Aquatic biodiversity enhances multiple nutritional benefits to humans

Joey R. Bernhardt[a,b,1] and Mary I. O'Connor[a]

[a]Department of Zoology, Biodiversity Research Centre, University of British Columbia, Vancouver, BC V6T 1Z4, Canada; and [b]Department of Ecology and Evolutionary Biology, Yale University, New Haven, CT 06520

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Humanity depends on biodiversity for health, well-being, and a stable environment. As biodiversity change accelerates, we are still discovering the full range of consequences for human health and well-being. Here, we test the hypothesis—derived from biodiversity–ecosystem functioning theory—that species richness and ecological functional diversity allow seafood diets to fulfill multiple nutritional requirements, a condition necessary for human health. We analyzed a newly synthesized dataset of 7,245 observations of nutrient and contaminant concentrations in 801 aquatic animal taxa and found that species with different ecological traits have distinct and complementary micronutrient profiles but little difference in protein content. The same complementarity mechanisms that generate positive biodiversity effects on ecosystem functioning in terrestrial ecosystems also operate in seafood assemblages, allowing more diverse diets to yield increased nutritional benefits independent of total biomass consumed. Notably, nutritional metrics that capture multiple micronutrients and fatty acids essential for human well-being depend more strongly on biodiversity than common ecological measures of function such as productivity, typically reported for grasslands and forests. Furthermore, we found that increasing species richness did not increase the amount of protein in seafood diets and also increased concentrations of toxic metal contaminants in the diet. Seafood-derived micronutrients and fatty acids are important for human health and are a pillar of global food and nutrition security. By drawing upon biodiversity–ecosystem functioning theory, we demonstrate that ecological concepts of biodiversity can deepen our understanding of nature's benefits to people and unite sustainability goals for biodiversity and human well-being.

seafood | biodiversity–ecosystem functioning | ecosystem services

Species losses and range shifts because of climate change, harvesting, and other human activities are altering aquatic biodiversity locally and globally (1–5). In aquatic ecosystems, not only are some species severely depleted because of overfishing or habitat loss (3, 6–8), the ecosystem-level dimensions of biodiversity such as the total number of species and their functional diversity have also changed (9). Beyond the loss of particular species, changes in ecosystem-level dimensions of biodiversity threaten numerous ecosystem services to humans, which include the cultural, economic, or health benefits people derive from nature (10–13). In many regions, such as tropical coastal systems, the cumulative impacts of human activities are severe and associated with strong declines in taxonomic and ecological functional diversity (6) and coincide with regions with a high dependence of people upon wild-caught seafood for food and nutrition (14). In temperate regions, where some coastal communities depend on local wild seafood harvests to meet their nutritional needs (15, 16), species richness may be increasing as species recover from exploitation and warmer oceans allow species to expand their ranges into new territory (1, 2, 17).

There is growing concern that biodiversity change leads to changes in human health and well-being (10, 13, 18). Specific and quantitative links between aquatic biodiversity and human health that distinguish contributions of species diversity from those of biomass, as predicted by biodiversity–ecosystem functioning theory, have not been established. At a time of unprecedented global change and increasing reliance on seafood to meet nutritional demands (19), there is an urgent need to understand how changing aquatic ecosystem structure may alter the provisioning of seafood-derived human nutrition.

Seafood, consisting of wild-caught marine and freshwater finfish and invertebrates, provides an important source of protein and calories to humans. Additionally, unlike staple foods such as rice or other grains, seafood can address multiple dimensions of food and nutritional security simultaneously by providing essential micronutrients, such as vitamins, minerals, and polyunsaturated essential fatty acids critical to human health (19–22). Given the multiple attributes of seafood that are valuable to human health, it is possible that the diversity of an aquatic assemblage, distinct from the inclusion of any particularly nutritious species, could support human well-being consistent with a large body of evidence for biodiversity's major contributions to ecological functions (11, 23–26). Dietary diversity is a basic tenet of a nutritious diet (27) and it is widely appreciated that diets composed of more food groups and more species are more nutritious (28–31). Ecological measures of dietary diversity (diet diversity, species richness, functional diversity, and Simpson's index of evenness) have been associated with the nutritional value of diets in a range of contexts (27, 29, 32–38). These studies rely on relationships between species

Significance

Food security is not simply about maintaining yields, but it is also about the need for a stable supply of nutritionally diverse foods. Obtaining nutritious food is a major challenge facing humanity, and diverse aquatic ecosystems can help meet this goal. To test how aquatic biodiversity affects human health, we assembled a dataset of nutrients, contaminants, and ecological traits of 801 aquatic species. We used ecological models to quantify the role of species richness and ecological functional diversity and found that these biodiversity dimensions enhanced seafood micronutrient and fatty acid provisioning by the same mechanisms that link biodiversity to productivity in grasslands, forests, and other systems. Our results underscore the need to minimize aquatic biodiversity loss to sustain and improve human well-being.

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[1]To whom correspondence may be addressed. Email: joey.bernhardt@biodiversity.ubc.ca.

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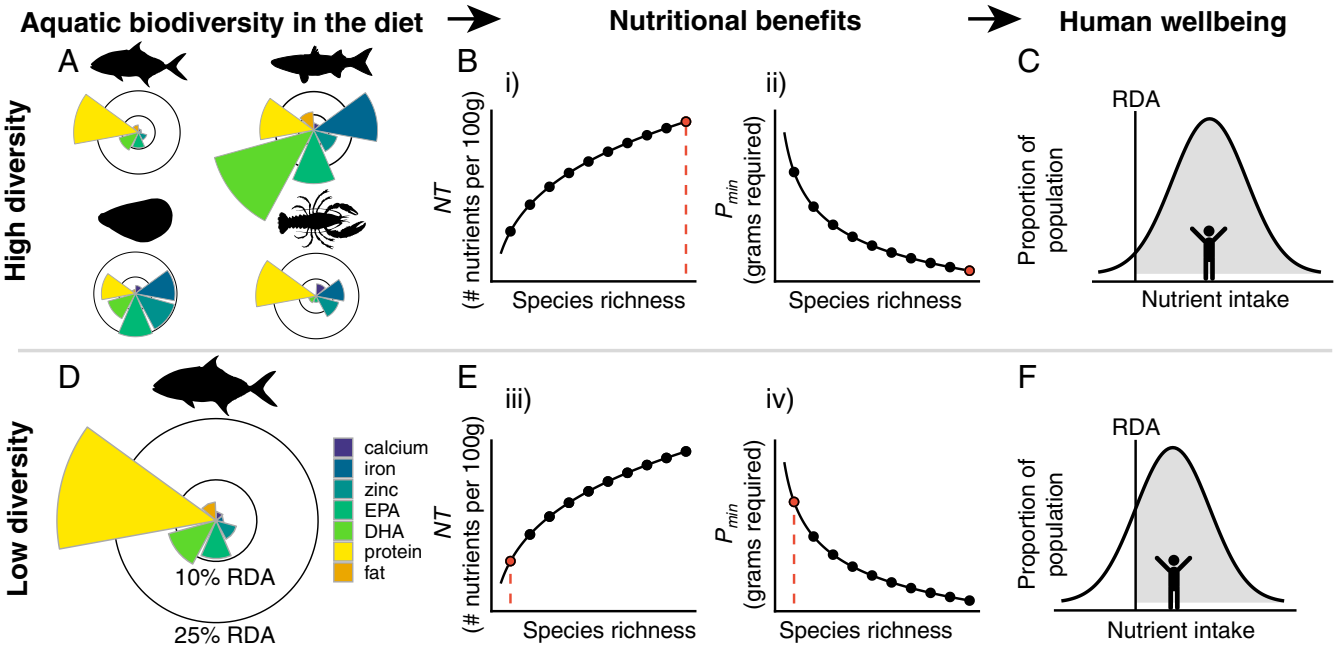

Fig. 1. Aquatic biodiversity increases human well-being because edible species have distinct and complementary multinutrient profiles (*A*) and differ in mean micro- and macronutrient content (shown here relative to 10 and 25% thresholds of recommended dietary allowance, RDA, guidelines) for representative finfish (*Abramis brama*, *Mullus surmuletus*), mollusc (*Mytilus galloprovincialis*), and crustacean species (*Nephrops norvegicus*). Biodiversity–ecosystem functioning theory predicts that nutritional benefits, including the number of nutrient RDA targets met per 100 g portion (*NT*; i, iii) and minimum portion size (P_{min}; ii, iv) (*B* and *E*), are enhanced with increasing seafood species richness. Orange dots in *B* and *E* correspond to potential diets of high and low biodiversity levels. Seafood consumers with limited access to seafood each day may not reach RDA targets if diets are low in diversity (*D–F* versus *A–C*; gray shading indicates proportion of population that meets nutrient requirements). DHA: docosahexaenoic acid, EPA: eicosapentaenoic acid.

included in the diet (or other food intake measures) and nutritional adequacy of reported diets. However, a simple correlation between dietary diversity and a measure of dietary benefits provides only partial support for a claim that biodiversity benefits human well-being, consistent with the same ecological processes by which biodiversity supports numerous ecosystem functions and services (23, 26). We build upon this foundation of empirical relationships between diet diversity and diet quality by placing this question in the quantitative ecological theoretical framework that relates biodiversity to function (24, 25), thereby laying the groundwork for additional development of links between biodiversity science and our understanding of human well-being.

Ecological theory predicts that biodiversity can be ecologically and economically important, apart from the importance of total biomass or the presence of particular species (23, 39). According to theory and over 500 explicit experimental tests (23, 40, 41), diversity in ecological communities and agricultural systems enhances ecosystem functioning by two mechanisms: 1) more diverse assemblages may outperform less diverse assemblages of the same density or biomass of individuals because more diverse assemblages will include more of the possible species and are therefore more likely to include high-performing species, assuming random processes of including species from the species pool (a *selection effect*), or 2) more diverse assemblages of a given density (or biomass) contain species with complementary functional traits, allowing them to function more efficiently (a *complementarity effect*) (25, 39). For aquatic animals, increased diversity enhances productivity of fish biomass (42) and also enhances temporal stability of biomass production and total yields (43, 44), providing economic and nutritional benefits to humans related to increased stability of harvests and production of biomass for consumption (43). However, when considering aquatic species from the perspective of human nutrition, functions other than biomass production become relevant because total seafood biomass consumption is not predictive of micronutrient benefits from seafood (45, 46).

Here, we test a hypothesis central to ecological theory in the 21st century: whether biodiversity per se (species richness and ecological functional diversity), distinct from the identities and abundance of species, enhances human well-being (Fig. 1). We chose a measure of human well-being distinct from provision of protein, calories, or total yields—the micronutrient and essential fatty acid benefits of seafood. For increasing biodiversity per se (as opposed to increasing total seafood consumption) to enhance nutritional benefits as predicted by biodiversity–ecosystem functioning theory (25, 47), the amounts of various nutrients within edible tissues must differ among species, and furthermore, nutrient concentrations must trade off among species, such that species that have relatively high concentrations of some nutrients also have relatively low concentrations of others (25). Specifically, a "biodiversity effect" (*sensu* ref. 25) on nutritional benefits requires that concentrations of multiple nutrients are negatively correlated with each other, or uncorrelated, when compared among species, creating a complementary distribution of nutrients across species. In contrast, if nutrient concentrations in edible tissue are positively correlated for multiple nutrients across species such that, for example, a species containing high amounts of iron also has a high essential fatty acid concentration, thereby containing multiple nutrients in high concentrations simultaneously, seafood species or ecological functional diversity in the diet would not be important. In the case of positive correlations among nutrient concentrations, the ecosystem service of nutritional benefits would be enhanced by consuming more fish biomass or by selecting a few highly nutritious species, without considering species richness or ecological functional diversity.

We aimed to bridge two distinct theoretical frameworks—the biodiversity–ecosystem functioning theory and human nutrition science—by quantitatively testing for effects of aquatic species richness and ecological functional diversity (48, 49) in seafood diets on nutritional benefits via complementarity or selection effects. We used the public health measure of recommended dietary allowance (RDA) index to quantify nutritional benefits. RDAs are nutrient-based reference values that indicate the average daily dietary intake level that is sufficient to meet the nutrient requirement of nearly all (97 to 98%) healthy individuals in a particular life stage and gender group (50). Here, we used the RDA for females aged 19 to 50 y (*SI Appendix*, Tables S1 and S2; see *SI Appendix*, Table S1 for definitions of key terms). We measured nutritional value in terms of concentrations relative to RDAs, and we refer to these recommended amounts (or portions thereof) as "RDA targets" (*SI Appendix*, Tables S1 and S2 and *Metrics*). We quantified nutritional value in two ways: 1) the minimum amount of seafood tissue (in grams) required to meet given RDA targets (either for a single nutrient or the five micronutrients and fatty acids simultaneously; referred to as "minimum portion size required," P_{min} [*SI Appendix*, Table S1, Eq. A1, and *Metrics*]) and 2) the number of nutrients that meet an RDA target in a single 100 g seafood portion (*NT*, *SI Appendix*, Table S1, Eq. A2). By considering nutritional value per unit biomass in both metrics, we avoided confounding diversity of seafood consumed with the total amount consumed (*Metrics*). We first tested two hypotheses: 1) seafood species richness increases *NT* because of complementarity in nutrient concentrations among species, and 2) seafood species richness increases the nutritional value of a 100 g edible portion of seafood, thereby lowering the minimum portion size, P_{min}, and improving the efficiency with which seafood consumers reach nutritional targets (Fig. 1). Following biodiversity–ecosystem functioning theory, we predicted that increased species richness is correlated with ecological functional diversity (51) in potential seafood diets and that ecological functional diversity is related to diversity in the concentration of essential elements and fatty acids that have nutritional value to human consumers, such that species and ecological functional diversity yields increased nutritional benefits. We also tested the hypothesis that seafood diversity increases total intake of heavy metal contaminants because some aquatic animals are known to bioaccumulate toxic metals in their tissues. For this reason, variation in bioaccumulation among species could lead to a biodiversity effect on contaminant intake that is detrimental to human health.

In a global analysis of over 5,040 observations of nutrient concentrations in 547 aquatic species (*SI Appendix*, Fig. S1), we considered the provision of nutritional benefits to human consumers. To assess whether the relationships between biodiversity and human nutrition benefits depend on the geographic extent (global or local) over which seafood are harvested or accessed (11), we tested whether seafood species richness is associated with higher nutritional value at local scales (versus global scale) in traditional Indigenous seafood diets in North America (*SI Appendix*, Methods 1.4). Seafood is critical for Indigenous groups, who on average consume seafood at a rate that is 15 times higher than the global average per capita consumption rate (16). To test our hypotheses at the geographic scale of local consumer communities, we complemented our global analysis with additional analyses of 25 to 57 species in 14 geographically constrained groups of species consumed together as part of traditional Indigenous diets (*SI Appendix*, Methods 1.4).

Results

Diversity of Seafood Nutrient Concentrations. Biodiversity effects via complementarity or selection require that species differ in their functional traits. We found that the global species pool was highly diverse with regard to concentrations of the micronutrients iron, zinc, calcium, and two fatty acids, docosahexaenoic acid (DHA) and eicosapentaenoic acid (EPA), in edible fish tissue relative to RDAs for those micronutrients and fatty acids (Fig. 2; micronutrient and fatty acid geometric coefficients of variation [CV]: ln[iron] = 3.28, ln[calcium] = 3.56, ln[EPA] = 2.62, ln[zinc] = 3.02, and ln[DHA] = 2.17; note the log scale). We observed limited variation in protein concentrations (ln[protein] CV = 0.04). The frequency distribution of trait values such as nutrient concentrations across species may indicate the potential strength of biodiversity effects, with lognormal distributions (such as we observed for micronutrients and fatty acids) more likely to confer strong effects of biodiversity than normal distributions with low dispersion (as we observed for protein). Most species did not meet a single micronutrient or fatty acid RDA in a 100 g portion: fewer than half of the 547 species we examined reached an RDA target of 10% RDA for calcium, iron, and the essential fatty acid EPA in a standard 100 g edible portion of a single species (*SI Appendix*, Table S3).

