

Global patterns in marine predatory fish

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Large teleost (bony) fish are a dominant group of predators in the oceans and constitute a major source of food and livelihood for humans. These species differ markedly in morphology and feeding habits across oceanic regions; large pelagic species such as tunas and billfish typically occur in the tropics, whereas demersal species of gadoids and flatfish dominate boreal and temperate regions. Despite their importance for fisheries and the structuring of marine ecosystems, the underlying factors determining the global distribution and productivity of these two groups of teleost predators are poorly known. Here, we show how latitudinal differences in predatory fish can essentially be explained by the inflow of energy at the base of the pelagic and benthic food chain. A low productive benthic energy pathway favours large pelagic species, whereas equal productivities support large demersal generalists that outcompete the pelagic specialists. Our findings demonstrate the vulnerability of large teleost predators to ecosystem-wide changes in energy flows and hence provide key insight to predict the responses of these important marine resources under global change.

Marine top predators influence the structure and dynamics of food webs by imposing mortality and behavioural changes on prey and feeding on parallel pathways of energy from both the pelagic (open water) and benthic (bottom) zone of the ocean^{1–3}. Many of these predator species have declined in population sizes and distribution ranges, which in several cases has resulted in large-scale changes in ecosystems, involving trophic cascades^{2–4}.

Large teleost fish are a dominant group of predators in the global oceans, support lucrative commercial and recreational fisheries and provide food for human populations worldwide^{5–7}. These predators clearly differ in morphology and feeding habits across the world. In tropical and subtropical regions, teleost predators are often fast, mobile species that feed within the pelagic zone^{8,9}, while in boreal and temperate regions the largest teleost species are typically slower growing, demersal (bottom-living)¹⁰ and adapted to feeding on both pelagic and benthic organisms^{6,11–14}. Despite their importance for structuring marine ecosystems and their significant socio-economic value, the underlying factors determining the global distribution and productivity of these two groups of marine predatory fish are poorly known. Here, we test the specific hypothesis that spatial patterns in the distribution and productivity of these groups are primarily driven by pronounced global differences in the productivity of a pelagic and a benthic energy pathway in marine food webs worldwide (Fig. 1).

We examine this hypothesis by assessing the relative productivity of large marine teleost fish using global fisheries landings data¹⁵ across 232 marine ecoregions¹⁶. For each ecoregion, we calculate the average proportion of large pelagic versus demersal fish landings between 1970 and 2014. We show that in this case, the proportion of landings represents a good estimate of the dominant predatory feeding strategy in the sea. We develop a food-web model with two energy channels—one pelagic and one benthic—to formally test our hypothesis and predict the biomass fraction of pelagic versus demersal predatory fish worldwide.

Results

The proportion of large pelagic and demersal teleost predators varies strongly in fisheries landings across the globe (Fig. 2). As

expected, large pelagic fish dominate in the tropics and subtropics, while large demersal fish prevail in temperate and polar regions in both hemispheres. Despite the pronounced latitudinal gradients, some areas in the tropics have a relatively low proportion of large pelagic fish (for example, the Gulf of Mexico and Brazilian shelf), primarily due to high landings of demersal fish species; for example, the highly abundant largehead hairtail (*Trichiurus lepturus*).

Whether landings data can predict biomass (and as such the dominant predatory fish feeding strategy in the sea) has been disputed¹⁷. Here, we use weight fractions in landings and do not predict absolute biomass. Nevertheless, average landings and biomass¹⁸ are highly correlated for 71 pelagic and demersal predatory fish stocks (Supplementary Fig. 1; $P < 0.001$, coefficient of determination = $r^2 = 0.78$). The weight fraction in landings also corresponds well with the fraction in biomass over time, based on assessed pelagic and demersal fish stocks¹⁸ from nine different large marine ecosystems (Supplementary Fig. 2; $P < 0.001$, $r^2 = 0.91$). The proportions of pelagic and demersal fish landings weighted with the economic value of species¹⁹ (that is, a crude measure of potential fisheries preferences) demonstrate a similar global pattern (Supplementary Fig. 3; $P < 0.001$, $r^2 = 0.97$), highlighting that price differences between both groups are overshadowed by the considerably larger differences in the weight of the landings of the two groups. Further robustness checks show that the global patterns remain highly similar if large elasmobranchs (Supplementary Fig. 4; $P < 0.001$, $r^2 = 0.98$) or illegal, unregulated and unreported catches and discards are included in the analysis ($P < 0.001$, $r^2 = 0.99$). The robustness of our result to the potential biases described above provides strong support for using the weight fraction of pelagic versus demersal fish based on global landings as our response variable to estimate the dominant predatory fish feeding strategy in the sea.

We hypothesize that the relative production of pelagic and demersal predatory fish is dependent on the differences in the inflow of energy at the base of the pelagic and benthic pathway (Fig. 1). Most of the ocean net primary production (NPP) occurs in the pelagic layer. Yet, in some regions, sufficient carbon reaches the bottom via sinking and other active transport processes to support

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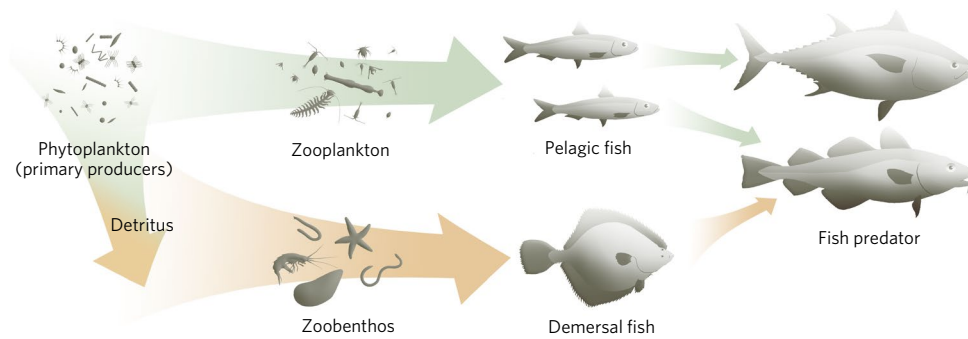


Fig. 1 | Conceptual figure illustrating the competitive interactions between large pelagic specialists and large demersal generalists that feed on smaller pelagic and/or demersal fish and invertebrates. The smaller pelagic and demersal fish feed on zooplankton or zoobenthos.

