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Uneven progress in tackling malnutrition has kept food and nutrition security high on the development agenda globally[1,3]. Micronutrients, such as iron and zinc, are a particular focus; it is estimated that nearly two billion people lack key micronutrients[7], underlying nearly half of all deaths in children under the age of five years[1], and reducing GDP in Africa by estimates of up to 11%[2,3,7]. Consequently, efforts to tackle malnutrition have shifted from a focus on increasing energy and macronutrients (e.g. protein) towards ensuring sufficient consumption of micronutrients[3]. People gain nutrients from a mix of locally produced and imported food products. Fish, harvested widely and traded both domestically and internationally, are a rich source of bioavailable micronutrients, which are often deficient in diets that rely heavily on plant-based sources[6,8]. Fish could therefore help address nutritional deficiencies if there are sufficient quantities of fishery-derived nutrients accessible in places where deficiencies exist. However, addressing this major food policy frontier has been elusive, in part because the nutrient composition of fish varies significantly among species, and data remain sparse for most species[5].

Here we determine the contribution marine fisheries can make to addressing micronutrient deficiencies. First, using strict inclusion protocols (methods), we developed a database of 2,267 measures of nutritional composition, from 367 fish species, spanning 43 countries, for seven nutrients essential to human health: calcium, iron, selenium, zinc, vitamin A, omega-3 (n-3 fatty acids), and protein. We then gathered species-level environmental and ecological traits that capture elements of diet, thermal regime, and energetic demand in fish[9,10] to develop a series of Bayesian hierarchical models that determine drivers of nutrient content (Methods).

Our models successfully predicted nutrient concentrations, with posterior predictive distributions consistently capturing both the observed overall mean and individual values of each nutrient[11] (Extended Data Figs. 1 and 2; Methods). We found that calcium, iron, and zinc – nutrients critical in preventing public health conditions such as stunting and anaemia[7,12] – were in higher concentrations in tropical fishes (Fig. 1). Tropical soils are often zinc and calcium deficient because these nutrients are easily exported from land to sea during strong pulse rainfall events common in the tropics; this process may elevate levels of these nutrients in marine food-webs[13]. Higher concentrations of calcium, zinc and omega-3 were found in small fish species. Small fish consumption is promoted, particularly in Asia and Africa[14,15,] as a rich source of micronutrients and, although these high concentrations are often linked to the practice of consuming fish whole[15], we also detected elevated levels of these nutrients in muscle tissue.

Greater concentrations of omega-3 – which supports neurological function and cardiovascular health[16] – was found in species that are pelagic feeders, are from cold regions, and approach their maximum size more slowly (Fig. 1). Pelagic feeders consume plankton, the main source of omega-3 in aquatic systems[17], whereas species adapted to a colder thermal regime, have a greater need for energy storage compounds and fat, including fatty acids[18]. Selenium concentrations were higher for species found at greater depths and lower for species in tropical waters, whereas lower concentrations of vitamin A were found in species from cold regions, with high trophic levels and short, deep body shapes. Concentrations of protein were greater in higher trophic level species, and those with a pelagic feeding pathway, and lower in species found in cold regions, and with a flat or elongated body shape (Fig. 1).

Given the alignment between our posterior predictions and observed data (Extended Data Fig. 2), we used our trait-based models of nutrient concentration, and traits for species within the landed catch of the world's marine fisheries[19], to produce the first global estimates for nutritional concentration (Fig. 2) and nutritional yield (Extended Data Fig. 3) of marine fisheries (Methods). These data reflect catches from within a country's Economic Exclusive Zone (EEZ) that are landed and consumed domestically, landed outside the country by foreign fleets, or traded internationally[19]. We include both officially recorded and reconstructed unrecorded catches (see Methods for comparisons), but do not include discards. There was no correlation between the concentration of nutrients per unit catch and either total nutrient yield or total fishery yield (Extended Data Fig. 4), suggesting the nutrient quality of fishery landings is influenced by species composition rather than the quantity landed; and thus, fish-based food policy guidelines [e.g. 20] should specify for what types of fish consumption is advised.

High concentrations of iron and zinc (>2.5mg 100^{-1}g and >1.8 mg 100^{-1}g respectively, of raw, edible portion) are found in the species caught in a number of African and Asian countries (Fig. 2, Extended Data Table 1), the same regions at greatest risk of deficiencies in these nutrients[7,12]. This suggests that, in areas of critical public health concern, a single portion (100g) of an average fish provides approximately half the recommended dietary allowance (RDA) of iron and zinc for a child under the age of five years. Calcium concentrations are high (>200mg/100g raw, edible portion) in the species caught in the Caribbean region, an area with a high prevalence of deficiency risk[7], again highlighting the potential contributions fish can make to targeted health interventions in these areas. Concentrations of selenium and omega-3 are high (>25ug 100^{-1}g, >0.5g 100^{-1}g respectively, of raw, edible portion) in fish species caught from high latitude regions including parts of Russia, Canada, Northern Europe, and Alaska (Fig. 2, Extended Data Table 1). This is consistent with omega-3 observed as abundant in marine foods consumed by Arctic indigenous populations such as the Inuit of Nunavik, Canada[21]. Furthermore, these high selenium concentrations are found in some of the areas where selenium deficiencies are common[22], yet a single portion of an average fish (Methods) from these waters contains enough selenium to meet the daily RDA for a child under the age of five years, and nearly half that required by adults.

While recognising challenges of fisheries sustainability, and potential climate-driven declines in yields[23], the availability of high concentrations of key nutrients in areas at risk of nutrient deficiencies suggests that marine fisheries could be critical in helping close nutrient gaps. To assess this, we calculated nutrient yields (per capita) using the estimated national nutrient yield in our models and the human population living within 100 km of the coast (which represents 39% of the global population[24]; Methods). We focus on calcium, iron, zinc, and vitamin A, which constitute a major burden of malnutrition, particularly within low-income countries[1,7,12]. For each nutrient and country, we compare this to published dietary deficiency risks[12], seafood consumption rates[25], and RDA[26] (Methods). We specify RDA averaged for the population aged five years and over, and children between six months and four years (Fig. 3). The latter category represents a vulnerable proportion of the population, in which interventions have the greatest potential long-term effects on growth, development, and health.