Biodiversity Increased the Nutritional Content of an Edible Portion of Seafood. We found that seafood species richness not only enhanced nutritional value for consumers selecting seafood from our global species dataset but that seafood species richness per se was essential to meeting nutritional targets for seafood diets with limited biomass consumption. Increasing seafood species richness allowed simulated diets to reach more RDA targets per 100 g of tissue so that nutritional value increased with species richness even as total biomass consumption (e.g., total seafood portion size) remained constant. We quantified the minimum amount of seafood, in grams, that would be required to reach an RDA target (*SI Appendix*, Table S2) at each of 10 levels of species richness (referred to as minimum portion size, P_{min}, for which lower values signify higher nutrition benefits to consumers per gram seafood consumed, *Metrics*). We then estimated the biodiversity effect using Eq. 3 (*Statistical Analyses and Hypothesis Testing*), in which b_{Pmin} is the scaling coefficient that describes how function (here, P_{min}) varies with species richness; higher absolute values of b_f (where f is an ecosystem function) indicate a steeper relationship between biodiversity and function and can be used to compare "biodiversity effects" among studies and systems (12, 52). As species richness increased in potential diets, P_{min} declined, and RDA targets for each micronutrient or fatty acid were achieved with less total seafood intake (Fig. 3*A*, $b_{Pmin} < 0$ for every micronutrient and fatty acid: calcium −0.32 [95% CI −0.35, −0.28], iron −0.24 [95% CI −0.27, −0.22], zinc −0.26 [95% CI −0.28, −0.23], EPA −0.25 [95% CI −0.27, −0.23], and DHA −0.22 [95% CI −0.23, −0.21]). Increasing species richness reduced the minimum portion size required, P_{min}, in our sample diets, independent of systematic changes in the identity of species included (*Stastical Analysis and Hypothesis Testing*), because the diets were assembled using random samples of the species pool. The restricted variation and symmetrical distribution in protein concentrations (Fig. 2 *Upper*), combined with high levels of protein in all edible tissues, lead to no benefit and a minimal detrimental effect of seafood species richness on protein provisioning (Fig. 3*A*, $b_{Pmin} = 0.0071$ 95% CI 0.0062, 0.0080). In other words, the ecosystem service of protein provisioning was adequately provided by total seafood edible biomass and not improved by species richness or even species identity. The findings for the micronutrients and fatty acids are consistent with demonstrations that variety and diversity in diets is important for nutrition (28, 29), but we extend these findings to show seafood species richness allows consumers to gain more nutritional benefit without consuming more total seafood biomass, and explicitly relate this pattern with general effects of biodiversity in ecological systems.

We then considered the effects of seafood species richness on the provisioning of multiple nutrients simultaneously (*Metrics*).

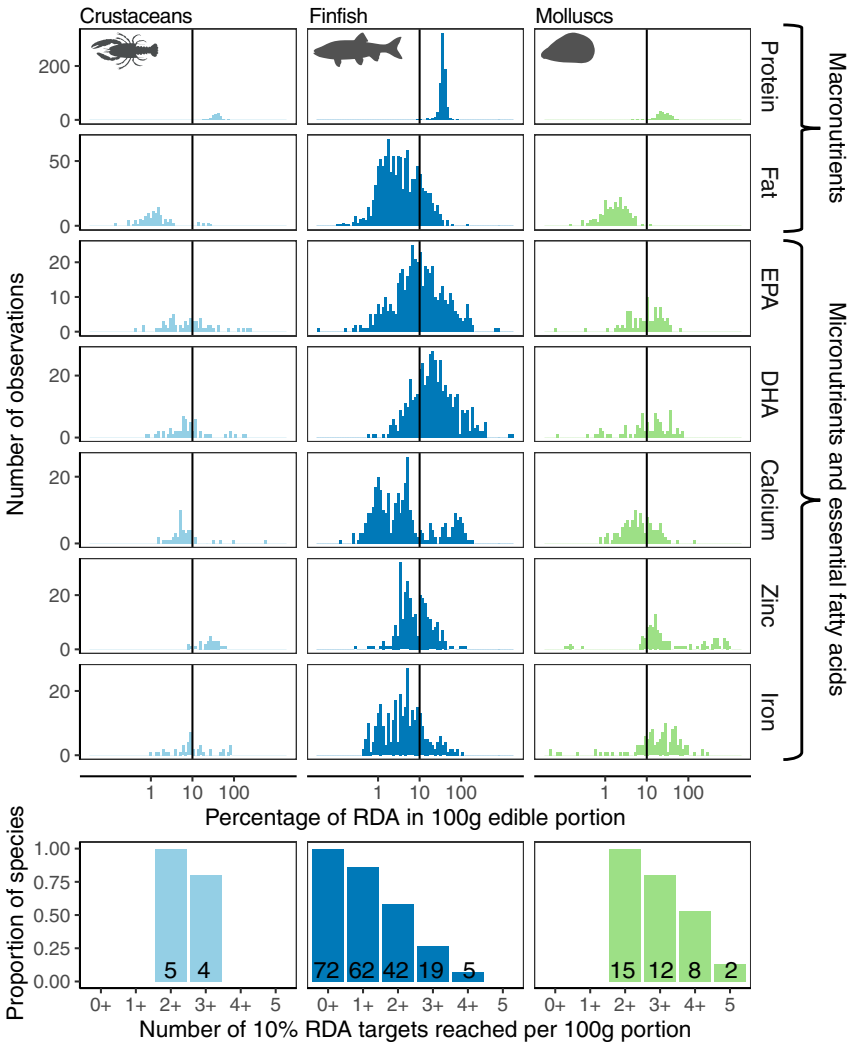

Fig. 2. Variation in nutrient concentrations differs among taxonomic groups. (*Upper*) Frequency of reported protein, fat, micronutrient and fatty acid content in 100 g of the edible portion of 547 seafood species. Note the *x*-axis is plotted on a log scale. (*Lower*) Proportion of species, and number shown on each bar, with available data that reach 10% of RDA targets for any one, two, or up to five of the micronutrients and fatty acids examined here.

This is referred to as a multifunctional benefit of biodiversity (53, 54) and takes into account possible trade-offs or correlations among functions; in this case, concentrations of micronutrients and fatty acids. For some ecosystem services (e.g., water quality or ecotourism), benefits of biodiversity accumulate when multiple ecosystem functions are considered simultaneously (54–56). Consistent with biodiversity–ecosystem functioning theory, we found that in the case of a multifunctional metric of an ecosystem service defined from the human beneficiary's perspective (i.e., multiple micronutrient and fatty acid targets reached simultaneously), biodiversity benefits for the multifunctional service are greater than for individual functions (b_{Pmin} for all five micronutrients and fatty acids simultaneously = −0.42 [95% CI −0.47, −0.38] versus single nutrients b_{Pmin} range from −0.32 [95% CI −0.35, −0.28] for calcium to −0.22 for DHA [95% CI −0.23, −0.21]) that comprise the ecosystem service (Fig. 3 *A* and *B*). Increasing seafood species richness from one to 10 species in 1,000 simulated, resampled diets drawn from our global species pool allowed diets to meet RDA targets for five essential microelements and fatty acids simultaneously more than twice as efficiently (i.e., a median of 494.19 g of tissue required with one species versus median of 213.34 g of tissue required with 10 species) (Fig. 3 *A* and *B*). Then, we assessed the effects of biodiversity when the total biomass of seafood consumed was held constant, at 100 g, by counting the number of nutrients for which RDA targets were reached in a 100 g portion (*NT*). We found positive effects of biodiversity on the number of nutrients that met RDA targets, *NT*, in a single 100 g portion (Fig. 3*C*): diets with higher species richness reached more nutritional targets (higher *NT*) per 100 g serving than diets of the same fish biomass comprising fewer species (b_{NT} = 0.20 [95% CI: 0.20 to 0.21]; Fig. 3*C*). These findings were robust to different RDA target levels (for P_{min}, they were independent of RDA target level, and for *NT*, they were positive over the range from 1 to 40% RDA per 100 g portion; *SI Appendix*, Fig. S2). These results reveal biodiversity effects of seafood quantitatively comparable with the widely recognized relationship between biodiversity and productivity (26, 47, 52) and demonstrate a benefit of biodiversity for human nutritional well-being over and above the benefits of consuming a particular amount (biomass) or identity of aquatic species.

Increasing Seafood Diversity Increased Contaminant Exposure. We considered a range of trace elements, which, at high concentrations, are known to be harmful to human health (57). We focused on four heavy metals considered as contaminants (methylmercury,

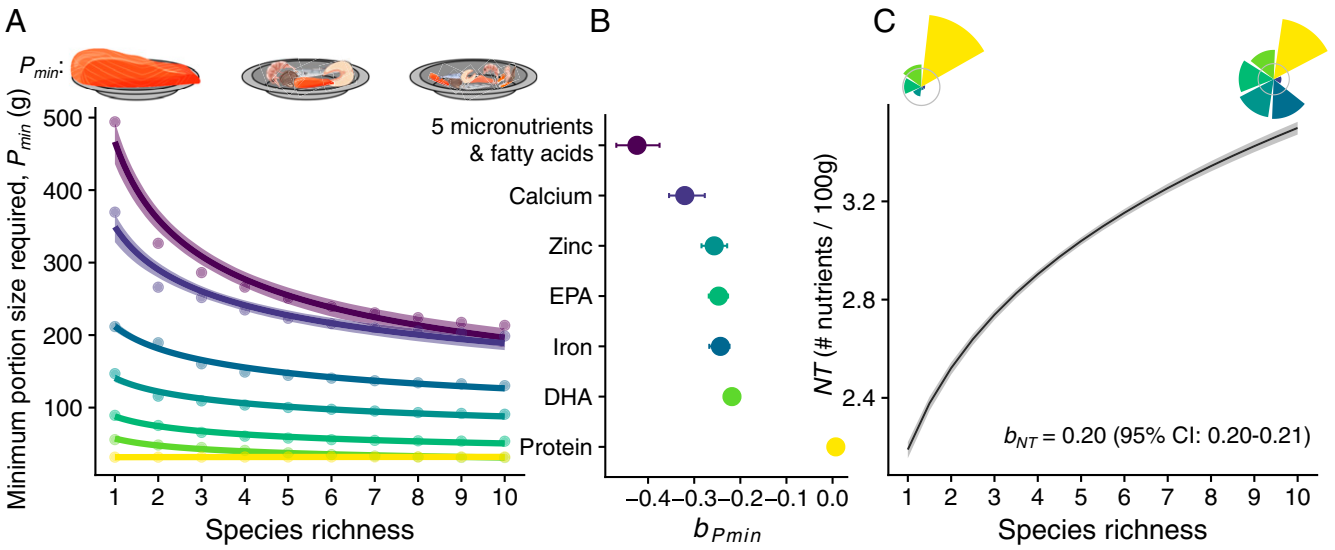

Fig. 3. Aquatic biodiversity enhances nutritional benefits. (*A*) Seafood species richness improves the efficiency with which human diets can meet RDA targets by reducing the minimum portion size required, P_{min}, to meet RDA targets (measured in grams of seafood). P_{min} is shown for micronutrients, fatty acids, and protein separately (points are median values for calcium, iron, zinc, EPA, DHA, and protein, lines show the fit of Eq. 3 to the data, and shading refers to 95% CI) as well as for the five micronutrients and fatty acids simultaneously (top purple line). Colors corresponding to each nutrient in *A* are shown in *B*. (*B*) Estimates (± 95% CI) for the scaling parameter that relates species richness to P_{min} (b_{Pmin}) (Eq. 3). (*C*) Species richness increases the number of distinct nutrient RDA targets met in a 100 g seafood portion (*NT*); black line and 95% CI correspond to the fit of Eq. 2 to mean *NT* derived from resampled diets from the global seafood species pool. Flower plots in *C* summarize the micronutrient and fatty acid concentrations relative to 10% RDA (gray circle) in two representative diets at low and high species richness levels. Data shown in *A* and *C* are derived from n = 1,000 resampled diets.

cadmium, arsenic, and lead) for which there exist public health guidelines for upper tolerable limits and for which seafood is potentially a major source of dietary intake (*SI Appendix*, Fig. S1 and Table S2). We examined the concentrations of these elements in the muscle tissues of 353 seafood species (thereby excluding parts such as viscera, liver, and bones). We found that the same mechanisms that lead to a positive relationship between seafood species richness and nutritional benefits also contributed to exposure to a wider range of contaminants with higher species richness. We observed high levels of variation in contaminant concentrations across species (Fig. 4 *A*–*D*), and as we observed for the micronutrients and fatty acids, these distributions were often right skewed such that most species contained low contaminant concentrations, and few contained high concentrations. On average, muscle tissue concentrations of contaminants were weakly positively correlated across species, such that species that contained high concentrations of one contaminant also contained high concentrations of another (average pairwise correlation = 0.09) (*SI Appendix*, Fig. S3). When considering multiple contaminants simultaneously, increasing seafood species richness increased the number of contaminants that exceeded their upper tolerable limits (PTDI) in a 100 g portion, referred to as *NC* (*SI Appendix*, Table S1, Eq. A4), (b_{NC} = 0.10, 95% CI 0.084, 0.12) (Fig. 4*E*). When we considered the effects of biodiversity on exposure to each contaminant separately, we found that increasing species richness generally increased contaminant content per 100 g, but the strength of this effect varied among contaminants. For example, increasing species richness from one to 10 species was associated with doubling methylmercury concentrations on average, thereby reducing the maximum portion size before exceeding PTDI, referred to as P_{max} (*SI Appendix*, Table S1, Eq. A3) (b_{Pmax} = −0.25 95% CI −0.27, −0.22). For lead, however, the biodiversity effect was weaker (an order of magnitude smaller than for methylmercury). Increasing species richness from one to 10 species was associated with only a 10% increase in average lead concentrations and a small reduction in maximum portion size, P_{max} (b_{Pmax} = −0.039, 95% CI −0.049, −0.034). For cadmium,

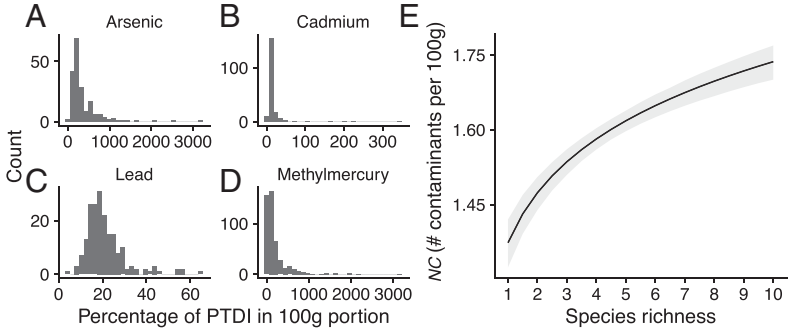

Fig. 4. Frequency histograms of concentration of arsenic (*A*), cadmium (*B*), lead (*C*), and methylmercury (*D*) in edible muscle tissues of North American aquatic species relative to PTDI. (*E*) Increasing seafood species richness increases the number of contaminants which exceed the upper tolerable limit (PTDI) in a 100 g portion (*NC*). Black line indicates the mean *NC* from 1,000 bootstrapped samples of seafood diets sampled from the North American seafood contaminant dataset, and gray shading refers to 95% CIs. Slope, b_{NC} = 0.10, 95% CI 0.084, 0.12.

b_{Pmax} = −0.12 (95% CI −0.13, −0.12), and for arsenic, b_{Pmax} = −0.17 (95% CI −0.19, −0.14). These differences in the strength of biodiversity effects among contaminants are linked to the shape of the distribution of their concentrations among fish species (i.e., normal versus lognormal) (Fig. 4 *A–D*), and the more skewed the distribution, the stronger the biodiversity effect.