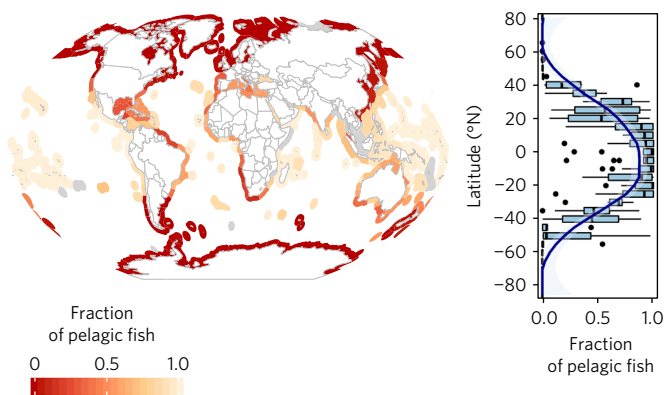


Fig. 2 | Average weight fraction of large pelagic fish compared with large demersal fish in fisheries landings between 1970 and 2014. Large pelagic fish are the dominant group of fish in most tropical and subtropical areas, whereas large demersal fish are dominant in temperate regions and the exclusive group at the poles. The grey ecoregions in the map were excluded from the analysis due to limited data availability (see Methods). The boxplots show the ecoregions ($n = 217$) in bins of 5° latitude, the midline of the box shows the median of the data, the limits of the box show the first and third quartile, and the whiskers extend to a maximum of 1.5 times the interquartile range. The line was derived with a LOESS smoother.

high production of benthic organisms. There are multiple environmental conditions that can influence the downward flux of carbon to the seafloor. First, there is a clear relation with bathymetry, as in deeper oceans only a fraction of the production from the pelagic zone may reach the seabed²⁰. The proportion of NPP that reaches the bottom also varies with latitude. This happens because low water temperatures decelerate remineralization processes and subsequently increase the proportion of NPP available for export^{21,22}, but also because seasonal variability in NPP may result in a temporal mismatch between phytoplankton and zooplankton production, leading to a larger fraction of (ungrazed) NPP sinking to the bottom during the spring bloom in seasonal environments²³. Finally, it has been suggested that the proportion of NPP sinking to the seabed is dependent on the depth of the photic zone and either the total NPP or chlorophyll concentration²⁴.

We approximated the difference in pelagic and benthic production by calculating the ratio of the fraction of NPP that remains in the photic zone (F_{photic})²⁴ versus the fraction of NPP that reaches the seabed (F_{seabed}) (see Supplementary Fig. 5). Using nonlinear regression models, we found that the ratio of F_{photic} versus F_{seabed} explains a substantial part of the global variability in the proportion of large pelagic versus demersal fish landings (Fig. 3; deviance

explained = 68%, $P < 0.001$; see other environmental predictors in Supplementary Table 1). The results show how in most tropical and subtropical areas a highly productive pelagic energy pathway favours large pelagic fish, while in many temperate and polar regions more equal productivities of the two pathways favour large demersal fish (feeding as a generalist on both pelagic and demersal resources).

To further test our hypothesis, we developed a food-web model with two energy channels to predict the biomass fraction of large pelagic species across ecoregions (Fig. 1 and Supplementary Tables 2 and 3). The pelagic and benthic energy pathways are modelled as two separate channels that have their own resource carrying capacity. The carrying capacity of the pelagic resource is calculated by multiplying a total resource carrying capacity constant (R_{max}) by F_{photic} , whereas the carrying capacity of the demersal resource is calculated by multiplying R_{max} by F_{seabed} . The resources are both preyed on by an intermediate trophic level, representing smaller fish and invertebrates, while two groups of predators are included at the top of the energy pathways: a pelagic specialist feeding exclusively on a pelagic diet and a demersal generalist feeding on both energy pathways.

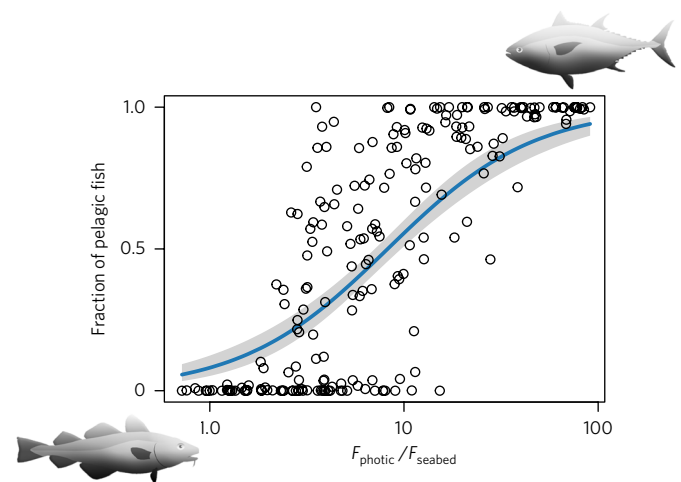


Fig. 3 | Relationships between the fraction of large pelagic fish in fisheries landings and the ratio of F_{photic} versus F_{seabed} for all ecoregions with available data ($n = 217$). Large demersal fish are dominant at approximately equal pelagic-to-benthic NPP ratios, while pelagic fish are dominant in areas where a high fraction of NPP remains in the photic zone (and/or where a low fraction of NPP reaches the seabed) (generalized additive model, $P < 0.001$, deviance explained = 68%). The fit is indicated by the solid line, while the grey area shows the 95% confidence interval.