Fish-derived calcium, iron, zinc, and vitamin A yields of a large number of countries could contribute a significant proportion of the RDA for their coastal populations. For eight countries, these yields exceed requirements for at least one of these nutrients (Fig. 3a-d). Of those countries, only Iceland has mild dietary deficiency risks (<20%)[12,27] (Fig. 3a-d). Very high nutrient yields and prevalence of dietary deficiency risk coincide for at least two nutrients in

Namibia, Mauritania, and Kiribati (Fig. 3a-d). In these countries, a small fraction of available fisheries production, has the potential to close nutrient gaps. For example, iron dietary deficiency risk in Namibia is severe (47%)[12], but just 9% of the fish caught in her EEZ is equivalent to the dietary iron requirements for her entire coastal population.

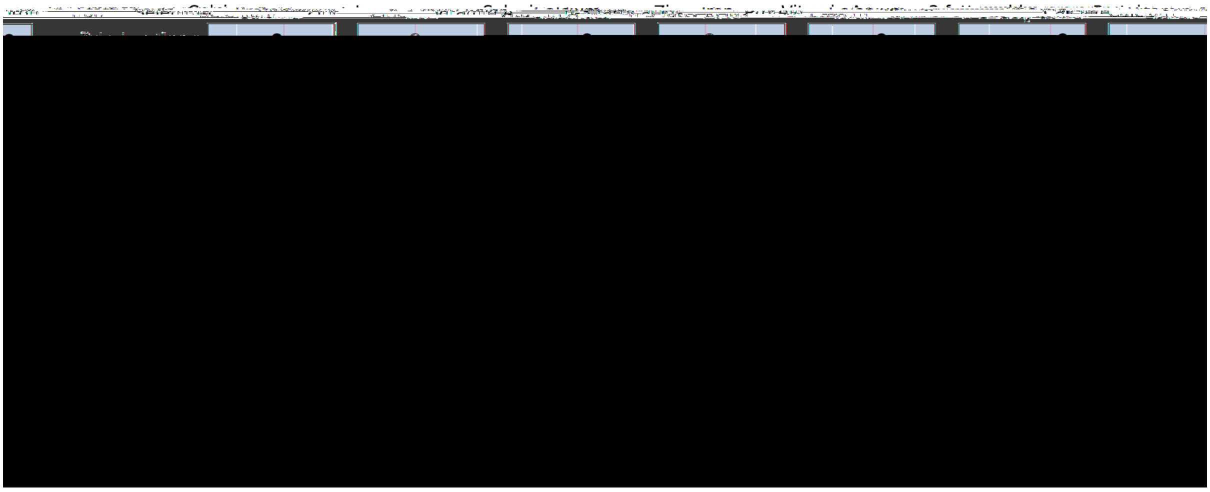
Fisheries clearly have an important place in food and nutrition policy. This contribution could be particularly significant if targeted towards the most vulnerable groups within society, such as children under the age of five, capturing the period when most growth-faltering occurs. Over 50% of coastal countries have moderate to severe deficiency risks (>20%)[12,27] and nutritional yields that exceed the RDA needed for all children under five in the coastal population (Fig. 3e-h). Most notably in Kiribati, calcium dietary deficiency risk is severe (82%)[12], but just 1% of fish caught in her EEZ equals the calcium requirements for all children under five years. For a further 22 countries, predominantly in Asia and west Africa, the dietary requirements for all children under five years is equivalent to 20% or less of current catches. That targeted approaches could only require a fraction of current landings, suggests a nutrition-sensitive fisheries approach could align with environmental efforts to reduce current harvest levels.

Nutrient surpluses of some coastal countries where nutritional needs are not being met highlights that large yields do not necessarily lead to food and nutrition security. International fishing fleets and trade deals[19], physical, economic, or institutional access to the right food[28], food preferences and cultures, waste, and reduction to fish oil for animal feed[29], can all act as barriers or avenues to these resources meeting local nutritional needs. For example, trade and foreign fishing are dominant in countries with large nutrient yields, where high rates of dietary deficiency risk exist (Methods; Extended Data Table 2). Understanding why, when there is an adequate supply of nutrients, populations are still at risk of dietary deficiency, will require a multiscale socio-economic research agenda, that situates fish in the broader food system, accounting for patterns of production, distribution, preparation, and consumption.