Biodiversity Benefits Were Consistent at Local and Global Scales. Consistent with the positive biodiversity effects we observed when sampling diets from a global seafood species pool, we also found benefits of seafood diversity in a local context. We analyzed the effects of biodiversity on nutrient content in 14 traditional Indigenous North American diets of seafood harvested and consumed locally. We found a consistent, beneficial effect of biodiversity on *NT* and P_{min}, although the magnitude of the biodiversity effect was generally lower at the local scale than the global scale (*SI Appendix*, Fig. S4) (global b_{Pmin} = −0.42 [95% CI −0.47, −0.38] versus mean local b_{Pmin} = −0.25 ±0.0091 SE and global b_{NT} = 0.20 [95% CI 0.20, 0.21] versus mean local b_{NT} = 0.097 ±0.0082 SE). This finding is consistent with lower nutritional functional diversity (NFD, *SI Appendix*, Table S1) *sensu* ref. 34 (mean local *NFD* = 2.77 ±0.17 SE versus global *NFD* = 3.87) and higher nutritional functional evenness in local diets (mean local *NFEve* = 0.82 ±0.0037 SE versus global *NFEve* = 0.57) (*SI Appendix*, Methods 3 and Fig. S5), suggesting that functional consequences of changes to diversity in local seafood diets may be buffered by higher nutritional redundancy among species.

Nutritional Traits Covary with Ecological Traits. We found that nutrient concentrations varied substantially among species in ways that differed for different nutrients (Fig. 2)—a condition necessary for biodiversity per se to increase nutritional benefits. The diversity that we observed in the nutrient content of edible portions (Fig. 2) was partly explained by ecological attributes and functional traits: habitat, trophic position, body size, diet source, and feeding mode (*SI Appendix*, Tables S4–S8). When considering all five micronutrients and fatty acids (calcium, iron, zinc, EPA, and DHA) together, finfish, crustaceans, and molluscs differed significantly in their multinutrient profiles (*SI Appendix*, Table S1, permutational multivariate ANOVA [PERMANOVA], $F_{2,103}$ = 3.429, P = 0.006). Among finfish, nutrient concentrations depended on which tissues were included in the edible portions (significant "body part" effect shown in *SI Appendix*, Tables S4 and S6–S11). Finfish species whose edible portions included organs such as liver or bones had higher nutrient concentrations in the edible portion than those whose edible portions were restricted to muscle tissue (ANOVA P < 0.01 for calcium, iron, and zinc concentrations; *SI Appendix*, Fig. S6). Principal components analysis of multiple nutrient concentrations in species showed that essential element (calcium, iron, and zinc) concentrations were typically negatively correlated with essential fatty acid concentrations (EPA and DHA) (*SI Appendix*, Fig. S7), allowing complementarity among species to increase nutritional benefits. Specifically, high EPA and DHA concentrations traded off against low calcium and zinc concentrations, and vice-versa (negative pairwise Pearson correlation coefficients; *SI Appendix*, Fig. S7). When considering muscle tissues or muscle and skin tissues of finfish only (thereby eliminating the influence of body parts such as bones on nutrient concentration), concentrations of calcium, iron, zinc, EPA, and DHA were associated with ecological traits across species, including habitat and diet source (e.g., demersal versus pelagic), body size, and trophic position (Fig. 5). Relationships between species' nutrient tissue concentrations and their habitats and trophic positions have been predicted by ecological stoichiometry theory (58). Relationships between ecological traits and nutrient concentrations differed for different nutrients. For example, tissue concentrations decreased with body size for calcium but not for the other microelements, EPA or DHA (Fig. 5 and *SI Appendix*, Figs. S8–S10 and Tables S4–S8). Species at lower trophic positions had higher zinc concentrations in their tissues than species at higher trophic positions, but we did not observe this relationship for other nutrients (*SI Appendix*, Tables S4–S8). These examples illustrate that trade-offs and variation in nutrient concentrations across species were associated with variation in different ecological traits and roles that species play in ecosystems.

Nutritional Value Was Linked to Diversity of Ecological Functions. Ecological functional diversity of a species assemblage captures variation in traits and ecological roles of species (48, 49) and is understood to play an important role in the relationship between biodiversity and ecosystem function (Fig. 6*A*). We assessed the relationship between ecological functional diversity of seafood species diets (independent from species richness) and nutritional value. Consistent with observations for ecosystem functions such as productivity and biomass, nutritional benefits and ecological functional diversity were positively related, such that seafood diets with higher ecological functional diversity also provided

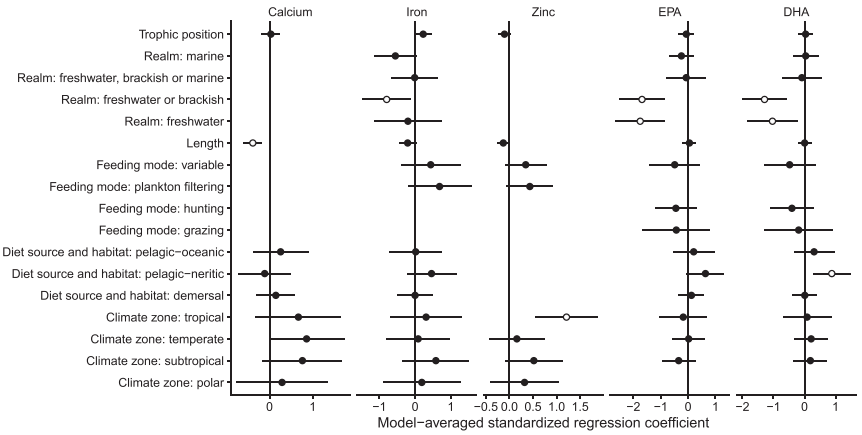

Fig. 5. Nutrient concentrations in finfish muscle tissue vary with ecological traits in ways that differ among the essential trace elements (calcium, iron, zinc) and the essential fatty acids (EPA and DHA). Model-averaged standardized regression coefficients and 95% CIs from phylogenetic least squares regression (see *SI Appendix*, Methods 4 for full model description) are shown for samples including muscle or muscle and skin tissues only. Traits for which there is no symbol did not appear in any of the models in the top 95% set (with cumulative sum of Akaike weights ≤ 0.95). Open symbols indicate coefficient estimates for which 95% CIs do not encompass zero. Note that *x*-axes differ across panels for clarity of presentation. Number of species: n = 155 for EPA, n = 159 for DHA, n = 104 for calcium, n = 99 for iron, and n = 90 for zinc. For model results including tissues other than muscle tissue, see *SI Appendix*, Tables S4–S11.

higher nutritional value (i.e., were more likely to reach five micronutrient and fatty acid RDA targets simultaneously, $NT = 5$) (Fig. 6*B*). Ecological functional diversity increased with species richness (*SI Appendix*, Fig. S11), and higher levels of ecological functional diversity were also associated with lower minimum portion size required (*SI Appendix*, Fig. S12). Because aquatic assemblages with higher ecological functional diversity have been shown to exploit more diverse resources, transform and transport energy and materials more efficiently, produce higher yields, and be more productive and resilient over time (42, 59–61), it is possible that the provisioning of multiple micronutrients and fatty acids occurs in tandem with a range of other ecological functions.

Discussion

Biodiversity of seafood provides high levels of nutritional benefits to humans because nutrient concentrations vary substantially among species in ways that differ for different nutrients (Figs. 2 and 5 and *SI Appendix*, Fig. S7). The effects of species richness observed for nutritional benefits equal or exceed mean observed diversity effects documented for plant and forest species richness and productivity (12, 40, 52, 62). Our findings build on evidence showing that biodiversity in marine systems enhances ecological functions by extending this paradigm to human nutrition. In agro-ecosystems, specific combinations of species such as corn, pumpkin, and beans have been planted to exploit complementary traits (shade provisioning, nitrogen fixation, and biomass production) to attain higher yields, more resilient crops, and enhanced nutritional benefits (35). By demonstrating that nutritional benefits of seafood can be understood as a consequence of seafood species richness and ecological functional diversity, we have shown that diverse seafood assemblages also provide nutritional and other ecological benefits simultaneously.

Our analysis provides robust evidence that biodiversity is critical to multifunctionality of ecosystem services when function thresholds are grounded a priori in multivariate metrics meaningful for human well-being such as RDA. Our approach overcomes the critique that multifunctionality is not enhanced by biodiversity (63) but rather a statistical artifact of how multifunctionality was commonly estimated. Our findings are robust to a range of RDA target levels (*SI Appendix*, Fig. S2). In the case of P_{min}, we found that the benefit of biodiversity was consistent across all RDA target levels considered, and in the case of NT, we found beneficial effects of biodiversity across a range of levels of nutritional value that are significant for human nutrition (i.e., 1 to 40% RDA per 100 g portion), highlighting the importance of species richness in seafood diets. More generally, ecosystem service benefits, as defined in metrics of human well-being rather than the traits of the species pool under consideration (e.g., biomass or stability of the food web), typically are produced by several underlying ecosystem functions (54). The strong effects of diversity on multifunctional benefits observed here may also apply to relationships between diversity and other services, for example, desired filtration rates of pollutants in wetlands (64), or desired pest consumption rates in agricultural systems (65).

Physiological and Ecological Mechanisms Underlying Nutritional Benefits and Risks. When comparing the magnitude of the biodiversity–ecosystem function scaling parameter b among the nutrients and contaminants, we found that the magnitude of b (Eq. **1**) was higher for nutrients with more skewed distributions of tissue concentrations (Figs. 2 and 4 and *SI Appendix*, Fig. S7). For all of these highly skewed distributions, we observed a strong biodiversity effect (i.e., high values of b). However, for protein and lead in muscle tissues, we observed symmetrical tissue concentration distributions. In these two cases, the biodiversity effect was either nonexistent (in the case of protein) or very weak (in the case of lead). This finding suggests that biodiversity effects may increase when the trait distribution is skewed and includes some species with extreme trait values, known as "functionally specialized" and "functionally unique" species (9, 66, 67). Understanding the drivers of the tissue concentration distribution among species may lend insights into how biodiversity effects may change as the nutrient under consideration changes or as the environment changes.

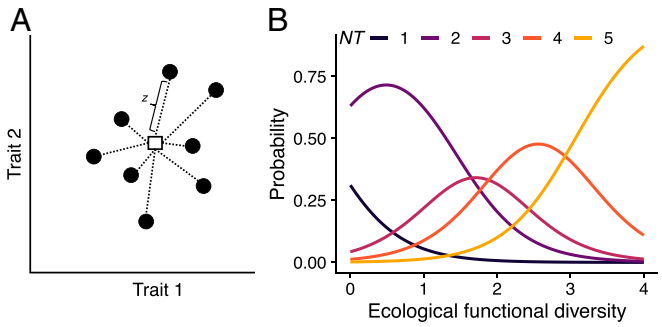

Fig. 6. (*A*) Ecological functional diversity, EFD, captures variation in the ecological traits and ecological roles of species and can be quantified as the average of the distances between species' trait values (circles) and the center of functional trait space (square, indicated by z, adapted from ref. 93). (*B*) Seafood diets with higher levels of EFD are associated with higher levels of nutritional benefits (i.e., higher number of RDA targets per 100 g portion). Probability of reaching five micronutrient and fatty acid RDA targets simultaneously in a single 100 g portion ($NT = 5$, light orange line) increases as the EFD of the diet increases. Probabilities predicted from ordinal logistic regression (log odds of functional diversity = 2.08, 95% CI [0.52, 3.64], n = 1,000 resampled diets).

Increasing seafood species richness increases nutritional benefits as well as contaminant exposure. Increasing biodiversity can have negative consequences for some ecosystem functions, despite positive consequences for others. On balance, the benefits of diversity may outweigh the negative effects on function when considering multiple functions together (68). Here, we found that the same mechanisms (lognormal and complementary tissue concentration distributions among species) that contributed to the positive relationship between biodiversity and human nutritional benefits also applied to contaminant exposure. As a result, increasing seafood species richness comes with both benefits and risks (69–71). However, interpreting our results in the context of public health outcomes is complicated by the fact that epidemiological evidence on health outcomes of contaminant exposure is mixed and likely dependent on complex social and health risks. The health risks of contaminant exposure depend on other health factors such as smoking or nutrients in the diet (72, 73) and disease status. Complex interactions among multiple diet and health risk factors (74) were beyond the scope of this study but would be necessary to understand exposure risks from seafood consumption in any particular community. Nonetheless, our results suggest that while increasing biodiversity increases contaminant exposure, it also increases nutritional benefit and reduces the portion sizes required to meet nutritional demands. Finding a balance between seafood biodiversity, seafood biomass consumption, and the resulting risks and benefits will be critical for both human and ecosystem health.

Aquatic Biodiversity and Food Security in a Changing World. Seafood-derived nutrition plays an important role in food security. The link that we have demonstrated between seafood biodiversity (species richness and ecological functional diversity) and nutrition in an ecological framework unites three of the United Nations Sustainable Development Goals focused on biodiversity, hunger, and well-being (75). More than two billion people suffer from micronutrient deficiencies (76, 77), and many of the most nutritionally vulnerable populations—those that are deficient in essential micronutrients and fatty acids during

particularly sensitive stages of life (i.e., pregnancy, breastfeeding, and childhood)—may rely heavily on local aquatic ecosystems to meet their nutritional demands (15, 19, 22, 78). These populations may have access to a limited amount of locally available seafood tissue each day, suggesting that nutritional efficiency (i.e., lower P_{min}) provided by biodiversity in wild-caught seafood may be particularly important for these populations. Regions of high nutritional vulnerability continue to experience major changes in biodiversity and ecosystem structure (6, 17, 79), and climate change is compounding threats to the sustainability of capture fisheries (2, 80). Our results suggest that declines in these aspects of diversity in wild aquatic ecosystems could make achieving sustainability goals for food security via seafood even more difficult. Seafood diets composed of more species, and groups of species with higher levels of ecological functional diversity, are more likely to provide more nutrients per unit biomass than less diverse seafood diets while also maintaining high levels of ecosystem function (26). This finding bridges the growing understanding of hidden hunger and food security with the large theoretical and empirical understanding of relationships between biodiversity, ecosystem function, and benefits to people. Biodiversity in natural aquatic systems can be maintained by reducing pollution and overharvest and by allowing ecosystems to adapt to climate change, and these measures could also benefit humanity directly through seafood provisioning.

Conclusions

Nutritional value appears to be derived from ecological diversity, suggesting links between the complexity of aquatic ecosystems and their capacity to produce nutritional benefits. While the role of seafood is well recognized as an important source of protein in the human diet, the role of seafood biodiversity as an important aspect of the provision of essential micronutrients has been overlooked. Our results reveal that aspects of ecological structure including species and ecological functional diversity enhance nutritional benefits while also increasing contaminant exposure, thereby linking the processes that structure ecosystems with their potential benefits and risks to human nutrition and health.

Methods

To test our hypotheses about aquatic species diversity and potential nutritional benefits for human well-being, we assembled a database of nutritional values by synthesizing observations from existing data (*SI Appendix*, Methods and Fig. S1). To build the database, we identified quantitative and comparable measures of nutritional content for the edible portions of aquatic species (*Quantifying Nutritional Value for Single Nutrients*). We then identified metrics for relating nutrient content to human health (*Defining Nutritional Benefits and Risks for Multiple Nutrients or Contaminants Across Diverse Species Groups*). We repeated this exercise for contaminants (*Quantifying Contaminant Exposure in Terms of Human Health Risks*). Next, we adapted an approach from biodiversity–ecosystem functioning theory for quantitatively assessing the potential nutritional value of seafood diets varying in their species composition and diversity for multiple nutrients separately and simultaneously (*Modeling the Biodiversity Effect for Sample Diets*). To test predictions of biodiversity–ecosystem functioning theory, we simulated potential diets at global and local scales and fit models to test for effects of species richness and ecological functional diversity (*Simulating Seafood Diets and Estimating Nutritional Benefits at Different Seafood Species Richness Levels*; and *Testing Hypotheses That Biodiversity Enhances Nutritional Benefits*). *SI Appendix*, Fig. S1 provides a graphical overview of our analyses.