The food-web model predicted global patterns in pelagic versus demersal predators largely corresponding to the proportions of large pelagic fish derived from landings (Fig. 4a,b; $r^2=0.58$). However, some areas showed a strong mismatch between model predictions and landings data (Fig. 4b,c). Interestingly, the largest differences can be observed at high latitudes in the Southern Ocean and the temperate North Pacific, where the model predicts a higher production of pelagic specialists compared with the proportions derived from landings. We expect that the model predictions are realistic because large pelagic predators are indeed present and highly abundant in many of these areas. However, these are not predatory fish but fast, pelagic-feeding endotherms that maintain a high body temperature and activity despite the cold waters. For example, the Aleutian Islands, Kamchatka shelf, Antarctica and South Georgia (Fig. 4c, red areas) harbour high biodiversity and densities of penguins and pinnipeds^{25–27}. While this lends support to our model predictions, we stress the need for further research on the complementary roles of marine endo- and ectotherm predators. There is also a mismatch in ecoregions in the tropics where the model predicts higher production of demersal generalists compared with the proportions in landings (Fig. 4c, blue areas). In these regions, the energy fluxes to the seabed are predicted to be relatively high (Supplementary Fig. 5), thereby potentially supporting a high production of demersal generalists. The high fraction of NPP predicted to reach the seabed is consistent with other studies that used alternative methods to predict the carbon flux to the seabed on a global scale²³. In many of these areas, relatively high catch rates of sharks and rays can be observed¹⁵—species that are often demersal generalists and, as such, are similar to demersal teleost predators. Although the contribution of large sharks and rays to overall fisheries landings is marginal (Supplementary Fig. 4), which is potentially the result of long-term overfishing²⁸, including elasmobranch predators in the analysis increases the number of demersal generalists substantially near Australia, Peru and Chile in areas where the model predicts higher production of demersal generalists compared with the proportions in landings (Fig. 4c and Supplementary Fig. 4). An alternative explanation for the lower proportion of demersal generalists in the landings might be the ability of pelagic predators to disperse widely⁹ and dampen local differences in the fish abundances of the two predatory groups that have originated from variation in the energy flux to the seabed.

Discussion

Our study supports the hypothesis that the inflow of energy at the base of the pelagic and benthic channel determines the dominant feeding strategy of large teleost predatory fish. Pelagic specialists dominate when energy is primarily channelled through the pelagic pathway, while demersal generalists outcompete the specialists when both pelagic and benthic resources are available. This explanation assumes that demersal generalists' niches and diets overlap with pelagic specialists because they exploit both benthic and pelagic resources. Overlapping diets have indeed been observed in areas where both groups of species co-occur^{11,29,30}. Furthermore, overlapping diets may occur even in the absence of direct spatial overlap between the predator groups due to pronounced habitat shifts of pelagic prey species through daily (vertical) and seasonal (onshore–offshore) migrations (for example, refs^{31,32}). Since both large pelagic and demersal predators may access and feed on these highly mobile prey—but at different times, in different areas and even on different life stages—they engage in exploitative competition. Niche overlap is lower in deep sea environments where demersal species are less able to exploit pelagic resources. Even though reduced niche overlap in deep sea environments is not explicitly represented in our model or data analysis, it is implicitly captured because the fluxes are typically low in deep sea areas and consequently pelagic specialists are dominating. Although the degree of