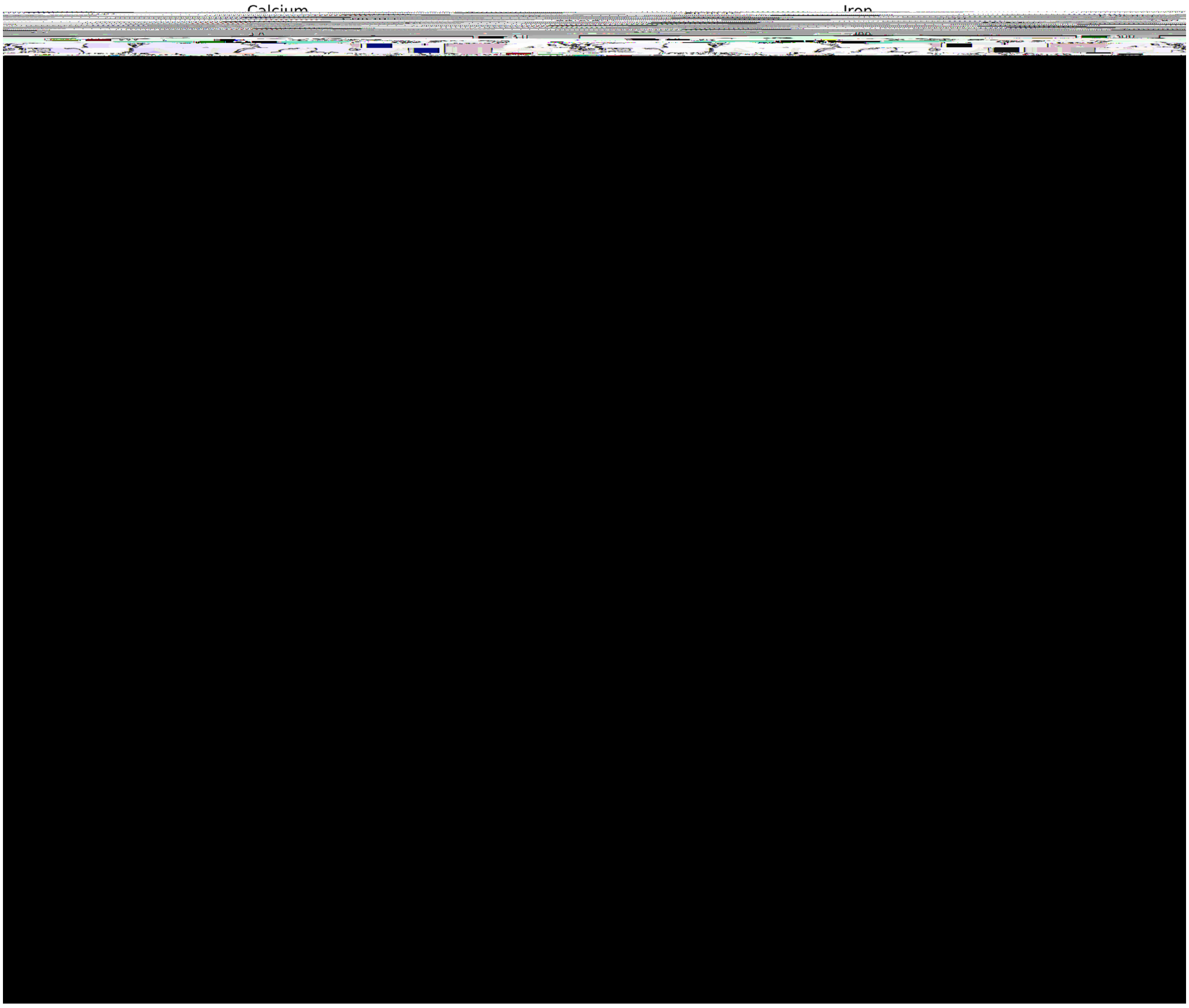
Our results identify the current world distribution of nutrients from fisheries catch. In doing so, we demonstrate that for a number of nutrients essential to human health current production has the potential to significantly and positively impact the nutritional status of some of the most nutrient-deficient countries globally, even at reduced catch levels. Given that fish are in many instances a more affordable animal-source food[4], with a lower environmental impact[20], and nutrient supply from fisheries is comparable to that from other animal-source foods[30], fisheries should be a core component of food and nutrition policy. However, current fisheries policy remains orientated towards maximising profit or yield. Reorienting fisheries policy towards a more efficient distribution of consumption, aimed at meeting nutritional needs, could close nutrient gaps in geographies of critical food and nutrition concern such as west and sub-Saharan Africa. Achieving this will require concerted efforts to understand how existing policies can be redirected towards desired food and nutrition outcomes. Ultimately, multiple approaches and actors must work in concert to tackle malnutrition [20]. Fisheries should thus form part of an integrated approach that is informed from health, production, development, and environmental sectors.

1. Global Nutrition Report 2017: *Nourishing the SDGs*. (Development Initiatives, Bristol, 2017).
2. Horton, S. & Steckel, R. H. in *How Much have Global Problems Cost the World?* (ed. Lomborg, B.) 247–272 (Cambridge University Press, 2013).
3. Haddad, L. et al. A new global research agenda for food. *Nature* 30–32 (2016).
4. Kawarazuka, N. & Béné, C. The potential role of small fish species in improving micronutrient deficiencies in developing countries: Building evidence. *Public Health Nutr.* 1927–1938 (2011).
5. Vaitla, B. et al. Predicting nutrient content of ray-finned fishes using phylogenetic information. *Nat. Commun.* 3742 (2018).
6. Thilsted, S. H. et al. Sustaining healthy diets: The role of capture fisheries and aquaculture for improving nutrition in the post-2015 era. *Food Policy* 126–131 (2016).
7. Kumssa, D. B. et al. Dietary calcium and zinc deficiency risks are decreasing but remain prevalent. *Sci. Rep.* 1–11 (2015).
8. Hotz, C. & Gibson, R. S. Traditional food-processing and preparation practices to enhance the bioavailability of micronutrients in plant-based diets. *J. Nutr.* 1097–1100 (2007).
9. Hixson, S. M., Sharma, B., Kainz, M. J., Wacker, A. & Arts, M. T. Production, distribution, and abundance of long-chain omega-3 polyunsaturated fatty acids: a fundamental dichotomy between freshwater and terrestrial ecosystems. *Environ. Rev.* 414-424 (2015).
10. McGill, B. J., Enquist, B. J., Weiher, E. & Westoby, M. Rebuilding community ecology from functional traits. *Trends Ecol. Evol.* 178–185 (2006).
11. Gelman, A., Meng, X-L. & Stern, H. Posterior predictive assessment of model fitness via realized discrepancies. *Statistica sinica* 733-760 (1996).
12. Beal, T., Massiot, E., Arsenault, J. E., Smith, M. R. & Hijmans, R. J. Global trends in dietary micronutrient supplies and estimated prevalence of inadequate intakes. *PLoS One* e0175554 (2017).
13. Lal, R. Managing soils for a warming earth in a food-insecure and energy-starved world. *J. Plant Nutr. Soil Sci.* 4–15 (2010).
14. Marinda, P. A., Genschick, S., Khayeka-Wandabwa, C., Kiwanuka-Lubinda, R. & Thilsted, S. H. Dietary diversity determinants and contribution of fish to maternal and under-five nutritional status in Zambia. *PLoS One* e0204009 (2018).
15. Thilsted, S. H., Roos, N. & Hassan, N. The role of small indigenous fish species in food and nutrition security in Bangladesh. *Naga* 82–84 (1997).
16. Calder, P. C. Marine omega-3 fatty acids and inflammatory processes: Effects, mechanisms and clinical relevance. *Mol. Cell Biol. Lipids* 469–484 (2015).
17. Parrish, C. C. Lipids in Marine Ecosystems. *ISRN Oceanogr.* 604045 (2013).
18. Arts, M. T., Brett, M. T. & Kainz, M. J. *Lipids in aquatic ecosystems*. (Springer, 2009).
19. Pauly, D. & Zeller, D. Catch reconstructions reveal that global marine fisheries catches are higher than reported and declining. *Nat. Commun.* 10244 (2016).
20. Willett, W. et al. Food in the Anthropocene: the EAT-Lancet Commission on healthy diets fomr sustainable food systems *Lancet* 447-492
21. Achouba, A., Dumas, P., Ouellet, N., Lemire, M. & Ayotte, P. Plasma levels of selenium-containing proteins in Inuit adults from Nunavik. *Environ. Int.* 8–15 (2016).