Metrics.

Quantifying nutritional value for single nutrients. We characterized an aquatic species' nutritional value by drawing on two well-established nutritional metrics: nutrient concentration (mg/100 g edible portion) and RDAs. RDAs are developed following health guidelines to quantify the recommended amount of a particular nutrient required to maintain health (50). We used RDAs established by the Food and Nutrition Board of the US Institute of Medicine to quantify the daily intake level of a nutrient needed to meet the requirements of 97 to 98% of healthy adults (females aged 19 to 50 y) (50) (*SI Appendix*, Table S2). We refer to an RDA-defined threshold as an *RDA target* (*SI Appendix*, Tables S1 and S2). We calculated a ratio of the nutrient content in a 100 g edible portion relative to the RDA (or fraction thereof) for that nutrient. For many species, nutrient concentrations in edible tissues provided only small fractions of the RDA (*SI Appendix*, Table S2). Following the Institute of Medicine, we chose an RDA target as 10% of RDA for a given nutrient in a single portion (*SI Appendix*, Table S2) because this is a minimum threshold for a food to be considered of nutritional benefit (50). We defined the minimum portion size required, P_{min}, as the minimum amount of edible seafood tissue (g) required to reach the RDA target for a given nutrient (or a set of nutrients, *Defining Nutritional Benefits and Risks for Multiple Nutrients or Contaminants Across Diverse Species Groups*) (*SI Appendix*, Table S1, Eq. A1). We quantified the sensitivity of our biodiversity findings to different threshold levels of RDA for both single nutrient analyses and multinutrient analyses and found that for P_{min}, they did not vary with threshold level, and for *NT*, they varied with threshold but were robust to RDA threshold levels between 1 and 40% RDA (*SI Appendix*, Fig. S2).

We examined data on concentrations of macronutrients including protein and fat as well as five micronutrients and essential fatty acids (n = 5,041 observations of nutrient concentrations, *SI Appendix*, Fig. S1*A*): metals beneficial at low concentrations but toxic at high concentrations (zinc and iron), one beneficial mineral (calcium), and the polyunsaturated fatty acids EPA and DHA. We chose these five micronutrients and fatty acids because we required that RDA standards exist for each one (50) and that each nutrient has known functions in organismal physiology and is considered "biologically essential" because it is required by organisms to grow or reproduce. The concentration of biologically essential nutrients in organisms' tissues are controlled homeostatically by organisms (81, 82) and therefore might be biologically related to ecological trait values we considered in our trait analysis.

Quantifying contaminant exposure in terms of human health risks. We characterized an aquatic species' contaminant content relative to established public health guidelines for exposure. We used the provisional tolerable weekly intake (PTWI) developed by the Food and Agriculture Organization of the United Nations (FAO)/World Health Organization Expert Committee on Food Additives (57), which estimates the amount of a substance in air, food, soil, or drinking water that can be assimilated weekly per unit body weight over a lifetime without appreciable health risk (57). To make this metric comparable to RDA targets defined above, we quantified contaminant exposure per day by dividing the PTWI by seven and using the body weight of a 70-kg person to calculate a daily tolerable limit for use in our analyses, which we refer to as provisional tolerable daily intake (PTDI; *SI Appendix*, Table S1). In our analyses, we consider a tolerable upper limit to be exceeded if an edible portion contains 100% or more of the PTDI. We examined the sensitivity of this choice of 100% threshold by considering lower values (e.g., 50%) and found that for all values between 50 and 100% of PTDI, our findings remain consistent.

Defining nutritional benefits and risks for multiple nutrients or contaminants across diverse species groups. To test our hypothesis that nutritional value may depend on seafood diversity in a way that considers multiple nutrients at the same time, we used two metrics that considered multiple micronutrients and fatty acids simultaneously (Fig. 1): 1) the minimum portion size introduced above, P_{min}, (*SI Appendix*, Table S1, Eq. A1), which quantifies the amount of tissue, in grams, required to reach the RDA target for five nutrients simultaneously and 2) the number of nutrients for which RDA targets are met in a standard 100 g edible portion, *NT* (*SI Appendix*, Table S1, Eq. A2). Note that our *NT* differs from another measure, NFD (34), which is a measure of nutritional profile in multivariate trait space and does not explicitly quantify the number of nutrient RDA targets met in a portion. Our *NT* is a measure of potential nutritional value and is derived from the biodiversity–ecosystem function perspective to allow us to compare nutritional value with other functions that depend on biodiversity (e.g., productivity, resource cycling). This measure does not consider the potential physiological interactions or co-benefits of consuming multiple nutrients that would be considered in metabolic models for human health. To test our hypothesis that contaminant exposure also varies with seafood diversity, we defined P_{max} as the amount of tissue beyond which a tolerable upper limit (PTDI) for a given contaminant would be reached (*SI Appendix*, Table S1, Eq. A3 and Methods 2). Analogous to the *NT* metric defined above for the nutrients, we defined the number of distinct PTDIs in a 100 g portion as *NC* (*SI Appendix*, Table S1, Eq. A4 and Methods 2). We chose to standardize *NT* and *NC* relative to 100 g of seafood per day because 100 g edible portion is a standard metric used in the food and nutrition literature (37, 83), and consumption rates of 100 g per day is within the range of daily consumption rates for many communities that rely heavily on seafood to meet nutritional needs and for whom seafood may also pose substantial contaminant exposure risks (16, 45, 84, 85).

Statistical Analyses and Hypothesis Testing.

Modeling the biodiversity effect for sample diets. To quantitatively compare effects of biodiversity among possible seafood diets varying in species richness, we modeled species richness effects as a power function:

$$Y = aS^b, \quad [1]$$

where the parameter b is referred to as the "biodiversity effect" and describes the relationship between a change in species richness, S, and a measure of function, Y, such as P_{min} or NT, where a is a constant (12, 52).

Simulating seafood diets and estimating nutritional benefits at different seafood species richness levels. We tested the effect of species richness, S, on nutritional value by randomly assembling diets from the global seafood species pool at varying levels of species richness (*SI Appendix*, Fig. S1*B*). In our analyses of NT, we kept the total biomass constant at each level of species richness (100 g). In analyses using the global dataset (547 species) (*SI Appendix*, Methods 1.1), we assembled diets from the entire global species pool, choosing species at random without replacement. This way of simulating diets certainly ignores economic, social, and cultural factors that affect which species people consume but allows us to consider the potential effect of biodiversity on diets before diets are filtered by these other processes. To assess potential effects of biodiversity on nutritional value for populations that consume seafood locally from a restricted species pool, we sampled diets from species contained within traditional diets in 14 Indigenous cultures in North America (*SI Appendix*, Methods 1.4).

We created sample diets by sampling 10 species at random from the global species pool and then assembling seafood diets from all possible combinations of these 10 randomly chosen species at 10 levels of species richness (1 to 10 species) to generate 1,023 simulated diets (*SI Appendix*, Fig. S1 *B, i*). At each level of species richness, we assembled diets following the typical experimental design employed to test the hypothesis that biodiversity affects ecosystem functioning, analogous to a biodiversity–ecosystem function experiment with a replacement design (86), where species' abundances in the diet decline proportionally as species richness increases such that each species contributed an equal proportion of biomass. For each diet at each level of species richness (i.e., $n = 1{,}023$), we calculated P_{min} (*SI Appendix*, Table S1, Eq. A1 and Fig. S1 *C, ii*; for either, one of six possible nutrients targets individually [protein, calcium, iron, zinc, EPA, and DHA] or five micronutrient and fatty acid [calcium, iron, zinc, EPA, and DHA] targets simultaneously). To estimate NT (*SI Appendix*, Fig. S1 *C, ii*), we quantified the number of distinct nutrient RDA targets by assigning each diet ($n = 1{,}023$) a set of zeros or ones according to whether that combination met the RDA target for each nutrient (*SI Appendix*, Table S1, Eq. A2). This approach allowed us to explore how likely it would be for potential human diets containing different numbers of seafood species to reach RDA targets for a given number of micronutrients and fatty acids (NT ranges between 0 and 5), assuming that seafood species were included in the human diet at different levels of richness at random. At each level of species richness, we averaged P_{min} and NT. We then repeated this process of random sampling 10 species from the species pool, assembling diets at each level of richness, estimating metrics of nutritional value, and averaging at each richness level 1,000 times, yielding 1,000 estimates of each metric at each richness level (*SI Appendix*, Fig. S1 *C, iii*).

Testing hypotheses that biodiversity enhances nutritional benefits. We tested the hypothesis that complementarity in nutrient concentrations among species increases nutritional benefits by increasing NT (*SI Appendix*, Fig. S1*D*). We quantified the effect of seafood species richness, S, on NT at each richness level estimated in *Simulating Seafood Diets and Estimating Nutritional Benefits at Different Seafood Species Richness Levels* ($n = 1{,}000$ estimates of NT per richness level) by fitting a power function of the form shown in Eq. 1,

$$NT = aS^{b_{NT}}, \quad [2]$$

where the parameter b_{NT} describes the relationship between a change in species richness, S, and a change in NT, and a is a constant.

We tested the hypothesis that complementarity in nutrient concentrations among species reduces the minimum portion size required, P_{min}, by estimating the effect of species richness, S, on P_{min} ($n = 1{,}000$ estimates of P_{min} per richness level) at each richness level using

$$P_{min} = aS^{b_{Pmin}}, \quad [3]$$

where the parameter b_{Pmin} describes the relationship between a change in species richness, S, and a change in P_{min}, and a is a constant (*SI Appendix*, Fig. S1*D*).

We estimated a and b in Eqs. 2 and 3 using nonlinear regression using the *nls.lm* function in the *minpack.lm* package in R (87). We conducted all analyses in R version 3.3.2 (88). To quantify uncertainty in parameter estimates associated with the fit of Eqs. 2 and 3 to our estimates of function (*Simulating Seafood Diets and Estimating Nutritional Benefits at Different Seafood Species Richness Levels*), we calculated bootstrapped CIs ($n = 1{,}000$ bootstraps) using nonparametric bootstrapping of mean centered residuals using the *nlsBoot* function in the R package *nlstools* (89). For both P_{min} and NT, we tested the hypothesis that biodiversity enhances nutritional benefits by assessing whether the estimate of the scaling exponent, b, had CIs not overlapping zero.

We tested the hypothesis that nutrient concentrations are related to species' ecological traits in two ways: 1) testing whether multinutrient profiles (i.e., concentrations of all five micronutrients and fatty acids) differ among major phylogenetic groups using PERMANOVA (*SI Appendix*, Methods 4) and 2) whether differences in single nutrient concentrations differ with species' ecological traits using phylogenetic least squares regression (*SI Appendix*, Methods 4). We quantified the relationship between nutritional benefits and ecological functional diversity (EFD, *SI Appendix*, Table S1) by estimating NT, P_{min}, and EFD, estimated as functional dispersion, of diets simulated from the global species pool (*SI Appendix*, Methods 5).

Uncertainties. There are several sources of uncertainty in our analyses. First, there are substantial sources of uncertainty in food composition estimates. The data in our dataset meet international standards for data quality and standardization, meaning that we followed guidelines for checking food composition data and converting units, denominators, and expressions (90). Still, tissue concentrations may vary depending on analytical techniques, laboratories, season, diet of the animal, life stage, etc. Some of these sources of uncertainty (e.g., differences in analytical techniques) are unavoidable consequences of synthesizing previously published data collected across many laboratories. We assumed that these uncertainties in the data were randomly distributed over our geographically and taxonomically diverse dataset. Further uncertainty is associated with how well our set of 547 species represents the global pool of seafood consumed. We do not know whether our sample is random or biased, though we can say that our dataset includes 41 of the 67 most consumed species worldwide [as determined by FAO production volumes (91), species with capture production of 150,000 tons or more, after removing species for which the majority of production volume is diverted to fish meal and oil (92), *SI Appendix*, Table S13]. A remaining source of variation among samples is likely due to natural sources of variation associated with seasonal and other sources of temporal variability, which we consider to be an important component of biodiversity.

Data Availability. Data and code are available at GitHub (https://github.com/JoeyBernhardt/Nutrient_analysis) and are archived using Zenodo with DOI: 10.5281/zenodo.4474988. Data are available on Dryad (https://doi.org/10.5061/dryad.rn8pk0p8t) (94).

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Supporting Information for

Aquatic biodiversity enhances multiple nutritional benefits to humans

Joey R. Bernhardt, Mary I. O'Connor
Correspondence to: joey.bernhardt@biodiversity.ubc.ca

This PDF file includes:

Part A: Supplementary Figures and Tables (Figures S1-S12; Tables S1 – S14)
Part B: Supplementary Methods
Supplementary References

Part A: Supplementary Figures and Tables

Part B: Supplementary Methods

Part A: Supplementary Figures and Tables

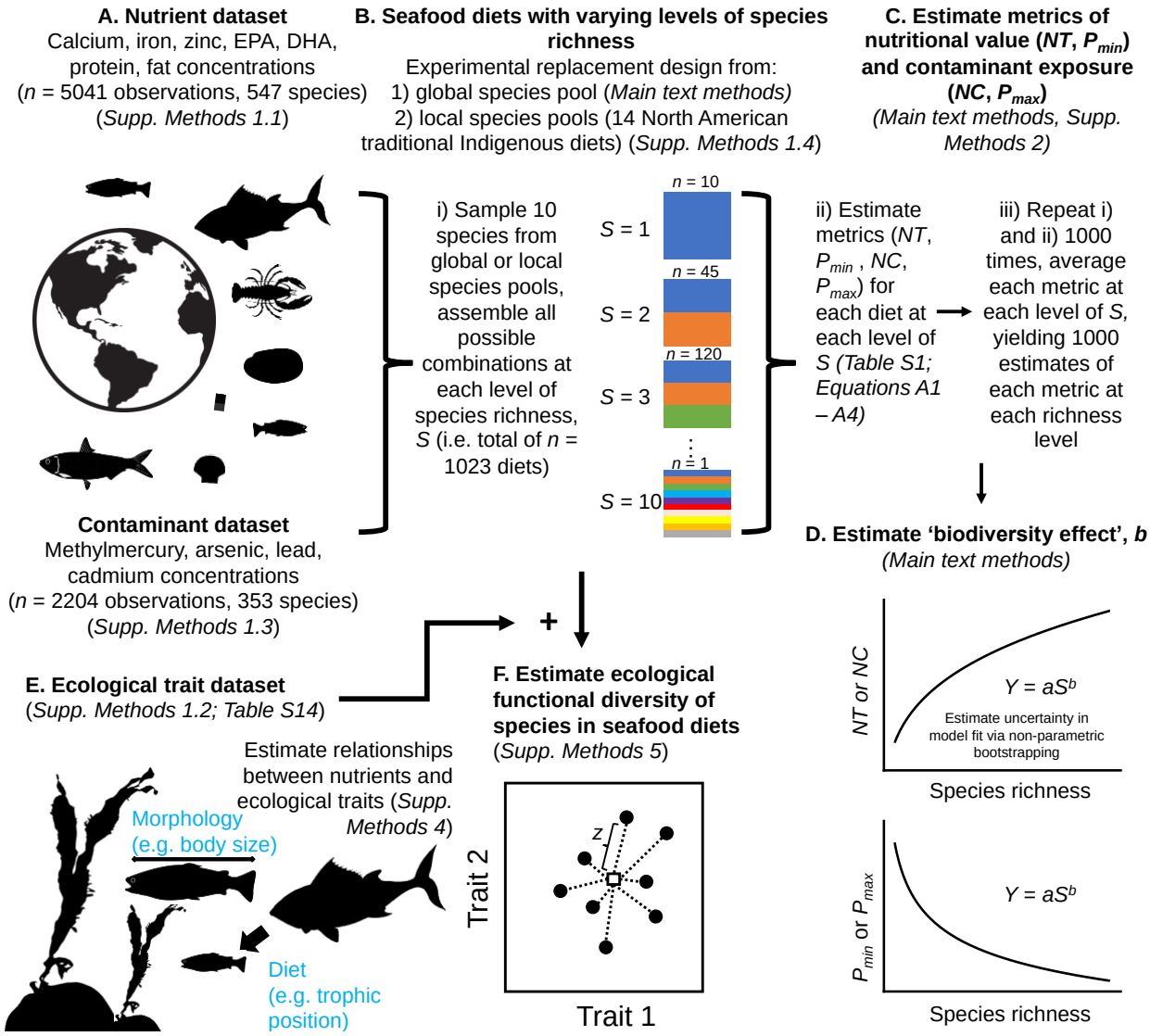

Figure S1. Graphical overview of some of the analyses used in this study, and references to relevant methods and definitions in the text. We began by assembling datasets of nutrient and contaminant concentrations in seafood tissues (A, Supplementary Methods 1.1). From these datasets, we assembled potential seafood diets at varying levels of species richness sourced from species pools at global and local scales, following a design analogous to a biodiversity-ecosystem function experiment with a replacement design (B, "Statistical Analyses and

Hypothesis Testing" Methods in main text, Supplementary Methods 1.4). We then estimated metrics of nutritional value and contaminant exposure (C, "Metrics" Methods in main text and Supplementary Methods 2), and the 'biodiversity effect' (D, "Statistical Analyses and Hypothesis Testing" Methods in main text). Finally, using a dataset of ecological traits for the species in seafood nutrient dataset (E, Supplementary Methods 1.2), we estimated the ecological functional diversity of seafood diets, to assess the relationship between metrics of nutritional value and ecological functional diversity (F, Supplementary Methods 5).