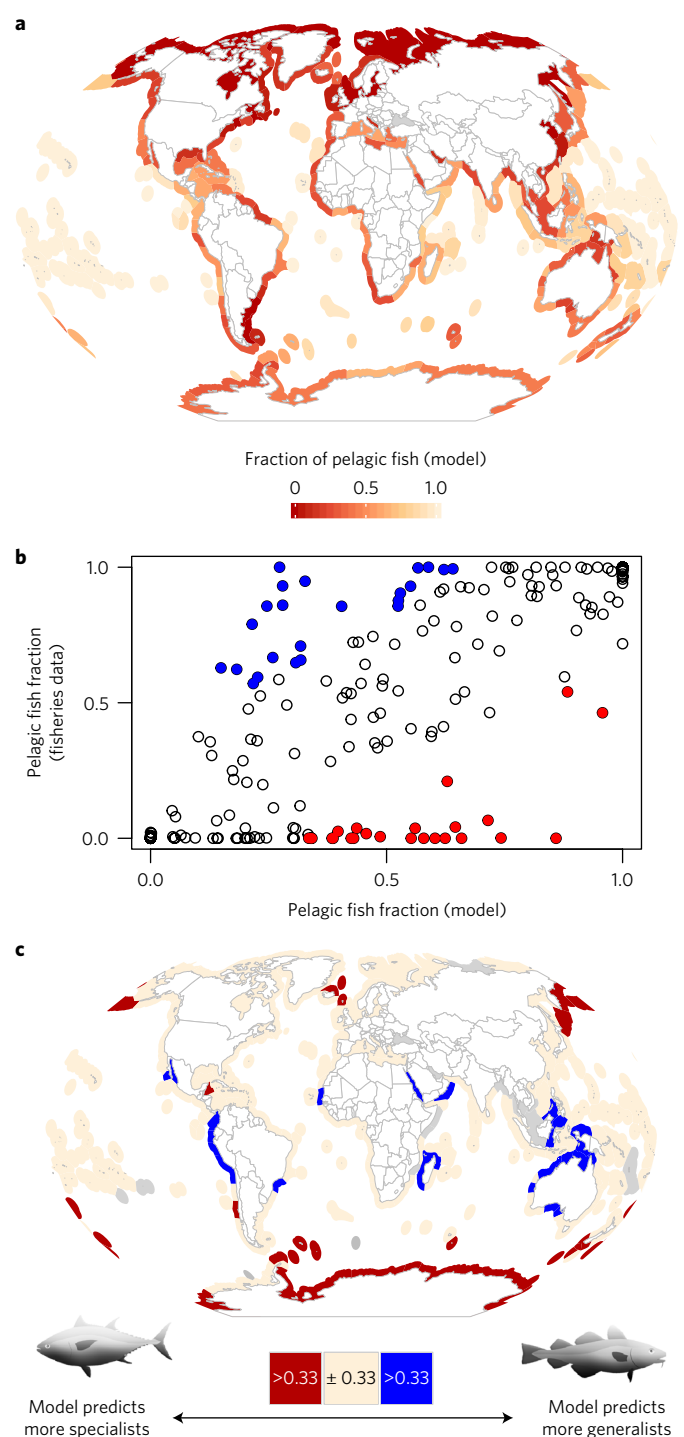


Fig. 4 | Predictions of the dominance of large pelagic specialists or demersal generalists across marine ecoregions using a food-web model. a, Map of the predicted weight fraction of large pelagic specialists compared with demersal generalists in the food-web model based on region-specific energy fluxes. **b**, Relationship between the fraction of large pelagic fish in fisheries landings data and the food-web model for each ecoregion ($y = 0.04 + 0.92x$, $r^2 = 0.58$, $P < 0.001$). The coloured points correspond to ecoregions with a large difference (>0.33) between the model predictions and the data; with either more pelagic specialists (red points) or demersal generalists (blue points) compared with the fisheries data. **c**, Map of all ecoregions with a large difference (>0.33) between the fraction of large pelagic fish in fisheries landings and the model, following **b**. The grey ecoregions were excluded from the analysis due to limited data availability.

dietary overlap and strength of competition between pelagic and demersal predators on a global scale are poorly known, our results suggest that competition between pelagic and demersal feeding strategies exists. Consequently, a decline in the productivity of the benthic energy pathway will shift dominance towards pelagic specialists (and vice versa).

We assumed that large pelagic teleost fish are superior in exploiting the pelagic resource compared with large demersal species. Large pelagic fish are highly adapted to feeding on fast-moving pelagic resources (such as forage fish) and have developed specific morphological features (for example, high muscle protein, a large gill surface area and the warming of muscles) to support an active pelagic lifestyle^{33,34}. Such physiological and morphological adaptations can explain the superiority of pelagic specialists to feed on pelagic prey compared with the more 'sluggish' demersal generalists. Yet, we lack the knowledge to explicitly account for the energetic costs associated with these physiological and morphological adaptations³³ in a food-web model, and also, to account for the costs of finding, capturing and digesting prey for both groups of species. Quantifying these energetic costs will allow for a further refinement of the food-web model and support estimates of fish production of both species groups across oceanic regions.

Our global analysis of predatory fish largely ignored the role of non-teleost fish and marine endotherm predators. The contribution of non-teleost predators in global fisheries landings is low (Supplementary Fig. 4). Yet, non-teleost predators are typically overfished²⁸ and abundances were probably much higher in the past and may increase again in the future. The potential increase in abundance highlights the need to understand the interplay between teleost and non-teleost predatory fish for future predictions of the global occurrence and productivity of fish predators. Additionally, it is unclear from our study under which environmental conditions endotherm predators are a highly abundant and dominant predatory species group. Following the results of our food-web analysis (Fig. 4), we hypothesized that pelagic-feeding endotherms are the dominant predatory group at high latitudes in the Southern Ocean and the temperate North Pacific. Yet, the complementary roles of marine endo- and ectotherm predators in relation to temperature and the productivity of the pelagic and benthic energy pathways needs further study.

When top predators feed on both pelagic and benthic prey resources, they act as couplers of these energy pathways. This coupling may infer stability to the food web if the predators balance the strength of their feeding interactions on pelagic and benthic prey with the relative difference in productivity (and turnover rates) of the pathways¹. We argue that not all predatory fish act as such 'balanced' couplers, as species can be specialized to exploit pelagic resources. This specialization implies that ecosystem-level variations in the productivity of the pelagic and benthic energy pathways will not only affect the occurrence and productivity of large predatory fish, but also the stability of the ecosystem.

There is large uncertainty related to current predictions of future fish and fisheries production, primarily since it is unclear how climate change will affect ocean primary production and how energy will be transferred to the upper trophic levels of marine ecosystems^{35,36}. Our findings suggest that changes in the global occurrence and productivity of large predatory fish can be anticipated by understanding how climate change will affect the base of pelagic and benthic food chains. Changes in the productivity of these energy pathways in response to climate change are expected^{37,38} and, in some instances, already observed; for example, large-scale changes in phytoplankton abundance and ocean primary production^{39,40}. For most continental shelf areas, climate change has been predicted to decrease detritus fluxes to the seafloor³⁵, thereby potentially limiting large demersal fish abundances and fisheries production. Accounting for the changes in the pelagic and demersal energy

pathways is therefore key to reliably predicting the effects of climate change on the upper trophic levels of marine ecosystems, as well as the impact on supported fisheries.

Methods

Global fisheries data. We used global fisheries landings data¹⁵ to determine general patterns in the feeding strategies of marine predatory fish between 1970 and 2014. The spatial fisheries landings data are predominately from global fisheries catch statistics assembled by the Food and Agriculture Organization of the United Nations and complemented by statistics from various international and national agencies. These datasets, with higher spatial resolution, were nested into the broader Food and Agriculture Organization regions, replacing the data reported at the coarser spatial resolution. The global fisheries landings data were mapped to 30 min spatial cells using information on the distribution of reported taxa and fishing fleets¹⁵. For the purpose of this study, we aggregated the data and examined fisheries landings data on a marine ecoregion scale¹⁶.