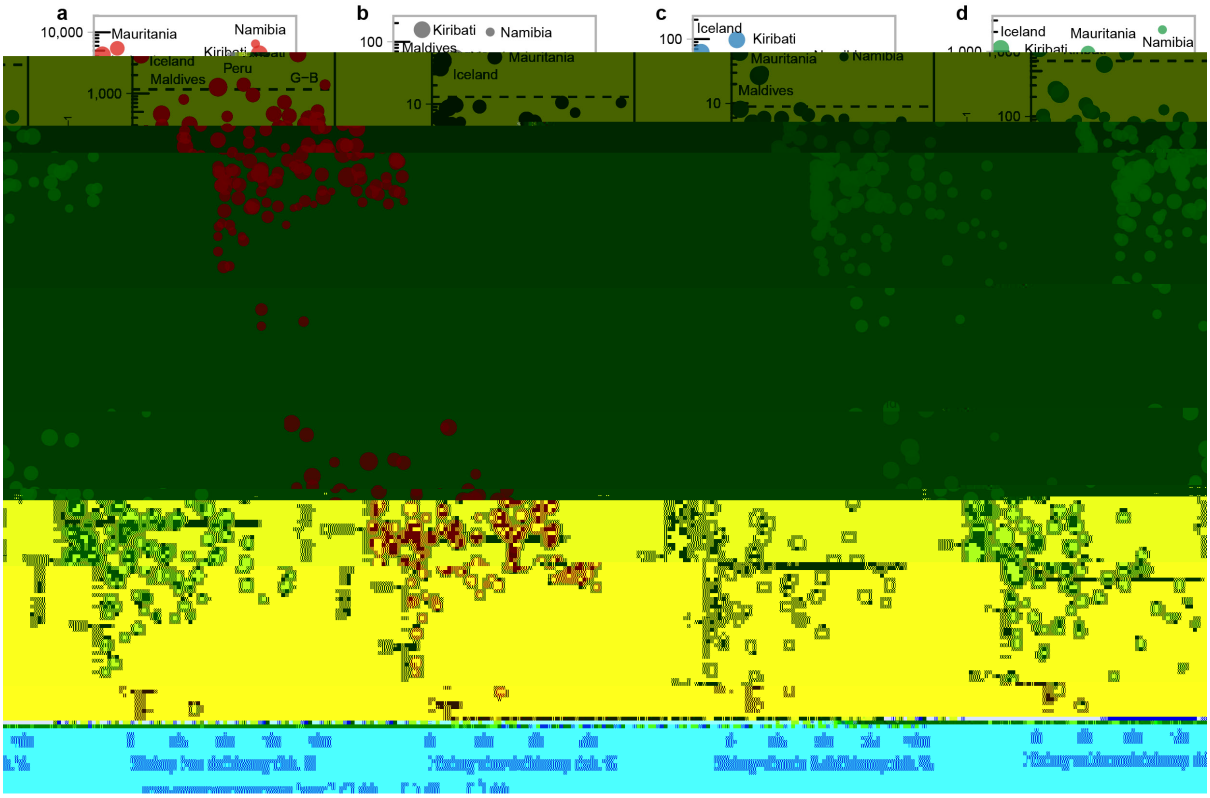
22. -linolenic acid, linoleic acid, and n–3 long-chain PUFA and risk of ischemic heart disease. *Am. J. Clin. Nutr.* 1097–1103 (2011).
23. Golden, C. D. et al. Nutrition: Fall in fish catch threatens human health. *Nature* 317–320 (2016).
24. Kummu, M. et al. Over the hills and further away from coast: global geospatial patterns of human and environment over the 20th–21st centuries. *Environ. Res. Lett.* 034010 (2016).
25. Micha, R., et. al. Global, regional and national consumption of major food groups in 1990 and 2010: a systematic analysis including 266 country-specific nutrition surveys worldwide. *BMJ open*. ***5***, p.e008705 doi.org/10.1136/bmjopen-2015-008705 (2015).
26. National Academies of Sciences, Engineering, and Medicine. *Dietary Reference Intakes Tables and Application.* 2017 Available at: national academies. org/HMD/Activities/Nutrition/SummaryDRIs/DRI-Tables. aspx.
27. Allen, L., de Benoist, B., Dary, O. & Hurrell R. *Guidelines on Food Fortification with Micronutrients*. (World Health Organization, Geneva, 2006)
28. Sen, A. *Poverty and Famines: an Essay on Entitlement and Deprivation*. (Oxford University Press, Oxford, 1982).
29. Fréon, P., Avadí, A., Vinatea Chavez, R. A. & Iriarte Ahón, F. Life cycle assessment of the Peruvian industrial anchoveta fleet: boundary setting in life cycle inventory analyses of complex and plural means of production. *Int. J. Life Cycle Assess.* 1068–1086 (2014).
30. Smith, M. R., Micha, R., Golden, C. D., Mozaffarian, D. & Myers, S. S. Global Expanded Nutrient Supply (GENuS) Model: A New Method for Estimating the Global Dietary Supply of Nutrients. *PLoS One* e0146976 (2016).