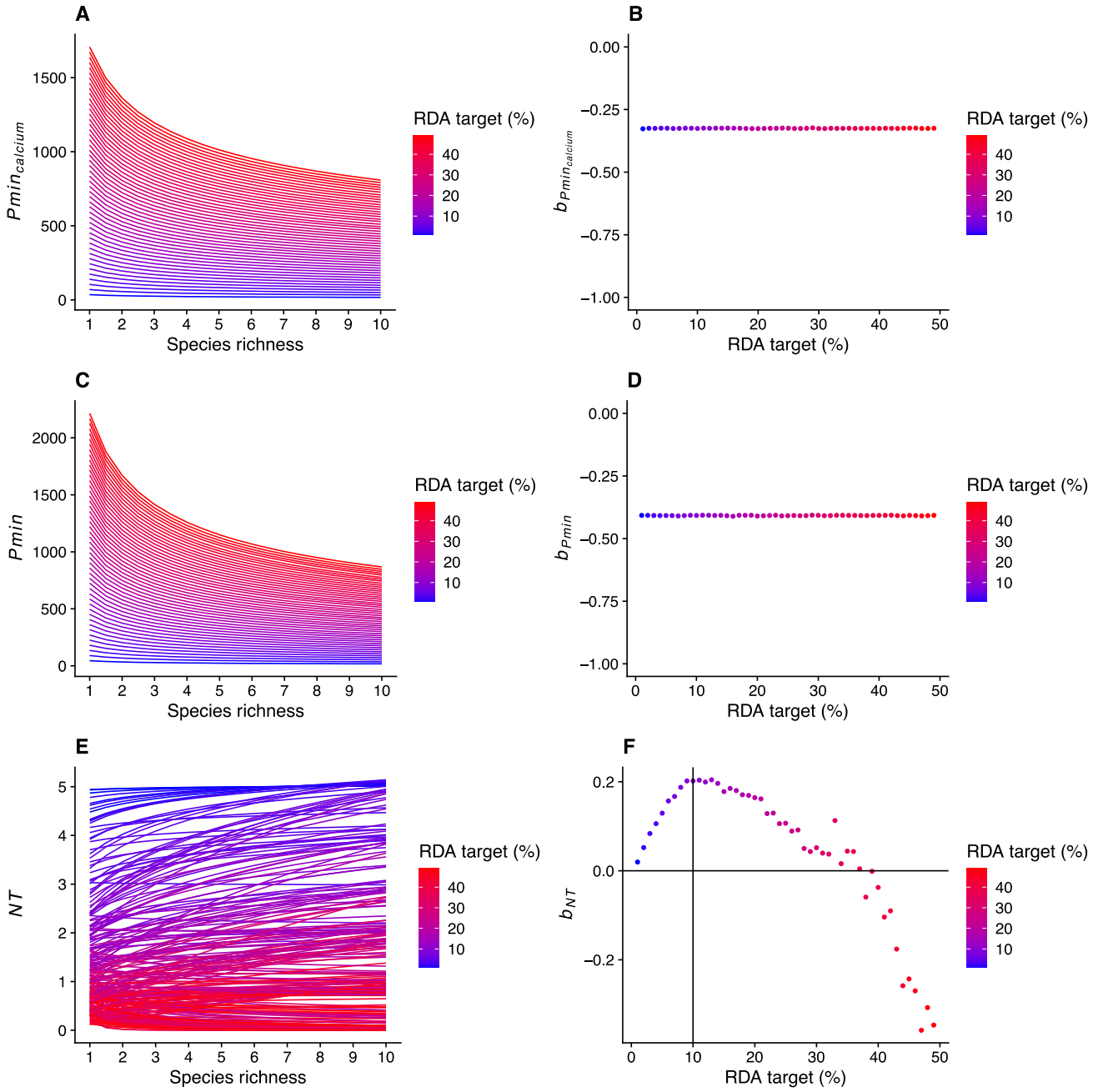

Figure S2. Minimum portion size (P_{min}, Main Text, Methods) required to reach RDA targets for a single nutrient (e.g. calcium) (**A**) and for the five micronutrients and fatty acids (**C**) depends on species richness and the percentage of RDA considered in the target. The effect of biodiversity on P_{min}, (estimated as the slope parameter, b_{Pmin}, in Equation 3, Main Text) remains constant

across all percentages of RDA, in the case of b_{Pmin} for a single nutrient (e.g. calcium), (**B**) and five micronutrients and fatty acids simultaneously (**D**). Each line shown in **A** and **C** is the mean P_{min} from 1000 simulated diets sampled from the global seafood nutrient dataset. Colours correspond to calculations of P_{min} using different RDA target levels, from 1% to 50% RDA. The effect of biodiversity on the number of nutrients that reach RDA targets (*NT*, Main Text Methods) depends on the RDA target level (**E, F**). Number of nutrients that reach RDA targets per 100g edible portion increases with seafood species richness (**E**). Colours correspond to calculations of *NT* using different RDA target levels, from 1% to 50% RDA. Each line shown here is the mean *NT* from 1000 simulated diets sampled from the global seafood nutrient dataset. The effect of biodiversity (estimated as the slope parameter, b_{NT}, in Equation 2, Main Text) on the number of nutrient targets reached (*NT*) is positive over a range of RDA target levels from approximately 1-40% (**F**).

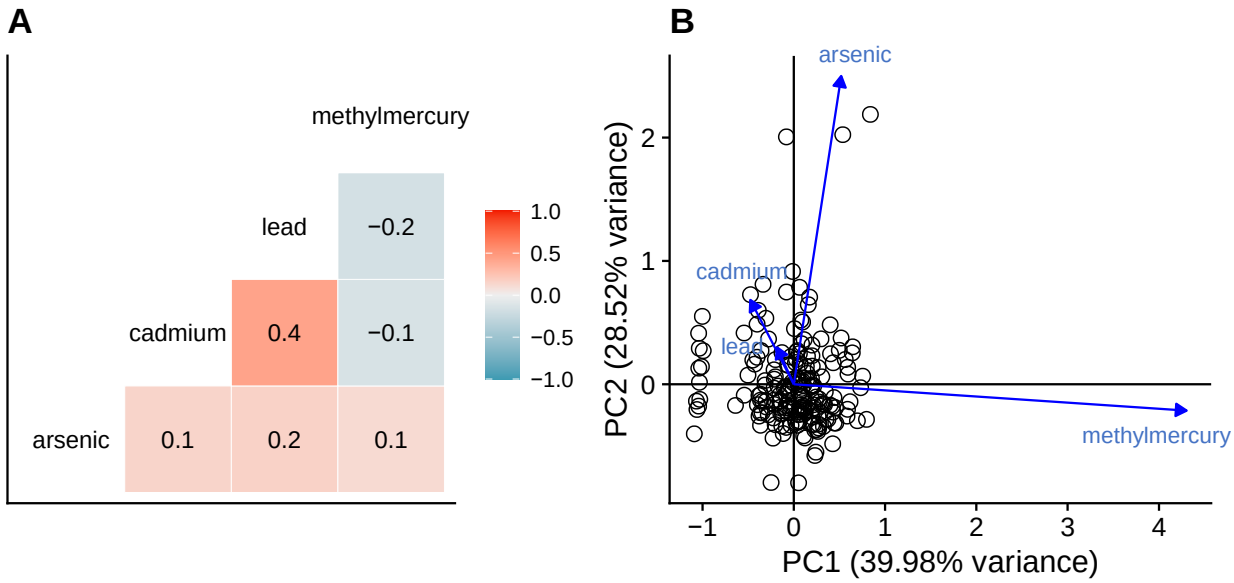

Figure S3. Pairwise Pearson correlation coefficients (A) and principal components analysis (B) of contaminant concentrations in muscle tissues of 200 North American seafood species (see SI Appendix Part B, Supplementary Methods 1.3 for information on contaminant data).

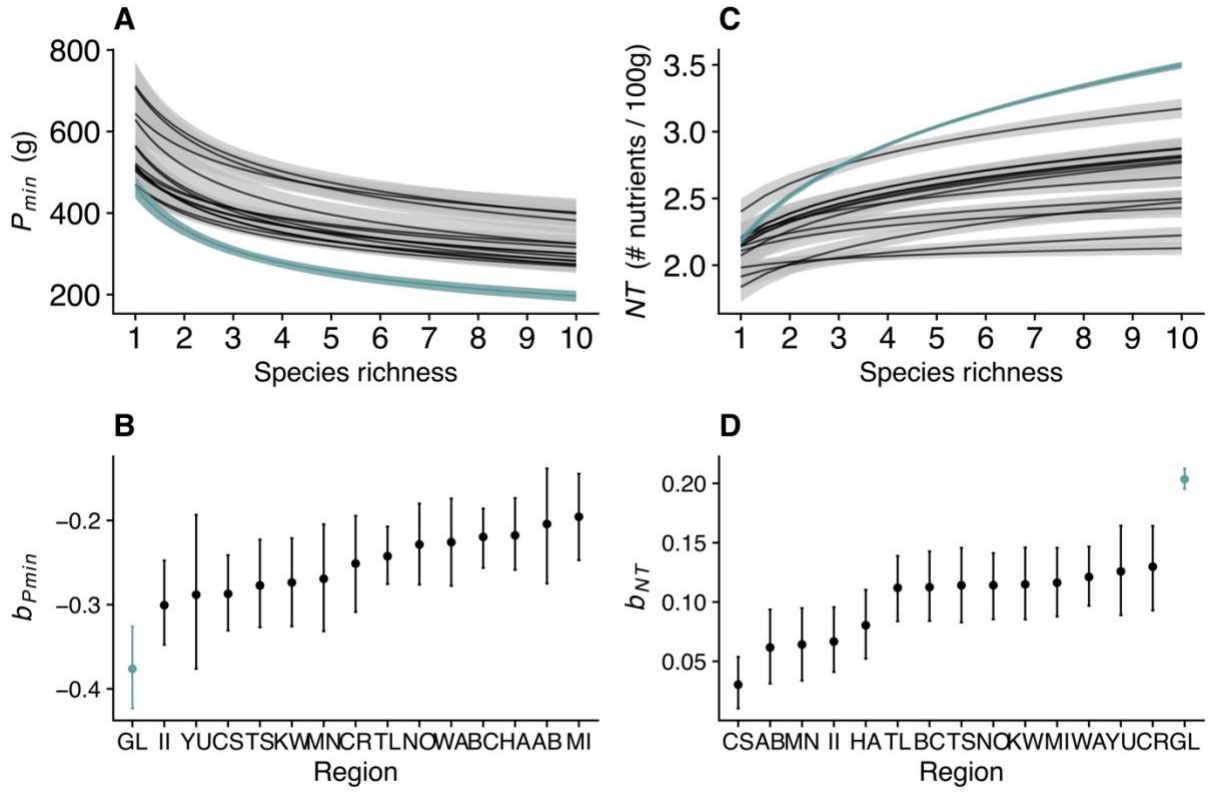

Figure S4. At global and local scales, biodiversity enhances nutritional benefits in terms of two metrics of nutritional benefit: minimum portion size required to reach five micronutrient and fatty acid targets, P_{min}, (A, B) and the number of nutrients that meet an RDA target, *NT* (C, D). Increasing seafood species richness sourced from local and global scales reduces the minimum portion size required to reach five micronutrient and fatty acid RDA targets (A, black lines are the fit of Equation 3 for each of fourteen traditional Indigenous diets in North America (local scales), green line is for a diet sourced from the global seafood market (global scale)). Increasing species richness increases *NT* at local and global scales (C, colour coding as in A). Each point in panel B and D corresponds to the *b* parameter estimate from Equation 3 (panel A) and Equation 2 (panel C) for one of fourteen local Indigenous diets (Table S12) and the global diet (GL; standardized to 40 species, Supplementary Methods 3). Points are mean ± 95% CI from non-parametric bootstrapping of the fit of Equations 2 or 3 to randomly assembled diets drawing

from the species included in the North American Indigenous diet species' lists (Supplementary Methods, section 1.4). Names of regions for each local diet are represented in two-letter abbreviations listed in Table S12.

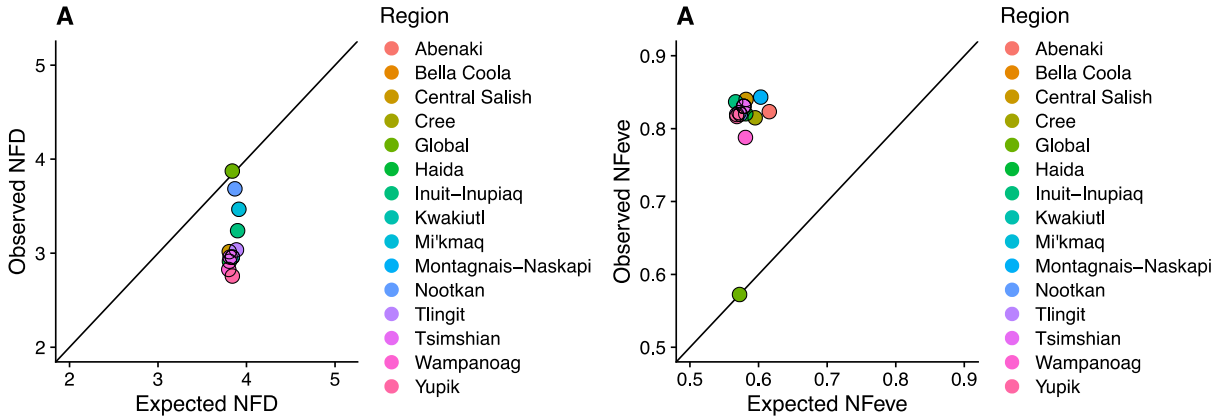

Figure S5. Observed *vs* expected nutritional functional diversity (*NFD*) and functional evenness (*NFEve*) in local North American traditional Indigenous seafood diets and global seafood diets. Local Indigenous diets tend to have lower *NFD* and higher *NFEve* than global seafood diets standardized to the same number of species (40 species); see Supplementary Methods section 3.