Feeding strategies of marine fish. To examine the productivity of marine teleost fish along the pelagic and benthic energy pathways, we classified fish into two general feeding strategies: either feeding exclusively on the pelagic pathway (pelagic fish) or (partly) relying on the benthic pathway for feeding (demersal fish). This was done using the functional group classification system developed in the Sea Around Us project (<http://www.seaaroundus.org/>). Data classified using the Sea Around Us project as shark, ray, any type of invertebrate or bathydemersal and bathypelagic fish (these groups include the mesopelagic fish) were removed (see Supplementary Table 4). This limited our analysis to teleost fish and the two dominant feeding strategies. The two feeding strategies were further divided on the basis of fish maximum size (<http://www.fishbase.org/search.php>). Large predatory species were classified as fish with a maximum size ≥ 90 cm. The choice of this maximum size limit did not affect our analysis as it can range from 70 to 150 cm without changing the results (Supplementary Fig. 6). Part of the fisheries landings had not been identified (for example, marine animals and marine fish not identified) and these observations were excluded. Other data were identified at too general a taxonomic grouping to derive the correct size class (for example, Gadiformes and Gadidae) and these landings data were assumed to represent species with maximum sizes smaller than 70 cm.

For each of the ecoregions, we calculated the average weight fraction of pelagic fish compared with demersal fish in the fisheries landings data between 1970 and 2014. This was only done for ecoregions where at least 60% of the landings data (in tonnes) could be classified into one of the functional groups from the Sea Around Us project (but note that the main findings are unaffected when more or less strict criteria for ecoregion selection are chosen). All fractions were averaged over at least 24 years of data (for 219 ecoregions, fractions were averaged over 45 years of data).

Besides the large predatory teleost fish, we also determined whether there were general patterns in the feeding strategies of teleost fish species with a maximum size < 90 cm (Supplementary Fig. 7). The results show that there is no clear latitudinal pattern and no relationship between the small pelagic fish fraction and $F_{\text{pelagic}}/F_{\text{benthic}}$. The pattern is not improved when pelagic and benthic invertebrate landings are included in the analysis (Supplementary Fig. 7).

Potential bias due to the use of fisheries landings. Our assessment of the global variation in the large predatory fish may be biased by our use of global fisheries landings data instead of biomass data. We included a variety of analyses to examine this potential bias. First, we examined with available stock assessments from the RAM Legacy Stock Assessment Database¹⁸ the relationship between catch and biomass of large teleost fish. For this analysis, data were available for 71 different large predatory fish stocks (38 pelagic and 33 demersal; Supplementary Table 5). For each stock, we averaged both the total biomass and total catch for all years with assessment data and examined across stocks the relationship between the average biomass and catch and whether this differs between both feeding groups (model comparison using Akaike information criterion scores). Afterwards, we tested the relationship between the weight fraction of pelagic fish versus demersal fish in catch and biomass over time. This was done by selecting pelagic and demersal fish in all size groups from the RAM Legacy Stock Assessment Database¹⁸ for nine different large marine ecosystems over multiple years. The large marine ecosystems and years were selected since they have data available on assessed fish stocks in both feeding strategies (see Supplementary Table 6). To further check the robustness of our findings, we examined how much the fraction of large pelagic and demersal fish varied when the fraction was corrected for the economic value of the species (assuming species are preferred by fisheries when they have higher economic value). Nominal economic values, standardized per unit weight, were derived for each species and year from Sumaila et al.¹⁹ and used to estimate the economic value of both feeding groups (standardized per unit weight) per ecoregion and year. When multiple species from the same feeding group were present in the landings in a particular ecoregion and year, the economic value of that feeding group was averaged by weighting all species with the landings. Afterwards, we calculated the price difference between pelagic and demersal fish for each year and ecoregion and averaged this across all years per ecoregion. A price-corrected weight fraction of

large pelagic fish was then calculated by: $wf \times (1 - pf) / (wf \times (1 - pf) + (1 - wf) \times pf)$, where wf is the weight fraction of large pelagic fish from fisheries landings and pf is the price fraction (a fraction of 0.9 means that pelagic fish are 9 times more valuable than demersal fish at similar tonnes of landings) (Supplementary Fig. 3). We also examined how the inclusion of large sharks and rays (taken from the fisheries landings database¹⁵) affected the global patterns in predatory fish. The classification of pelagic (oceanic) sharks and rays followed ref. ⁴¹ and all other taxa were classified as demersal generalists (the maximum body size was based on <http://www.fishbase.org/search.php>). Finally, we examined how estimates of illegal, unregulated and unreported catches and discarded fish affected our calculation of the weight fraction of large pelagic versus demersal fish. Estimates of illegal, unregulated and unreported catches and discarded fish were taken from the spatial fisheries landings database¹⁵ for each ecoregion and year.

Pelagic and benthic energy production. We hypothesized that the relative production of pelagic and demersal fish in fisheries landings across ecoregions is dependent on the differences in pelagic and benthic production. We approximated the difference in production by calculating the ratio of F_{photic} versus F_{seabed} . This was done by first calculating the fraction of NPP that sinks out of the photic zone (the pe -ratio) then by accounting for energy loss between the depth of the photic zone and the seabed.