Standardised effect sizes for environmental and ecological drivers of nutrient concentrations: diet (green), thermal regime (dark blue), and energetic demand (light blue). Parameter estimates are Bayesian posterior median values, 95% highest posterior density uncertainty intervals (UI; thin lines), and 50% UI (thick lines). Black dots indicate that the 50% UI does not overlap zero, indicating more than 75% of the posterior density was either positive or negative; and open squares indicate baseline category in the statistical model. Underlying sample sizes are calcium (n=170), iron (n=173), selenium (n=134), zinc (n=196), vitamin A (n=69), omega-3 (n=176), and protein (n=627). Note effect sizes are not on a common x-axis scale for clarity of presentation.



. Data based on annual catch composition between 2010-2014 (ref 19) showing concentrations of calcium (mg/100g), iron (mg/100g), selenium (µg/100g), zinc (mg/100g), vitamin A (µg/100g), omega-3 (g/100g), and protein (%) in each EEZ. Total catch is shown in the final panel. Data are plotted at the scale of a country's EEZ, except where a country's EEZ covers more than one ocean (e.g. Canada) where nutrient yield and concentrations are calculated and plotted separately.



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Nutritional yield per,) capita coastal resident) capita under 5-year-old coastal resident, by dietary deficiency risk[12] for all coastal countries based on, calcium; iron; zinc; vitamin A. Bubble size indicates national seafood consumption (g cap^{-1} day^{-1})[25]. Solid horizontal line denotes <5-year old RDA, dotted horizontal line denotes RDA for the rest of the population[26].

We compiled a database of 4188 measures of nutritional composition, from 419 finfish species, spanning 45 countries, based on:

1) Thomson Reuters Web of Science search of the scientific literature published between the years 1980 and 2015, using the search terms ‘content’ or ‘compos*’, and ‘nutrition* NEAR content NEAR fish* AND Marine*’.
2) FAO/INFOODS food composition for biodiversity database[31-33] produced by the Food and Agriculture Organisation (FAO) of the United Nations.
3) Key informant grey literature sources of finfish nutrient composition databases identified through snowballing of nutrition experts.

We extracted quantitative nutrient data from these sources on 14 nutrients essential to human health[34]; including, protein, minerals (iron, calcium, zinc, phosphorous, magnesium, selenium), vitamins (Vitamin A and B12), and fatty acids (polyunsaturated fatty acid (PUFA); the PUFA subsidiaries (omega-6, omega-3), and the omega-3 subsidiaries (eicosapentaenoic acid (EPA) and docosahexaenoic acid (DHA)). We only included sources in English, that were fully traceable and accessible, based on wild caught, marine finfish species, where analyses were conducted on fresh samples, reported nutrient content as a quantitative measure, and samples were taken from either the muscle, fillet, ‘edible portion’ or whole body.

We followed the FAO-INFOODS guidelines[35] for fatty acid conversions from percentage of total fatty acids to g/100g. Differences in sampling (e.g., wet weight, dry weight, whole, whole minus parts, muscle etc) were recorded and controlled for in our analyses (Methods below, Extended Data Fig. 5.)

Of the14 nutrients of interest, seven had sufficient replication for our analyses: calcium, iron, selenium, zinc, vitamin A, polyunsaturated fatty acids (PUFA), and protein. We focussed our PUFA on n-3 fatty acids (i.e. omega-3) because fish are known to be the richest source of these important long chain n-3 fatty acids, and few other sources exist[36]. The final database for the seven nutrients used here was comprised of 2,267 individual samples, from 367 species of finfish, spanning 43 countries.

Drawing on a body of theoretical, analytical, and empirical research in fish ecology[9,10,37-39] we identified a suite of characteristics related to diet, energetic demand, and thermal regime that are likely to influence nutritional quality of fish. We selected a trait-based approach to enable mechanisms of nutrient concentrations to be explored. However, we also allowed for inter-order variation among species in the structure of our hierarchical model to account for phylogeny[5].

We used FishBase[40] to source trait data on the identified characteristics for fish species in our nutrient database and the Sea Around Us Project landings data. An underlying assumption of this approach is that trait values are fixed for a species and do not change in time or space. Thus, spatial trends in nutrient concentrations are representative of shifts in the composition of the catch. Where trait data were missing for a particular species, genus level averages were calculated (mean for continuous traits and mode for categorical traits). Where genus level averages were not available due to missing data, family level average values were calculated. Traits were selected carefully to capture distinct elements of a species diet, energy demand, and thermal regime.

Diet. Diet directly influences the nutritional content of organisms through the concentration of bioavailable nutrients in their food[9,41]. Two diet variables were sourced for each species: feeding pathway, and trophic level. For feeding pathway, each species was first categorised based on their food source, as listed under “ecology”, “diet”, and “food items” in FishBase[40]. These food sources were then classified as either from a predominantly pelagic pathway (e.g. planktonic feeding) or benthic pathway (e.g. benthic algae, crustaceans). For carnivores, the prey items needed to be assessed in the same way to see if they reflect pelagic or benthic pathways. This represents the two dominant energy pathways for fish feeding in the marine environment, which are likely to influence the accumulation of nutrients[42]. Trophic level, directly extracted from FishBase[40], indicates how high in the foodweb a species is feeding, which can be important for the bioaccumulation or bioreduction of some nutrients[43].