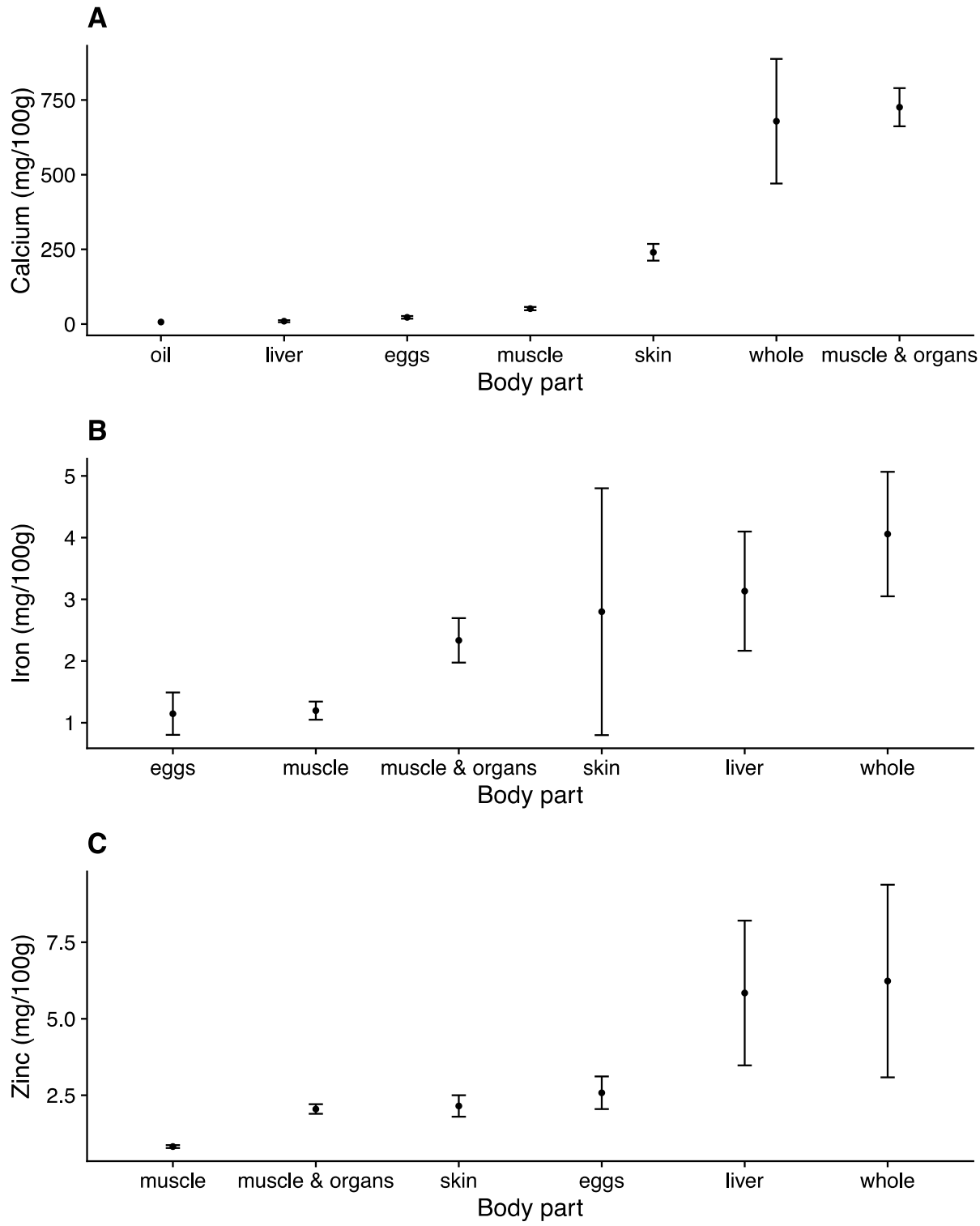

Figure S6. Variation in nutrient content per portion of finfish species associated with different body parts. Among finfish species, nutrient content varies by body part in the edible portion. Fish

species that are eaten whole or whose edible portions include organs such as skin, liver or bones have higher nutrient content for some nutrients than those whose edible portions are restricted to muscle tissue. Note that different edible portions may come from different species, and not all tissues are available for all species. (A) calcium, n = 343 observations, (ANOVA, $F_{6, 336} = 33.42$, $p < 0.01$), (B) iron, n = 316 observations (ANOVA, $F_{5, 310} = 4.36$, $p < 0.01$), (C) zinc n = 299 observations (ANOVA, $F_{5, 293} = 41.98$, $p < 0.01$). Points are mean ± standard error.

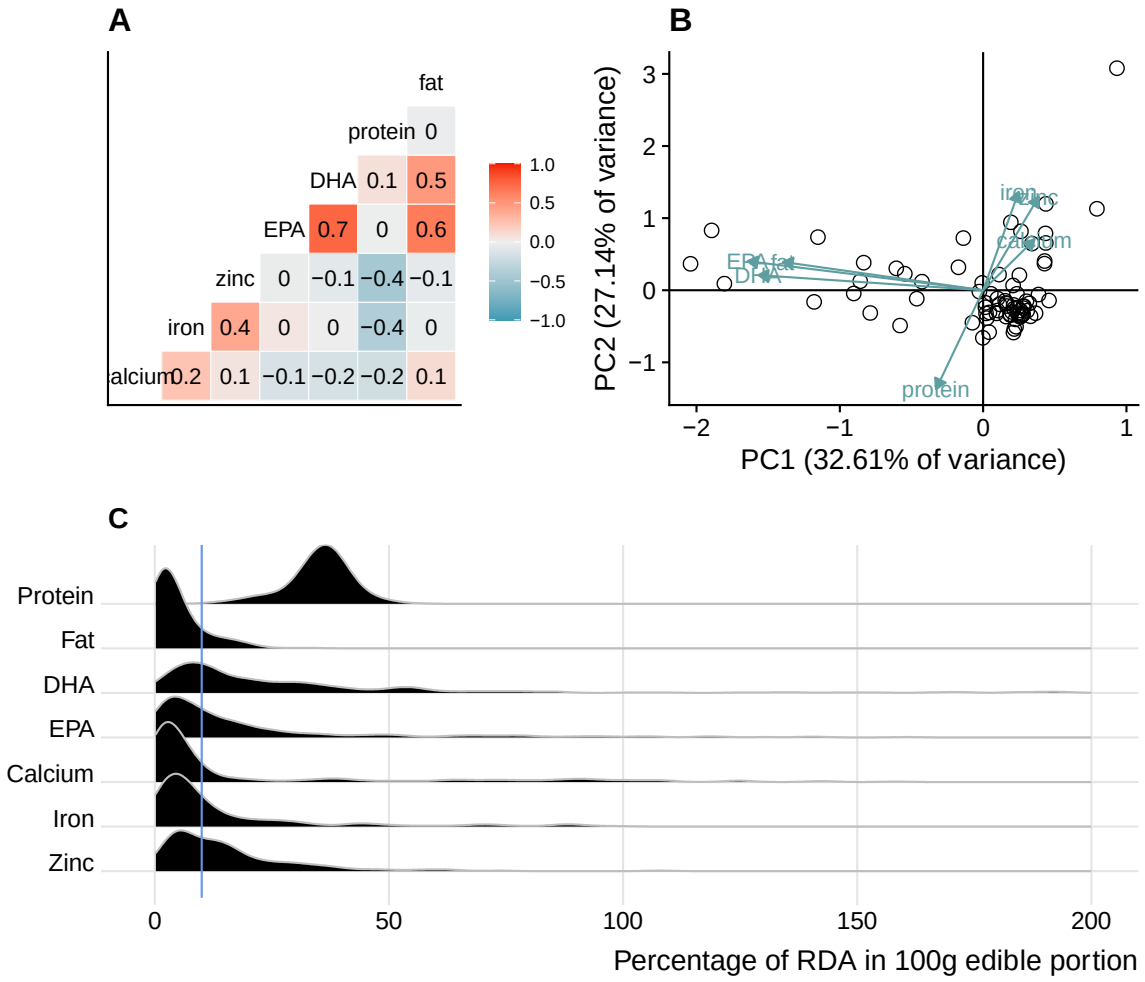

Figure S7. A) Pairwise Pearson correlation coefficients among concentrations of seven nutrients (five micronutrients and fatty acids plus protein and fat) in 120 species in the nutrient dataset for which data on all seven nutrients were available. B) Principal components analysis of seafood species' nutrient concentrations in edible portions for all seven nutrients showing trade-offs between the essential microelements (iron, calcium and zinc) and essential fatty acids (EPA and DHA). C) Distributions of average nutrient concentrations in seafood species tissues (for protein, n = 409, fat, n = 499, DHA, n = 275, EPA, n = 272, calcium, n = 236, iron, n = 234, zinc, n = 206), relative to 10% of RDA, shown in the blue vertical line.

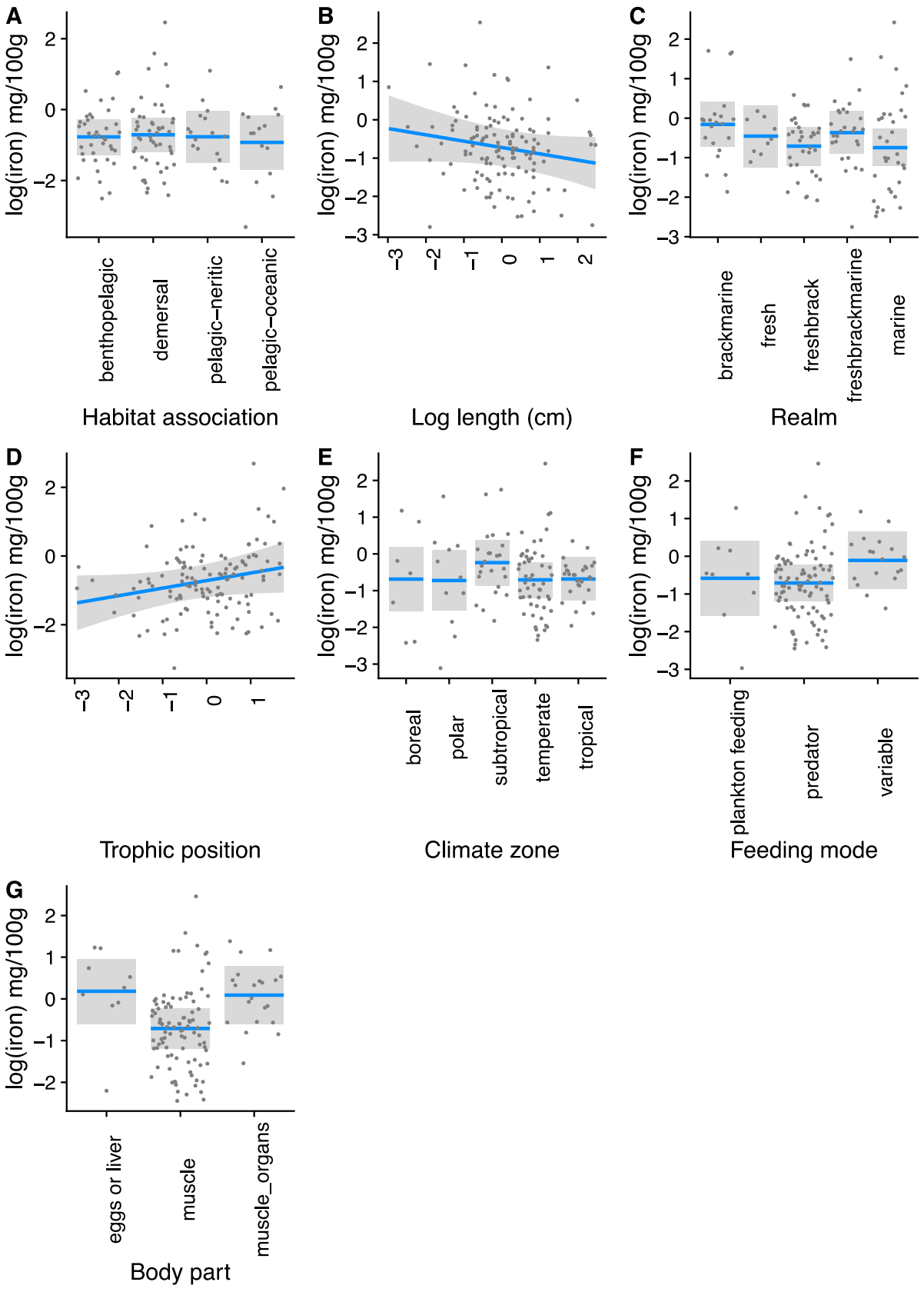
A
B
C
D
E
F
G
log(iron) mg/100g
benthopelagic
demersal
pelagic–neritic
pelagic–oceanic
Habitat association
Log length (cm)
brackmarine
fresh
freshbrack
freshbrackmarine
marine
Realm
Trophic position
boreal
polar
subtropical
temperate
tropical
Climate zone
plankton feeding
predator
variable
Feeding mode
eggs or liver
muscle
muscle_organs
Body part

Figure S8. Iron concentrations in edible finfish tissues vary with species' ecological traits. Partial regression plots from phylogenetic least squares regression (Supplementary Methods section 4) showing the effects of ecological traits on iron concentrations in seafood species edible tissues (finfish only), while holding all other variables constant (n = 123 species, R^2 = 0.26; for full model results and regression coefficient estimates, see Table S4). Note that different edible portions may come from different species, and data for nutrients in all tissue types were not available for all species; see Table S14 for predictors.

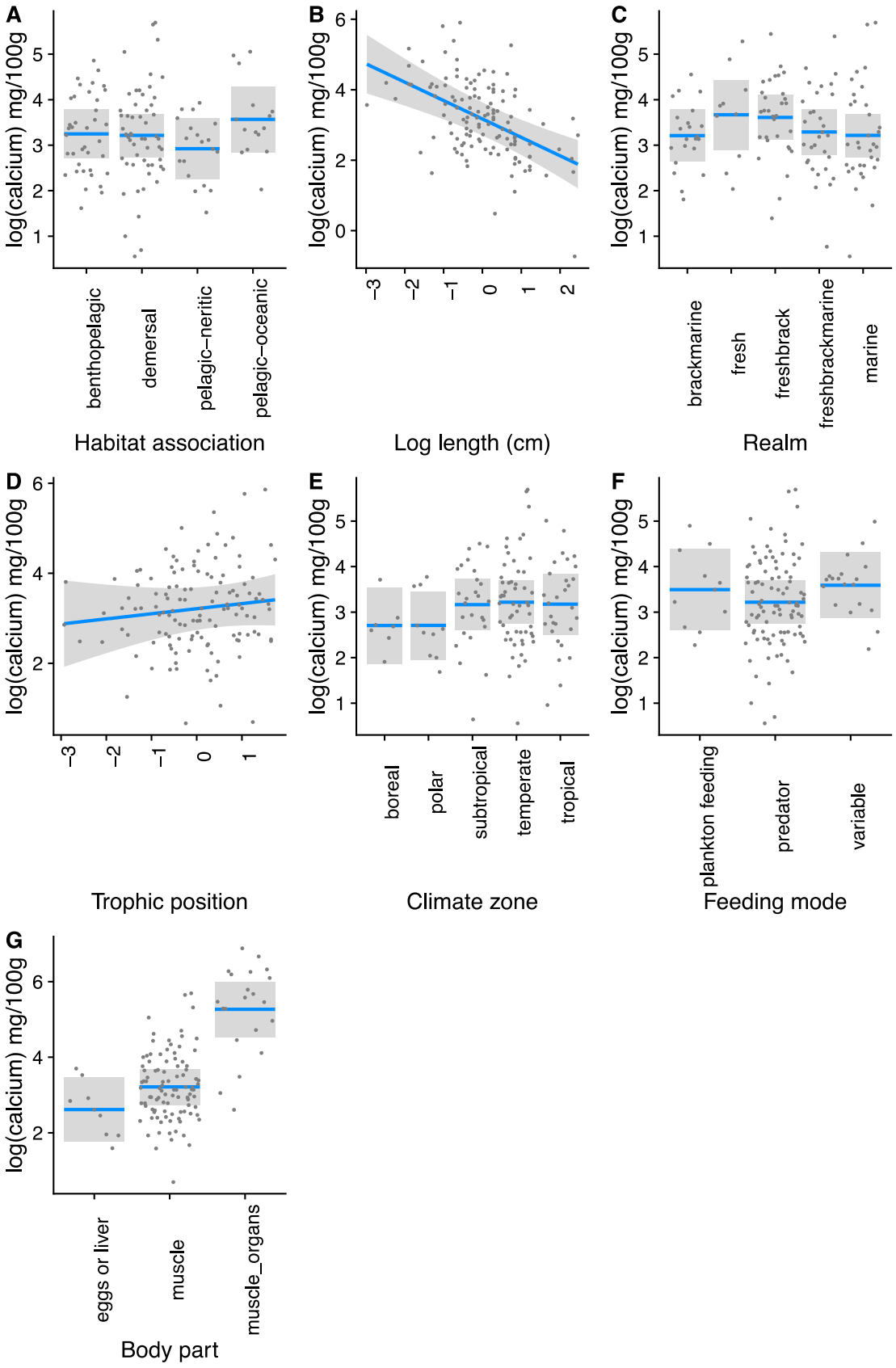
A
log(calcium) mg/100g
benthopelagic
demersal
pelagic–neritic
pelagic–oceanic
Habitat association
B
log(calcium) mg/100g
Log length (cm)
C
log(calcium) mg/100g
brackmarine
fresh
freshbrack
freshbrackmarine
marine
Realm
D
log(calcium) mg/100g
Trophic position
E
log(calcium) mg/100g
boreal
polar
subtropical
temperate
tropical
Climate zone
F
log(calcium) mg/100g
plankton feeding
predator
variable
Feeding mode
G
log(calcium) mg/100g
eggs or liver
muscle
muscle_organs
Body part