We used an empirical relationship introduced by Dunne et al.²⁴ to calculate the pe -ratio. This relationship captures ~60% of observed global variation in the pe -ratio using field-derived estimates of sea surface temperature (SST), primary production (NPP) and the photic zone depth (Zeu). In this calculation, increased temperature reduces the pe -ratio, while it is increased with increasing primary production and a smaller photic zone depth: $pe\text{-ratio} = -0.0101SST + 0.0582\ln\left(\frac{NPP}{Zeu}\right) + 0.419$. To estimate the pe -ratio on a global scale with the empirical model, we used the average annual sea surface temperature (in degrees Celsius) between 1998 and 2008 (<http://www.esrl.noaa.gov/psd/data/gridded/data.noaa.oisst.v2.html>) and the average daily NPP (mg chlorophyll a $m^{-3}d^{-1}$) from the vertically generalized production model using MODIS data from between 2003 and 2008 (<http://www.science.oregonstate.edu/ocean.productivity>)⁴² and we approximated the photic zone depth from average daily surface chlorophyll a concentrations (mg chlorophyll a $m^{-3}d^{-1}$) from the Sea-viewing Wide Field-of-view Sensor between 1998 and 2008 (<https://oceancolor.gsfc.nasa.gov/data/seawifs/>) (following ref. ⁴³; see ref. ⁴⁴ for original description). The sea surface temperature data were resampled to a $1/12^\circ$ grid to enable us to use more detailed information on spatial variation in bathymetry. The derived pe -ratios varied across the globe between 0.04 and 0.74 and were used to calculate F_{photic} (Supplementary Fig. 5), the predicted fraction of NPP that remains in the photic zone:

$$F_{\text{photic}} = 1 - r$$

where r is the pe -ratio.

The fraction of NPP that sinks out of the photic zone is reduced in energetic content before it reaches the seabed, especially in deeper oceans where only a fraction of the production from the pelagic zone may reach the seabed. To account for this effect, we accounted for energy loss, adjusting a function described in ref. ⁴⁵.

For all grid cells where the seabed depth is equal or shallower than the depth of the photic zone:

$$F_{\text{seabed}} = pe\text{-ratio}$$

For all other grid cells:

$$F_{\text{seabed}} = pe\text{-ratio} (\text{seabed depth/depth photic zone})^{-0.86}$$

Bathymetric data (m) were extracted per $1/12^\circ$ grid from the ETOPO1 Global Relief Model with sea ice cover⁴⁶.

The calculated fluxes in the pelagic and benthic zone only provide a first approximation of the relative productivity of the pathways. The estimates ignore different aspects that are known to influence pelagic and benthic energy pathways, such as the role of benthic primary producers (which, especially in coastal waters, contribute to a large part of the overall production⁴⁷), areas with high subsurface productivity (where NPP is underestimated when using satellite-derived NPP products^{48,49}) and any active transport processes to the seafloor^{50,51}. Despite these limitations, the predicted large-scale spatial variation in F_{photic} and F_{seabed} (Supplementary Fig. 5) seems to be consistent with other studies that used alternative methods^{23,52}.

Data aggregation per ecoregion and data analysis. Both F_{photic} and F_{seabed} were averaged per ecoregion. To account for latitudinal differences in grid size, all F_{photic} and F_{seabed} values per ecoregion were weighted with respect to latitude (weighting factor = $\cos(\pi/180 \times \text{degrees latitude})$) following ref. ⁵³. As fish production is expected to be highest in areas with high primary production⁵⁴, we also weighted F_{photic} and F_{seabed} per ecoregion with respect to grid cell differences in NPP.

Relationships between the fraction of pelagic fish and the ratio of F_{photic} versus F_{seabed} were examined using generalized additive models with a beta distribution (continuous probability distribution between 0 and 1) and (after model fit inspection) with a cauchit link function. The ratio of F_{photic} versus F_{seabed} was \log_{10} transformed, while the pelagic fish fraction was transformed to avoid zeros and ones following ref. ⁵⁵; $y = (y(n-1) + 0.5)/n$, where y is the pelagic fish fraction and n the number of ecoregions. Maps were produced using *rworldmap*⁵⁶.

Food-web model. Following the results of the fisheries data analyses, a food-web model was developed to study the competitive interactions between large pelagic specialists and demersal generalists across marine ecoregions. The benthic and pelagic energy pathways were modelled as two separate channels with their own resource carrying capacities with semi-chemostat dynamics. The carrying capacity of the pelagic resource (K_p) was calculated by multiplying the total resource carrying capacity (R_{max}) with F_{photic} , while the carrying capacity of the demersal resource (K_b) was calculated as R_{max} multiplied by F_{seabed} (see Supplementary Table 2 for model formulation). The resources were both preyed on by an intermediate trophic level, while two predatory species were included at the top of the energy pathways (following Fig. 1).

We hypothesized that large pelagic teleost fish are superior in exploiting the pelagic resource compared with large demersal species (see Discussion). To incorporate this in the model, feeding as a generalist comes at a cost and this cost was implemented with a lower attack rate of the generalist, meaning that the specialist is superior in exploiting the pelagic resource. The value of the attack rate parameter was selected to obtain an approximately equal number of ecoregions that overestimated the amount of either pelagic or demersal fish compared with fisheries landings. This resulted in an attack rate of the generalist that is 20% lower than the attack rate of the specialist. The attack rate value of the generalist can be lowered between 5% and 35% without reducing the r^2 of the statistical relationship between the landings data and model output strongly (r^2 is 0.58 when the generalist has a 20% lower attack rate; see Fig. 4).

Life Sciences Reporting Summary. Further information on experimental design and reagents is available in the Life Sciences Reporting Summary.

Data availability. A table is available as Supplementary Data with information per ecoregion on the fraction of pelagic fish in landings, environmental variables and the food-web model outcome. Detailed global fisheries landings data are available from Watson¹⁵.