Thermal Regime. The thermal regimes of water depth and the major geographic zones of the world influence a range of processes that may determine the assimilation or availability of nutrients, for example metabolism of organisms[44], and precipitation driven run-off of terrestrial nutrient sources[45]. We capture maximum depth and geographic zone for each species. Because temperature declines with depth, the maximum depth trait is correlated with temperature requirements[46]. Geographic zone was captured with four thermal regimes; tropical, subtropical, temperate, and cold. The ‘cold’ category includes polar and deep-water specialist species that are adapted to very cold water.

Energetic Demand. The allocation of energy and resources, including nutrients, to different aspects of life history, for example growth, reproduction, or somatic storage, is fundamental in animals[47]. Four variables were included to represent energetic demand: maximum length which is allometric with a range of characteristics such as home range and metabolism; age at maturity which captures the point at which resources are allocated to reproduction; K which captures the rate at which maximum size is approached and thus how energy is dedicated to body mass accumulation; and body shape which influences how a fish moves through its environment. All variables were extracted from FishBase[40]. Four categories of body shape were used; flat, elongate, short-deep, and fusiform. Eel-like shaped species (n=5 in our data) were grouped with elongate. Natural mortality (M) and reproductive guild were not included due to limited data on these life history traits across species.

While fish trait covariates were of substantive interest, other covariates related to sampling were not; however we included these ‘nuisance parameters’ because they could have potentially biased our results due purely to sampling (Extended Data Fig. 5). Therefore we controlled for variability in reported preparation (wet weight or dry weight) and sampling (whole, whole minus parts, muscle), source (Web of Science, key informant grey literature, FAO-INFOODS), by representing these conditions as covariates in our model. Finally, while multiple habitat categories are recorded in FishBase, it was unclear how this covariate would determine nutritional yield within a given ecosystem; we did however believe it might affect sampling and therefore chose to include it as a nuisance parameter..

We developed a series of Bayesian hierarchical models to predict the nutritional quality of marine finfish species, based on their environmental and ecological traits. None of the traits were sufficiently collinear to be problematic for the model. Where nutrient data were recorded at the genus level, these data were retained in the analysis if there were no species data for that genus within the dataset. If species-level data were available from a given genus, any genus-level data was removed due to non-independence among data points. We ran two sets of models, one where covariates were unstandardized and a second set where continuous explanatory variables were standardised by subtracting their mean and dividing by two standard deviations. The dependent variables, and maximum depth, maximum length, and growth rate were log-transformed to normalize the spread of these highly-skewed distributions. Our statistical models were hierarchically-structured, allowing for inter-order differences that were otherwise unaccounted for in our trait-focused models; this also provided posterior predictive distributions for unobserved species that represented the full uncertainty underlying their estimation. For each nutrient, our basic linear model structure was:

$$\mu \quad \beta_{0\,ORD} \quad \beta_{1\,HAB} \quad \beta_{2\,TR} \quad \beta_3 MAD \quad \beta_4 TL \quad \beta_5 PEL \quad \beta_6 LMX \quad \beta_{7\,BOD} \quad \beta_8 K$$
$$\beta_9 AM \quad \beta_{10\,HAB} \quad \beta_{11\,FOS} \quad \beta_{12\,SPM} \quad \beta_{13\,SEA}$$

where the β_x values represent covariate parameters for taxonomic order (ORD), thermal regime (TR), maximum depth (MAD), total length (TL), pelagic (PEL), maximum length (LMX), body type (BOD), growth parameter (K), and age at maturity (AM). It also included nuisance parameters for habitat category (HAB), the form of sample (FOS), sample preparation method (SPM), and the database used to acquire the data (SEA). This linear model was itself hierarchical, with the order-level intercepts (β_0) allowing for phylogenetic variation among groups.

Depending on assessed levels of fit to the model for each nutrient (see posterior checks below), we used this linear model in combination with one of three data likelihoods, either Normal ($Y_i \quad N \ \mu \ \sigma$ for calcium, omega-3 fatty acids, and selenium), non-central t ($Y_i \quad T \ \nu \ \mu \ \sigma$ for protein and vitamin A), or Gamma ($Y_i \quad \Gamma \ \alpha \ \alpha \ e^{\mu}$ for zinc and iron). The priors and hyperpriors for the various parameters were:

$$\beta_0 \quad N \ \gamma_0 \ \sigma_\gamma$$
$$\gamma_0 \ \beta_{1 \quad 13} \quad N$$
$$\sigma_\gamma \ \sigma \ \alpha \quad U$$
$$\nu \quad U$$

Models were all run in PyMC3 (ref 48) for 5000 iterations of the automatically-assigned No-U-Turn sampler. We examined posterior traces and Gelman-Rubin statistics[49] for evidence of model convergence and used posterior predictive distributions to check for model fit. Beginning with an assumed Normal data likelihood, if we found evidence for lack of convergence or poor model fit, we tried the alternative non-central t and Gamma likelihoods instead. Final models all had stable traces and Gelman-Rubin statistics very near one, supporting convergence, and posterior predictive distributions consistent with the observed data, supporting accurate predictions under each model (Extended Data Figs. 1 and 2).