Figure S9. Calcium concentrations in edible finfish tissues vary with species' ecological traits. Partial regression plots from phylogenetic least squares regression (Supplementary Methods section 4) showing the effects of ecological traits on calcium concentrations in seafood species edible tissues (finfish only), while holding all other variables constant (n = 127 species, R^2 = 0.60; for full model results and regression coefficient estimates, see Table S5). Note that different edible portions may come from different species, and data for nutrients in all tissue types were not available for all species; see Table S14 for predictors.

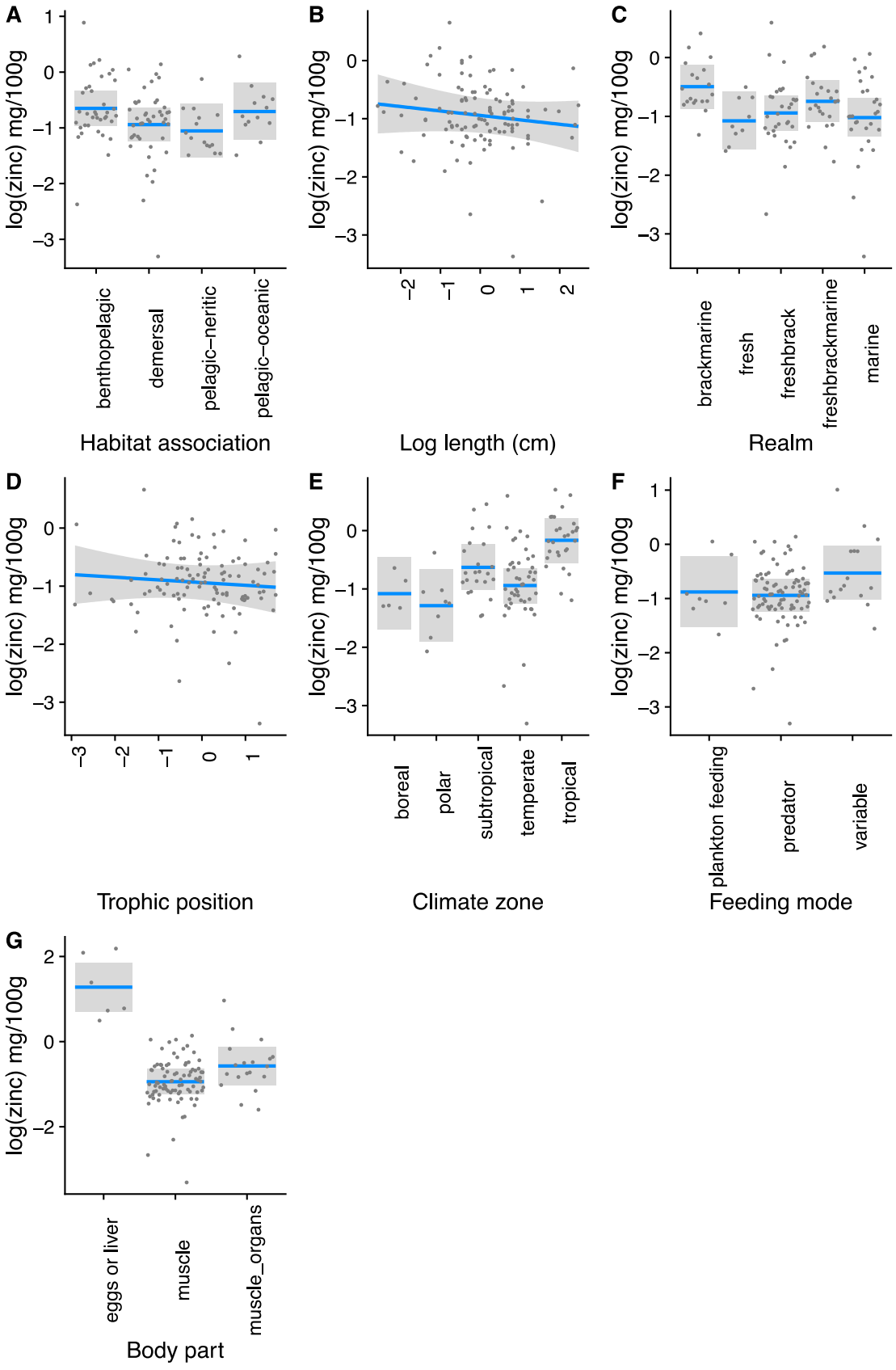
A
B
C
D
E
F
G
log(zinc) mg/100g
benthopelagic
demersal
pelagic–neritic
pelagic–oceanic
Habitat association
Log length (cm)
brackmarine
fresh
freshbrack
freshbrackmarine
marine
Realm
Trophic position
boreal
polar
subtropical
temperate
tropical
Climate zone
plankton feeding
predator
variable
Feeding mode
eggs or liver
muscle
muscle_organs
Body part

Figure S10. Zinc concentrations in edible finfish tissues vary with species' ecological traits. Partial regression plots from phylogenetic least squares regression (Supplementary Methods section 4) showing the effects of ecological traits on zinc concentrations in seafood species edible tissues (finfish only), while holding all other variables constant (n = 110 species, R^2 = 0.61; for full model results and regression coefficient estimates, see Table S6). Note that different edible portions may come from different species, and data for nutrients in all tissue types were not available for all species; see Table S14 for predictors.

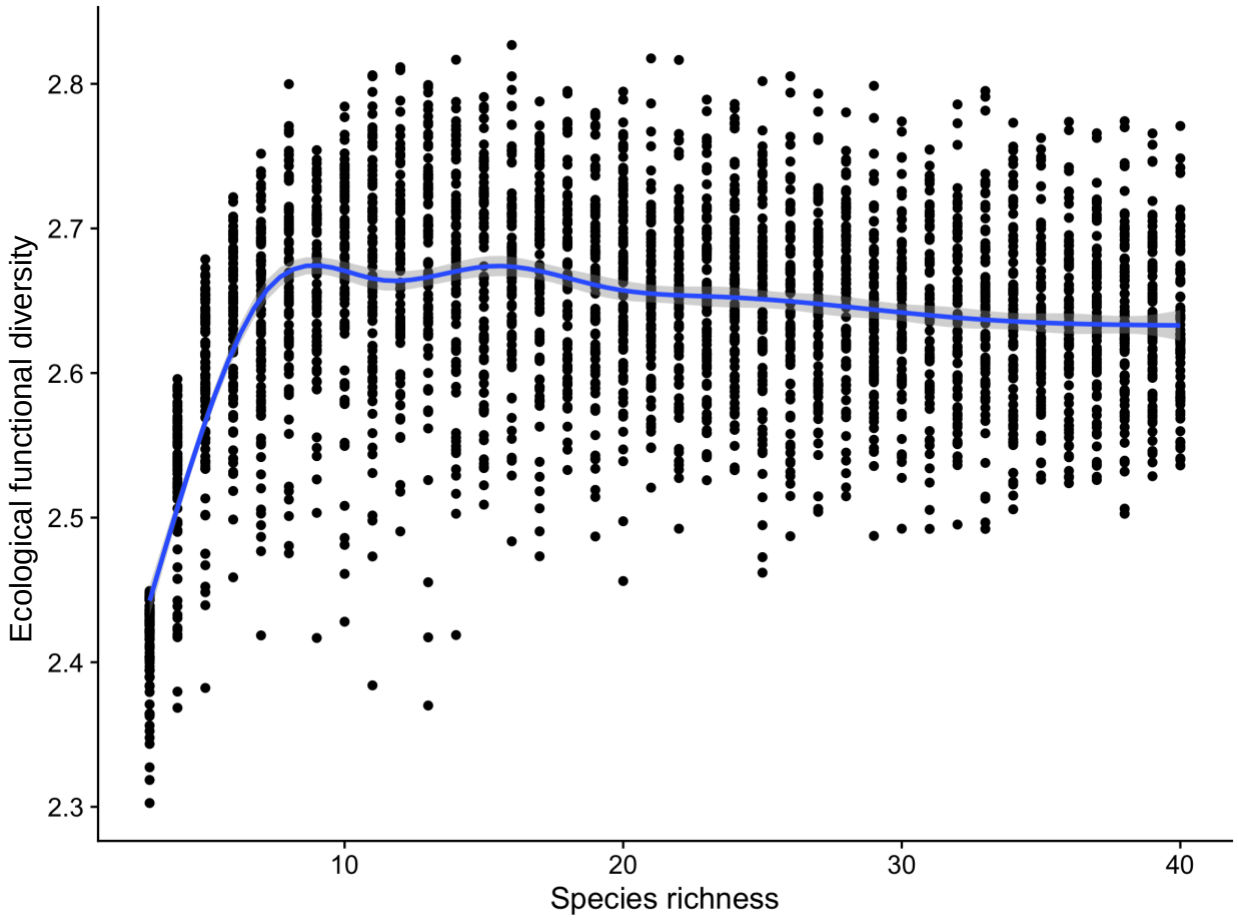

Figure S11. Ecological functional diversity of species from the global seafood species pool (Main text Methods, Supplementary Methods 5) measured as functional dispersion (i.e. the mean difference in multidimensional trait space of each individual species from the centroid of all species, **Figure 6A**) increases with species richness from three to ten species. Each point represents the ecological functional diversity estimated from randomly assembled seafood diets (resampled from the global seafood species dataset 100 times) at different levels of species richness (from three species to 40 species).

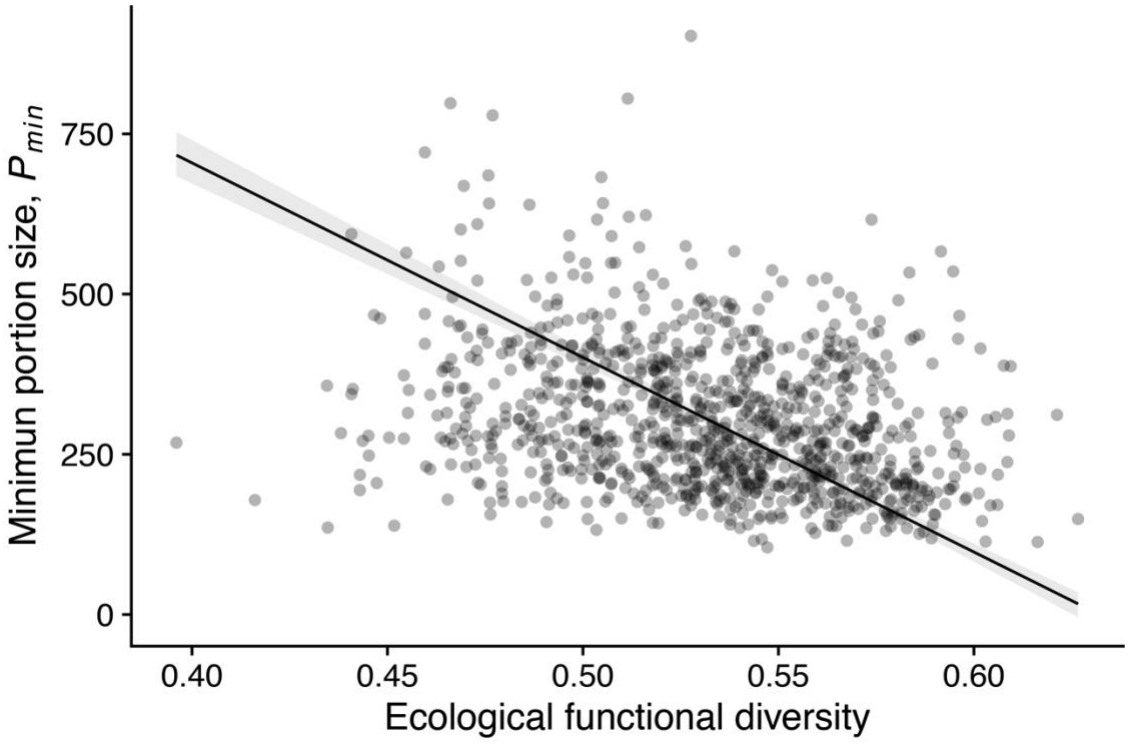

Figure S12. Diets with higher levels of ecological functional diversity (*EFD*, Supplementary Methods 5, Table S1) are associated with lower minimum portion sizes (P_{min}) required to reach five micronutrient and fatty acid RDA targets simultaneously. Each point corresponds to a seafood species diet with ten species (i.e. richness, S = 10), and 1000 randomly assembled diets from the global seafood species dataset are shown. For each of the 1000 simulated diets, P_{min} and *EFD* were calculated (Main text Methods and Supplementary Methods 5). Reduced major axis regression slope =-349.92, 95% CI -1436.16, -1268.86, R^2 = 0.0048.

Table S1. Definitions of key terms and references.