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References

- Rooney, N., McCann, K., Gellner, G. & Moore, J. C. Structural asymmetry and the stability of diverse food webs. *Nature* **442**, 265–269 (2006).
- Estes, J. A., Heithaus, M., McCauley, D. J., Rasher, D. B. & Worm, B. Megafaunal impacts on structure and function of ocean ecosystems. *Annu. Rev. Environ. Resour.* **41**, 83–116 (2016).
- Heithaus, M. R., Frid, A., Wirsing, A. J. & Worm, B. Predicting ecological consequences of marine top predator declines. *Trends Ecol. Evol.* **23**, 202–210 (2008).
- Baum, J. K. & Worm, B. Cascading top-down effects of changing oceanic predator abundances. *J. Anim. Ecol.* **78**, 699–714 (2009).
- The State of World Fisheries and Aquaculture 2016. Contributing to Food Security and Nutrition For All* (FAO, Rome, 2016).
- Link, J. S., Bogstad, B., Sparholt, H. & Lilly, G. R. Trophic role of Atlantic cod in the ecosystem. *Fish. Fish.* **10**, 58–87 (2009).
- Sibert, J., Hampton, J., Kleiber, P. & Maunders, M. Biomass, size, and trophic status of top predators in the Pacific Ocean. *Science* **314**, 1773–1776 (2006).
- Boyce, D. G., Tittensor, D. P. & Worm, B. Effects of temperature on global patterns of tuna and billfish richness. *Mar. Ecol. Prog. Ser.* **355**, 267–276 (2008).
- Worm, B. & Tittensor, D. P. Range contraction in large pelagic predators. *Proc. Natl Acad. Sci. USA* **108**, 11942–11947 (2011).
- Pauly, D., Watson, R. & Alder, J. Global trends in world fisheries: impacts on marine ecosystems and food security. *Phil. Trans. R. Soc. B* **360**, 5–12 (2005).
- Garrison, L. P. & Link, J. S. Dietary guild structure of the fish community in the northeast United States continental shelf ecosystem. *Mar. Ecol. Prog. Ser.* **202**, 231–240 (2000).
- Bulman, C., Althaus, F., He, X., Bax, N. J. & Williams, A. Diets and trophic guilds of demersal fishes of the south-eastern Australian shelf. *Mar. Freshw. Res.* **52**, 537–548 (2001).
- Byron, C. J. & Link, J. S. Stability in the feeding ecology of four demersal fish predators in the US Northeast Shelf Large Marine Ecosystem. *Mar. Ecol. Prog. Ser.* **406**, 239–250 (2010).