Using the Sea Around Us (SAU) catch reconstruction database[19], we extracted catches from each country's exclusive economic zone (EEZ) in tonnes and by species group for the period 2010-2014. Reported and unreported catches are generally available for consumption, but discards are not. We therefore extracted data on reported and unreported catches from each country's EEZ, and excluded discards from this data. Insufficient trait data exist for crustaceans[50], and the majority of landed catch are finfish. Therefore, all crustaceans, freshwater species, and cephalopods were removed from the database. We used the top 20 remaining species in our SAU database, which represent 100% of the catch of 31% of EEZs, over 90% of 74% of EEZs, and 75% of 95% of EEZs, to calculate the nutrient concentration of the catch from each EEZ over the 5-year period. The same procedure as used for the nutrient database, was used to assign the environmental and ecological traits to the species in the landed catch. Where Sea Around Us data were reported at family or genus level, we used the average trait value for that family or genus. All higher-level groupings (e.g. order and mixed categories), representing 18% of the finfish catch, were removed for the purpose of calculating EEZ nutrient concentrations. Higher level groupings were then reintroduced to calculate the EEZ nutrient yields. Our nutrient database included 17% of the species in the landed catch and we utilised the predictive capability of the trait-based model (Extended Data Figs. 1 and 2) for the remaining catch. Using the trait covariates from our predictive model, we calculated expected nutrient concentrations (per 100g raw, edible portion) based on the top 20 caught taxon grouping in the SAU database and the posterior distributions from our model. We then multiplied these values by total catch to estimate total nutritional yield per EEZ, based on reported SAU catches. There is some debate around the validity of the reconstructed unreported portion of these data, we therefore repeated all the analysis using only the reported catch and used correlation analyses to establish whether any bias was introduced. The spatial patterns in nutrient yields and nutrient concentrations are extremely similar between the reported+unreported and only reported data (Extended data Figs. 3 and 5). All nutrient yield correlation coefficients are > 98; and nutrient concentration >0.89 (Extended data Fig. 4); and reported+unreported nutrient yields are 19-29% greater than just reported nutrient yields.

There was no correlation between the concentration of nutrients per unit catch and either total nutrient yield or total fishery yield (Extended Data Fig. 6). This suggests that: first, nutrient concentrations are independent of total yield, and; second, the nutrient quality of fishery landings is influenced by species composition rather than the quantity landed. Fish-based food policy guidelines [e.g. 20] should thus specify for what types of fish consumption is advised.

for Bayesian hierarchical model used to predict nutrient concentrations from standardized covariates: https://gist.github.com/mamacneil/4358c6429a4dfa4a188e16bdce9c9376

Coastal population: We gathered data on each country's coastal population within a 100km coastal band and each country's population age structure in 2015[51]. To calculate coastal proportion, we created a 100km buffer along each country's coastline based on the Global Administrative Areas database (GADM v.2.8) and used this to calculate total human population, and population under 5 years, within 100km coastal band for each country in 2015 based on the Socioeconomic Data and Application Centre gridded population of the world database[52] and each country's population age structure[51]. In 2010, 39% of the world's population lived within 100km of the coast[24], and within our study the coastal population captured on average 74% of each country's population (ranging from 2% to 100%), or 49% of the population of all countries considered.

Nutrient yields and reference points: We focused on calcium, iron, zinc, and vitamin A, which are of great public health concern globally, and especially in low-income countries[7,12]. We calculated each country's per capita nutrient yield for the entire coastal population and separately for children under 5 years using the calculated fisheries-derived nutrient yields (methods above) and respective populations within the 100km coastal band. We use Recommended Dietary Allowance (RDA) for calcium, iron, zinc, and vitamin A as our dietary reference intake values. RDA is the intake level at which the dietary needs of nearly all (97% to 98 %) of the population will be met. We calculated average RDA for children under 5 years and for the rest of the population[26]. To calculate average RDA for children under 5 years, we assumed infants between birth and six months were exclusively breastfed, and would thus not consume fishery derived nutrients directly. We then calculated the average RDA for children between 6 months and 4 years (i.e. children <5years), assuming each country's population was evenly distributed across the first 5 years of life[26].

Prevalence of inadequate intake: We extracted data on the prevalence of inadequate intake of calcium, iron, zinc, and vitamin A for each country in 2011 from Beal et al[12]. Beal et al[12] combined food balance sheets from the FAO, UN population data, and nutrient intakes and requirements to calculate prevalence of inadequate intake based on the population weighted estimated average requirement and the distribution of the availability of each micronutrient.

Fish consumption rates: We extracted data on seafood consumption rates[25] as an indicator of how likely fish-based nutrition strategies were to be locally and culturally acceptable[29]. Countries that do not consume seafood are likely to face social, cultural, or religious barriers to the introduction of fish as a source of nutrients.

Fish trade could act as an engine of growth[53] enabling the import of large volumes of nutritious foods. Alternatively, in the absence of fair returns[54], fish trade could exacerbate food and nutrition insecurity[55]. Recent global analyses demonstrate the volume of fish exported from developing countries is equal to the volume imported, with developed countries importing high-priced seafood in exchange for low-priced seafood[56]. This work thus suggests developing countries are compensated for the quantities of seafood that they export with income; but, what remains unclear is whether the income from trade translates to the consumption of nutrient-rich foods, and how this pattern plays out in different countries. To address this gap, we analyse the role of trade and foreign fishing in the countries with potential nutrient supply and high prevalence of deficiencies.

For the countries whose nutrient yields (from catches in their EEZ's) exceed the RDA for their coastal populations, and for the same 5-year period (2010-2014), we use the FAO *fishery statistical collections* [57] (http://www.fao.org/fishery/statistics/global-commodities-production/en) to extract data on marine finfish imports and exports to examine the patterns of marine finfish trade; and the Sea Around Us catch reconstructions data to examine the prevalence of foreign fishing in their waters, to together establish how trade may affect food and nutrition security.

