term scientific trawl surveys from 15 Large Marine Ecosystems provide biomass estimates for regularly recorded taxa, and were obtained from a variety of sources. Biomass estimates for individual taxa were typically not corrected for differential catchability among taxa; furthermore, invertebrate biomass estimates were seldom included in the provided data. MTL time series from individual surveys were combined into a single global time series using a linear mixed effects model with 'Large Marine Ecosystem' modelled as a random effect. Stock assessment biomass values were obtained from the RAM Legacy database; total biomass was preferentially used in the analysis unless spawning biomass was the only time series available. Pearson correlations (r) were used to assess whether MTL followed the same trends in catches, surveys, and assessments, with statistical significance assessed after accounting for autocorrelation within time series.

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Supplementary Information is linked to the online version of the paper at www.nature.com/nature.

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Author Contributions T.A.B. designed the study, analysed the data, and wrote the paper; R.W. analysed the Sea Around Us Project catch data; E.A.F. designed and ran the ecosystem model analyses; S.J. analysed some trawl survey series; C.R.M. combined trawl survey data into a global time series; G.T.P. provided and calculated trophic level estimates; D.R. collated and analysed stock assessment data; and S.R.T. analysed the FAO and Sea Around Us Project catch data. All authors discussed the results and contributed to the manuscript.

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