14. López-López, L. et al. Is juvenile anchovy a feeding resource for the demersal community in the Bay of Biscay? On the availability of pelagic prey to demersal predators. *ICES J. Mar. Sci.* **69**, 1394–1402 (2012).
15. Watson, R. A. A database of global marine commercial, small-scale, illegal and unreported fisheries catch 1950–2014. *Sci. Data* **4**, 170039 (2017).
16. Spalding, M. D. et al. Marine ecoregions of the world: a bioregionalization of coastal and shelf areas. *BioScience* **57**, 573–583 (2007).
17. Branch, T. A. et al. The trophic fingerprint of marine fisheries. *Nature* **468**, 431–435 (2010).
18. Ricard, D., Minto, C., Jensen, O. P. & Baum, J. K. Examining the knowledge base and status of commercially exploited marine species with the RAM Legacy Stock Assessment Database. *Fish Fish.* **13**, 380–398 (2012).
19. Sumaila, U. R., Marsden, A. D., Watson, R. & Pauly, D. A global ex-vessel fish price database: construction and applications. *J. Bioeconomics* **9**, 39–51 (2007).
20. Suess, E. Particulate organic carbon flux in the oceans—surface productivity and oxygen utilization. *Nature* **288**, 260–263 (1980).
21. Pomeroy, L. R. & Deibel, D. O. N. Temperature regulation of bacterial activity during the spring bloom in Newfoundland coastal waters. *Science* **233**, 359–361 (1986).
22. Laws, E. A., Falkowski, P. G., Smith, W. O., Ducklow, H. & McCarthy, J. J. Temperature effects on export production in the open ocean. *Glob. Biogeochem. Cycles* **14**, 1231–1246 (2000).
23. Lutz, M. J., Caldeira, K., Dunbar, R. B. & Behrenfeld, M. J. Seasonal rhythms of net primary production and particulate organic carbon flux to depth describe the efficiency of biological pump in the global ocean. *J. Geophys. Res.* **112**, C10011 (2007).
24. Dunne, J. P., Armstrong, R. A., Gnanadesikan, A. & Sarmiento, J. L. Empirical and mechanistic models for the particle export ratio. *Glob. Biogeochem. Cycles* **19**, GB4026 (2005).
25. Tittensor, D. P. et al. Global patterns and predictors of marine biodiversity across taxa. *Nature* **466**, 1098–1101 (2010).
26. Mackintosh, N. A. The pattern of distribution of the Antarctic fauna. *Proc. R. Soc. Lond. B* **152**, 624–631 (1960).
27. Kaschner, K., Tittensor, D. P., Ready, J., Gerrodette, T. & Worm, B. Current and future patterns of global marine mammal biodiversity. *PLoS ONE* **6**, e19653 (2011).
28. Davidson, L. N. K., Krawchuk, M. A. & Dulvy, N. K. Why have global shark and ray landings declined: improved management or overfishing? *Fish Fish.* **17**, 438–458 (2016).
29. Drapeau, L., Pecquerie, L., Fréon, P. & Shannon, L. J. Quantification and representation of potential spatial interactions in the southern Benguela ecosystem. *African J. Mar. Sci.* **26**, 141–159 (2004).
30. Brodeur, R. D., Buchanan, J. C. & Emmett, R. L. Pelagic and demersal fish predators on juvenile and adult forage fishes in the Northern California Current: spatial and temporal variations. *CalCOFI Rep.* **55**, 96–116 (2014).
31. McDaniel, J., Piner, K., Lee, H. H. & Hill, K. Evidence that the migration of the northern subpopulation of Pacific sardine (*Sardinops sagax*) off the west coast of the United States is age-based. *PLoS ONE* **11**, e0166780 (2016).
32. Varpe, Ø., Fiksen, Ø. & Slotte, A. Meta-ecosystems and biological energy transport from ocean to coast: the ecological importance of herring migration. *Oecologia* **146**, 443–451 (2005).
33. Killen, S. S. et al. Ecological influences and morphological correlates of resting and maximal metabolic rates across teleost fish species. *Am. Nat.* **187**, 592–606 (2016).
34. Watanabe, Y. Y., Goldman, K. J., Caselle, J. E., Chapman, D. D. & Papastamatiou, Y. P. Comparative analyses of animal-tracking data reveal ecological significance of endothermy in fishes. *Proc. Natl Acad. Sci. USA* **112**, 6104–6109 (2015).
35. Stock, C. A. et al. Reconciling fisheries catch and ocean productivity. *Proc. Natl Acad. Sci. USA* **114**, E1441–E1449 (2017).
36. Brander, K. M. Global fish production and climate change. *Proc. Natl Acad. Sci. USA* **104**, 19709–19714 (2007).
37. Capotondi, A., Alexander, M. A., Bond, N. A., Curchitser, E. N. & Scott, J. D. Enhanced upper ocean stratification with climate change in the CMIP3 models. *J. Geophys. Res.-Oceans* **117**, C04031 (2012).
38. Sarmiento, J. L. et al. Response of ocean ecosystems to climate warming. *Glob. Biogeochem. Cycles* **18**, GB3003 (2004).
39. Richardson, A. J. & Schoeman, D. S. Climate impact on plankton ecosystems in the northeast Atlantic. *Science* **305**, 1609–1612 (2004).
40. Behrenfeld, M. J. et al. Climate-driven trends in contemporary ocean productivity. *Nature* **444**, 752–755 (2006).
41. Compagno, L. J. V. in *Sharks of the Open Ocean: Biology, Fisheries and Conservation* (eds Camhi, M. D., Pikitch, E. K. & Babcock, E. A.) Ch. 3 (Blackwell, Oxford, 2008).
42. Behrenfeld, M. J. & Falkowski, P. G. Photosynthetic rates derived from satellite-based chlorophyll concentration. *Limnol. Oceanogr.* **42**, 1–20 (1997).
43. Friedland, K. D. et al. Pathways between primary production and fisheries yields of large marine ecosystems. *PLoS ONE* **7**, e28945 (2012).
44. Morel, A. & Berthon, J.-F. Surface pigments, algal biomass profiles, and potential production of the euphotic layer: relationships reinvestigated in view of remote-sensing applications. *Limnol. Oceanogr.* **34**, 1545–1562 (1989).
45. Martin, J. H., Knauer, G. A., Karl, D. M. & Broenkow, W. W. VERTEX: carbon cycling in the northeast Pacific. *Deep Sea Res. A* **34**, 267–285 (1987).
46. Amante, C. & Eakins, B. W. *ETOPO1 1 Arc-Minute Global Relief Model: Procedures, Data Sources and Analysis* NOAA Technical Memorandum NESDIS NGDC-24 (NOAA, Boulder, 2009).
47. Ward, C. L., McCann, K. S. & Rooney, N. HSS revisited: multi-channel processes mediate trophic control across a productivity gradient. *Ecol. Lett.* **18**, 1190–1197 (2015).
48. Richardson, K., Visser, A. W. & Pedersen, F. B. Subsurface phytoplankton blooms fuel pelagic production in the North Sea. *J. Plankton Res.* **22**, 1663–1671 (2000).
49. Schullien, J. A., Behrenfeld, M. J., Hair, J. W., Hostetler, C. A. & Twardowski, M. S. Vertically-resolved phytoplankton carbon and net primary production from a high spectral resolution lidar. *Opt. Express* **25**, 13577–13587 (2017).
50. Jónasdóttir, S. H., Visser, A. W., Richardson, K. & Heath, M. R. Seasonal copepod lipid pump promotes carbon sequestration in the deep North Atlantic. *Proc. Natl Acad. Sci. USA* **112**, 12122–12126 (2015).
51. Davison, P. C., Checkley, D. M., Koslow, J. A. & Barlow, J. Carbon export mediated by mesopelagic fishes in the northeast Pacific Ocean. *Prog. Oceanogr.* **116**, 14–30 (2013).
52. Siegel, D. A. et al. Global assessment of ocean carbon export by combining satellite observations and food-web models. *Glob. Biogeochem. Cycles* **28**, 181–196 (2014).
53. Belkin, I. M. Rapid warming of large marine ecosystems. *Prog. Oceanogr.* **81**, 207–213 (2009).
54. Jennings, S. & Collingridge, K. Predicting consumer biomass, size-structure, production, catch potential, responses to fishing and associated uncertainties in the world's marine ecosystems. *PLoS ONE* **10**, e0133794 (2015).
55. Smithson, M. & Verkuilen, J. A better lemon squeezer? Maximum-likelihood regression with beta-distributed dependent variables. *Psychol. Methods* **11**, 54–71 (2006).
56. South, A. *rworldmap*: a new R package for mapping global data. *R J.* **3**, 35–43 (2011).

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Author contributions

P.D.v.D., M.L., B.R.M. and K.H.A. conceived the study. R.A.W. contributed fisheries landings data. P.D.v.D. performed the research with support from M.L. and K.H.A. P.D.v.D., M.L. and K.H.A. wrote the paper. All authors contributed to interpretation of the results and commented on the paper.

Competing interests

The authors declare no competing financial interests.

Additional information

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