Domestic fleets account for the greatest volumes of finfish catches (>79%) in Iceland, Maldives, and Namibia, whereas foreign fleets account for most of the fish caught in Kiribati and Mauritania (>69%). Namibia and Kiribati subsequently exports most of their fish landings (>90%), whereas the other nations export approximately half. For all countries, fish imports amount to a small fraction (<5%) of fish exports. Taken together, Namibia, Mauritania, and Kiribati, countries with high prevalence of nutritional deficiencies, have the equivalent of <13% of the fish caught in their waters available for domestic markets, whereas Iceland and Maldives, countries with low prevalence of nutritional deficiencies, have 68% and 39% available (Extended Data Table 2). Any income gained from the large quantities of fish trade and foreign fishing in Namibia, Mauritania, and Kiribati does not appear to substitute for the nutrients lost. These countries could benefit from policies that seek to divert a greater portion of fish for local consumption.

31. Rittenschober, D., Stadlmayr, B., Nowak, V., Du, J. & Charrondiere, U.R. Report on the development of the FAO/INFOODS user database for fish and shellfish (uFiSh) - Challenges and possible solutions. *Food Chem.* , 112-120 (2016).

32. Rittenschober, D., Nowak, V. & Charrondiere, U. R. Review of availability of food composition data for fish and shellfish. *Food Chem.* , 4303–10 (2013).

33. FAO-INFOODS v4.0 http://www.fao.org/infoods/infoods/tables-and-databases/faoinfoods-databases/en/ (2017)

34. Bogard, J. R., et. al. Nutrient composition of important fish species in Bangladesh and potential contribution to recommended nutrient intakes. *J. Food Compos. Anal.* , 120–133 (2015).

35. Charrondiere, U.R., et. al., Improving food composition data quality: three new FAO/INFOODS guidelines on conversions, data evaluation and food matching. *Food chemistry*, ***193***, 75-81 (2016).

36. Sidhu, K.S. Health benefits and potential risks related to consumption of fish or fish oil. *Regul. Toxicol. Pharmacol.* , 336–344 (2003).

37. Budge, S. M., Iverson, S. J., Bowen, W. D. & Ackman, R. G. Among- and within-species variability in fatty acid signatures of marine fish and invertebrates on the Scotian Shelf, Georges Bank, and southern Gulf of St. Lawrence. *Can. J. Fish. Aquat. Sci.* , 886–898 (2002).

38. Balter, M., What made humans modern? *Science*, ***295***, 1219-1225 (2002).

39. Mouillot, D., Graham, N. A. J., Villéger, S., Mason, N. W. H. & Bellwood, D. R. A functional approach reveals community responses to disturbances. *Trends Ecol. Evol.* , 167–177 (2013).
40. Froese, R. & Pauly, D. Ed. *FishBase.* www.fishbase.org, version (2018).
41. Willis, J.N. and Sunda, W.G. Relative contributions of food and water in the accumulation of zinc by two species of marine fish. *Marine Biology*, ***80***, 273-279 (1984).
42. Christensen, V. & Pauly, D. ECOPATH II — a software for balancing steady-state ecosystem models and calculating network characteristics. *Ecol. Modell.* , 169–185 (1992).
43. Van der Oost, R., Beyer, J. and Vermeulen, N.P. Fish bioaccumulation and biomarkers in environmental risk assessment: a review. *Environmental toxicology and pharmacology*, ***13***, 57-149 (2003).
44. Brown, J. H., Gillooly, J. F., Allen, A. P., Savage, V. M. & West, G. B. Toward a Metabolic theory of ecology. *Ecology* , 1771-1789 (2004).
45. Barlow, J. et. al. The future of hyperdiverse tropical ecosystems. *Nature,* , 517–526 (2018).
46. Dee, L. E. et al. Functional diversity of catch mitigates negative effects of temperature variability on fisheries yields. *Proc. R. Soc. B Biol. Sci.* , p.20161435 (2016).
47. Willmer, P., Stone, G. & Johnston, I. *Environmental Physiology of Animals*. (John Wiley & Sons, 2009).
48. Salvatier, J., Wiecki, T.V. & Fonnesbeck, C. Probabilistic programming in Python using PyMC3. *PeerJ Computer Science*, ***2***, p.e55 (2016).
49. Gelman, A. et al. *Bayesian Data Analysis* Vol. 2 (CRC, Boca Raton 2014).
50. Nash, K.L., Watson, R.A., Halpern, B.S., Fulton, E.A. & Blanchard, J.L. Improving understanding of the functional diversity of fisheries by exploring the influence of global catch reconstruction. *Scientific reports*, *7*, p.10746 (2017).
51.United Nations DESA Population Division https://population.un.org/wpp/Download/Standard/Population/ (2017)
52. Gridded Population of the World (GPW), v4 | SEDAC. Available at: http://sedac.ciesin.columbia.edu/data/collection/gpw-v4/sets/browse. (Accessed: 25th October 2018)
53. Cunningham, S. 2000. In A. Hatcher, & D. Tingley (Eds.), *International relations and the Common Fisheries Policy – Proceedings of the fourth Concerted Action workshop on economics and the Common Fisheries Policy* pp. 255–272. Portsmouth: Center for the Economics and Management of Aquatic Resources.
54. J. Alder, U.R. Sumaila. Western Africa: A fish basket of Europe past and present. *Journal of Environment and Development*, p. 156-178 (2004).
55. Ruddle, K. In K. Tsukamoto, T. Kawamura, T. Takeuchi, T.D. Beard, & M.J. Kaiser (Eds.), *Fisheries for global welfare and environment, 5th World Fisheries congress* pp. 399–411 (2008).
56. Asche, F., Bellemare, M.F., Roheim, C., Smith, M.D. and Tveteras, S. Fair enough? Food security and the international trade of seafood. *World Development*, ***67***, pp.151-160. (2015).
57. FAOSTAT 2019 http://www.fao.org/fishery/statistics/global-commodities-production/en (Accessed: 18th February 2019)

Data used for figures in this paper are available through the following GitHub link:https://gist.github.com/mamacneil/7f8907e97eeb56022bdcabdb8854949e

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