Term	Definition
Minimum portion size, P_{min}	Minimum amount of edible seafood tissue (g) required to reach a given RDA target for one nutrient or a set of nutrients. Given the total number of species *S* indexed by *j* and total number of nutrients *N* indexed by *i*, $$P_{min} = \arg\min_{P}\left(\sum_{i=1}^{N}\mathbb{1}\left\{\sum_{j=1}^{S}\frac{P}{S}content_{ij} \geq RDAtarget_i\right\} = N\right) \quad (A1)$$ where *P* is the total amount of edible seafood tissue; $content_{ij}$ is the nutritional content (mg) per 100g portion of species *j* and nutrient *i*, and $RDAtarget_i$ is the RDA target for nutrient *i*. The $\mathbb{1}$ refers to an indicator function, which takes on the value of 1 when the expression in the curly brackets is true (i.e. when the total nutrient content in the diet of *S* species, shown on the left-hand side of the "≥" is greater than or equal to the right-hand side of the expression, the RDA target), and 0 when the expression in the curly brackets is false (i.e. when total nutrient content summed across *S* species is less than the RDA target). The $\arg\min_{P}$ denotes that *P* is the argument that is being minimized. P_{min} is the minimum value of *P* (amount of edible tissue) required to reach a single RDA target (when $N = 1$) or set of RDA targets (when $N > 1$). In this paper, we considered the case when $N = 1$ for one nutrient, and $N = 5$ for five nutrients simultaneously. In other words, P_{min} is the minimum amount of edible tissue that reaches or exceeds a given number of RDA targets.
Number of nutrients, *NT*	Number of nutrients that reach a specific RDA target (for example, 10% RDA) in a single 100g portion of seafood (here *NT* ranges from 0-5). Given the total number of species *S* indexed by *j* and total number of nutrients (calcium, iron, zinc, EPA, DHA) *N* indexed by *i*,

	$$NT = \sum_{i=1}^{N} \mathbb{1}\left\{\sum_{j=1}^{S} \frac{1}{S} content_{ij} \geq RDAtarget_i\right\} \quad (A2)$$ where $content_{ij}$ is the nutrient content (mg) per 100g portion of species *j* and nutrient *i*, and $RDAtarget_i$ is the RDA target for nutrient *i*. The $\mathbb{1}$ refers to an indicator function, which takes on the value of 1 when the expression in the curly brackets is true (i.e. when the nutrient content of a 100g edible portion composed of *S* species is equal to or greater than the RDA for nutrient *i*), and 0 when the expression in the curly brackets is false (i.e. when the nutrient content of a 100g edible portion composed of *S* species is less than the RDA for nutrient *i*).
Maximum portion size, P_{max}	Maximum amount of edible seafood tissue (g) that may be consumed per day before one or more Provisional Tolerable Daily Intakes is exceeded. Given the total number of species, S, indexed by j and total number of contaminants (methylmercury, arsenic, cadmium or lead), C, indexed by k, $$P_{max} = \arg\max_{P}\left(\sum_{k=1}^{C} \mathbb{1}\left\{\sum_{j=1}^{S} \frac{P}{S} content_{kj} \leq PTDI_k\right\} = C\right) \quad (A3)$$ where $content_{kj}$ is the contaminant content (ug) per 100g of species *j* and contaminant *k*, and $PTDI_k$ is the Provisional Tolerable Daily Intake for contaminant *k*. The $\mathbb{1}$ refers to an indicator function, which takes on the value of 1 when the expression in the curly brackets is true (i.e. when the total contaminant content in the diet of *S* species, shown on the left-hand side of the "≤" is less than or equal to the right-hand side of the expression, the PTDI), and 0 when the expression in the curly brackets is false (i.e. when total contaminant content summed across *S* species is greater than the PTDI). The $\arg\max_{P}$ denotes that *P* is the argument that is being maximized. P_{max} is the maximum value of *P* (amount of edible tissue) which does not exceed one or more PTDIs. In this paper, we considered the case when $C = 1$. In other words, P_{max} is the maximum amount of edible tissue that does not exceed a given PTDI (i.e. remains below the PTDI).

Number of contaminants, *NC*	Number of contaminants that exceed the Provisional Tolerable Daily Intake in a single 100g portion of seafood (here *NC* ranges from 0-4). Given the total number of species *S* indexed by *j* and total number of contaminants (methylmercury, arsenic, cadmium, lead), *C*, indexed by *k*, $$NC = \sum_{k=1}^{C} \mathbb{1}\left\{\sum_{j=1}^{S} \frac{1}{S} content_{kj} \geq PTDI_k\right\} \quad (A4)$$ where $content_{kj}$ is the contaminant content (ug) per 100g portion of species *j* and contaminant *k*, and $PTDI_k$ is the Provisional Tolerable Daily Intake for contaminant *k*. The $\mathbb{1}$ refers to an indicator function, which takes on the value of 1 when the expression in the curly brackets is true (i.e. when contaminant content of a 100g edible portion composed of *S* species is equal to or greater than the PTDI for contaminant *k*), and 0 when the expression in the curly brackets is false (i.e. when the contaminant content of a 100g edible portion composed of *S* species is less than the PTDI for contaminant *k*).
Recommended dietary allowance (RDA)	Nutritional guideline describing the average daily level of intake sufficient to meet the nutrient requirements of nearly all (97%-98%) healthy people (here we refer to women aged 19-50)(1). RDAs are measured in mg/day.
RDA target	An RDA target is met if a given edible portion of seafood meets or exceeds the RDA (or a specified portion of RDA) for a given nutrient. In this study, we considered a threshold of 10% of RDA, meaning an RDA target is 10% of RDA (mg/day).
Provisional tolerable intake (weekly or daily)	An estimate of the amount per unit body weight of a potentially harmful substance or contaminant in food or water that can be ingested over a lifetime without risk of adverse health effects (2). We used an estimate of Provisional Tolerable Daily Intake (**PTDI**) by dividing the Provisional Tolerable Weekly Intake established by Joint FAO/WHO Expert Committee on Food Additives (JECFA) by (7).
Seafood	Freshwater or marine finfish or invertebrates potentially consumed in the human diet.

Species richness, *S*	Number of seafood species.
Ecological functional diversity, *EFD*	The diversity of ecological traits within a community or set of species (3–5). In this study, we measured ecological functional diversity as functional dispersion following Laliberte and Legendre 2010, (4), which measures the mean distance, in multivariate trait space, of each individual species from the centroid of all species (Main text Methods, Supplementary Methods 5).
Nutritional functional diversity, *NFD*	Estimates the diversity of nutrient concentrations in a diet based on an assessment of the entire nutritional diversity of a group represented as a functional dendrogram. Quantifies the degree of nutritional distinctiveness among species based on the dendrogram (6) (Supplementary Methods 3).
Multi-nutrient profile	The concentration of five micronutrients and fatty acids - calcium, iron, zinc, EPA and DHA in edible seafood tissues, characterized in multivariate space.

Table S2. Recommended Dietary Allowances (RDA) and Provisional Tolerable Intakes (PTWI).

A. Nutrients

Nutrient	RDA (per day)	unit	RDA target (10% RDA)
Zinc	8	mg	0.8
Calcium	1000	mg	100
Iron	18	mg	1.8
EPA	1	g	0.1
DHA	1	g	0.1
Protein	46	g	4.6
Fat	70	g	7

B. Contaminants

Contaminant	PTWI (ug/kg body weight/wk)	PTDI (ug per 70kg person per day)
Arsenic (total)	15	150
Cadmium	7	70
Lead	25	250
Methylmercury	1.6	16

Table S2. A) Recommended dietary allowances (RDA) for micro- and macronutrients considered in this study. RDAs are average daily dietary intake levels that are sufficient to meet the nutrient requirement of nearly all (97 to 98%) healthy individuals in a particular life stage and gender group. Here we used the RDAs for females aged 19-50 (1, 7, 8). **B**) Provisional Tolerable Weekly Intake (PTWI) limits for heavy metals. PTWIs estimate the amount per unit body weight of a potentially harmful substance or contaminant in food or water that can be ingested over a lifetime without risk of adverse health effects. Here we used the PTWI established by the Joint FAO/WHO Expert Committee on Food Additives (JECFA)(2). To make our contaminants analysis consistent with the nutrient analyses, which was conducted for a daily diet (i.e. with reference to daily RDA) we calculated a Provisional Tolerable Daily Intake PTDI,

by dividing the PTWI by 7, for a 70kg person, which allowed us to determine the upper tolerable limit per person, per day.

Table S3. Species in the global seafood species nutrient dataset that reach RDA targets.

Nutrient	Crustacean %	Crustacean n	Finfish %	Finfish n	Mollusc %	Molllusc n	All %	All n
Calcium	16.67	18	32.6	181	26.32	38	30.38	237
DHA	44	25	72.77	224	60	30	68.82	279
EPA	50	26	46.82	220	66.67	30	49.28	276
Fat	9.52	42	16.08	398			15.45	440
Iron	47.06	17	23.03	178	82.5	40	34.89	235
Protein	100	33	100	322	100	60	100.00	415
Zinc	100	10	46.34	164	90.91	33	56.04	207

Table S3. Percentage of species in the seafood nutrient dataset that reach 10% of RDA in a 100g edible portion, and total number of species (*n*) grouped by taxonomic group.

Table S4. Dependence of Iron (Fe) concentrations in edible finfish tissues on ecological traits.

Term	w_{ip}	1	2	3	4	5	6	7	8	β_i	Lower 95% CI	Upper 95% CI
Body part: muscle	1	+	+	+	+	+	+	+	+	**-0.75**	**-1.45**	**-0.05**
Body part: muscle & organs (incl. bones)	1	+	+	+	+	+	+	+	+	0.04	-0.77	0.86
Length	0.76	-0.21		-0.13	-0.16	-0.13	-0.19			-0.19	-0.41	0.02
Trophic position	0.8	0.14	0.17				0.15	0.08	0.19	0.15	-0.06	0.35
Feeding mode: hunting	0.35		+	+					+	-0.26	-1.08	0.57
Feeding mode: variable	0.35		+	+					+	0.25	-0.6	1.1
Climate zone: polar	0.05				+					-0.2	-1.19	0.8
Climate zone: subtropical	0.05				+					0.3	-0.55	1.16
Climate zone: temperate	0.05				+					-0.18	-0.98	0.62
Climate zone: tropical	0.05				+					-0.04	-0.9	0.82
Diet source: demersal	0.08					+	+	+	+	0.03	-0.4	0.46
Diet source: pelagic-neritic	0.08					+	+	+	+	0.24	-0.35	0.84
Diet source: oceanic	0.08					+	+	+	+	-0.09	-0.77	0.59
Realm												
Pagel's λ		0	0	0	0	0	0	0	0			
R^2		0.16	0.16	0.16	0.17	0.15	0.16	0.14	0.17			
Δ AICc		0	1.86	2.83	4.9	5.88	6.04	7.07	7.16			
Akaike weight		0.5	0.2	0.12	0.04	0.03	0.02	0.01	0.01			
Cumulative weight		0.5	0.7	0.82	0.86	0.89	0.91	0.93	0.94			

Table S4. Results from phylogenetic least squares regression model selection and model averaging for models relating iron concentrations in edible finfish species tissues to finfish species' traits (n = 123 species) (see Supplementary Methods 4 for full model description). Models are ranked in order of increasing AICc differences (Δ AICc). All models in the 95%

confidence model set are shown here (cumulative sum of Akaike weights <= 0.95). Akaike weights indicate the relative likelihood of a model, given the set of models being considered. Model-averaged standardized regression coefficients, β_i, with 95% CI, were averaged across all models in the best set and weighted by each model's Akaike weight. β_i were calculated with β_i = 0 when variable *i* was not included in a model. β_i with 95% confidence intervals not encompassing 0 are shown in bold. Relative variable importance (w_{ip}) is the sum of the relative variable importance across all models including that variable (*10*). Traits for which there is not a coefficient estimate did not appear in any of the models in the top 95% set (with cumulative Akaike weight <= 0.95). Note that different edible portions may come from different species, and not all tissues are available for all species.

Table S5. Dependence of Calcium (Ca) concentrations in edible finfish tissues on ecological traits.

Term	w_{ip}	1	2	3	4	β_i	Lower 95% CI	Upper 95% CI
Body part: muscle	1.00	+	+	+	+	0.64	-0.05	1.33
Body part: muscle & organs (incl. bones)	1.00	+	+	+	+	2.83	2.04	3.63
Length	1.00	-0.45	-0.45	-0.51	-0.50	**-0.47**	**-0.68**	**-0.26**
Trophic position	0.45	-0.04			-0.05	-0.04	-0.24	0.16
Feeding mode: hunting	0.29		+			0.01	-0.67	0.68
Feeding mode: variable	0.29		+			0.36	-0.41	1.13
Diet source: demersal	0.35			+	+	-0.18	-0.59	0.24
Diet source: pelagic-neritic	0.35			+	+	-0.51	-1.06	0.05
Diet source: pelagic-oceanic	0.35			+	+	0.06	-0.56	0.69
Climate zone								
Realm								
Pagel's λ		0	0	0	0			
R^2		0.56	0.56	0.57	0.57			
Δ AICc		0.00	0.42	0.66	2.76			
Akaike weight		0.34	0.28	0.24	0.09			
Cumulative weight		0.34	0.61	0.86	0.94			

Table S5. Results from phylogenetic least squares regression model selection and model averaging for models relating calcium concentrations in edible finfish species tissues to finfish species' traits (n = 127 species) (see Supplementary Methods 4 for full model description). Models are ranked in order of increasing AICc differences (Δ AICc). All models in the 95% confidence model set are shown here (cumulative sum of Akaike weights <= 0.95). Akaike weights indicate the relative likelihood of a model, given the set of models being considered. Model-averaged standardized regression coefficients, β_i, with 95% CI, were averaged across all models in the best set and weighted by each model's Akaike weight. β_i were calculated with β_i = 0 when variable i was not included in a model. β_i with 95% confidence intervals not

encompassing 0 are shown in bold. Relative variable importance (w_{ip}) is the sum of the relative variable importance across all models including that variable (*10*). Traits for which there is not a coefficient estimate did not appear in any of the models in the top 95% set (with cumulative Akaike weight <= 0.95). Note that different edible portions may come from different species, and not all tissues are available for all species.

Table S6. Dependence of Zinc (Zn) concentrations in edible finfish tissues on ecological traits.

Term	w_{ip}	1	2	β_i	Lower 95% CI	Upper 95% CI
Body part: muscle	1.00	+	+	**-2.27**	**-2.84**	**-1.70**
Body part: muscle & organs (incl. bones)	1.00	+	+	**-1.92**	**-2.61**	**-1.24**
Feeding mode: hunting	0.91	+		-0.37	-0.83	0.08
Feeding mode: variable	0.91	+		0.17	-0.38	0.73
Climate zone: polar	1.00	+	+	-0.10	-0.83	0.64
Climate zone: subtropical	1.00	+	+	0.50	-0.11	1.11
Climate zone: temperate	1.00	+	+	0.17	-0.41	0.76
Climate zone: tropical	1.00	+	+	**1.01**	**0.37**	**1.64**
Trophic position	0.09		-0.13	**-0.13**	**-0.26**	**-0.01**
Diet source						
Length						
Realm						
Pagel's λ		0	0			
R^2		0.56	0.53			
Δ AICc		0.00	4.57			
Akaike weight		0.81	0.08			
Cumulative weight		0.81	0.90			

Table S6. Results from phylogenetic least squares regression model selection and model averaging for models relating zinc concentrations in edible finfish species tissues to finfish species' traits (n = 113 species) (see Supplementary Methods 4 for full model description). Models are ranked in order of increasing AICc differences (Δ AICc). All models in the 95% confidence model set are shown here (cumulative sum of Akaike weights <= 0.95). Akaike weights indicate the relative likelihood of a model, given the set of models being considered. Model-averaged standardized regression coefficients, β_i, with 95% CI, were averaged across all models in the best set and weighted by each model's Akaike weight. β_i were calculated with β_i =

0 when variable *i* was not included in a model. β_i with 95% confidence intervals not encompassing 0 are shown in bold. Relative variable importance (w_{ip}) is the sum of the relative variable importance across all models including that variable (*10*). Traits for which there is not a coefficient estimate did not appear in any of the models in the top 95% set (with cumulative Akaike weight <= 0.95). Note that different edible portions may come from different species, and not all tissues are available for all species.

Table S7. Dependence of DHA concentrations in edible finfish tissues on ecological traits.

Term	w_{ip}	1	2	β_i	Lower 95% CI	Upper 95% CI
Body part: muscle	1.00	+	+	**-2.04**	**-3.01**	**-1.07**
Body part: muscle & organs (incl. bones)	1.00	+	+	**-1.45**	**-2.59**	**-0.30**
Feeding mode: hunting	1.00	+	+	-0.33	-0.96	0.30
Feeding mode: variable	1.00	+	+	-0.45	-1.18	0.27
Length	1.00	0.03	-0.03	0.00	-0.21	0.21
Diet source: demersal	0.53	+		-0.01	-0.38	0.37
Diet source: pelagic-neritic	0.53	+		**0.66**	**0.14**	**1.18**
Diet source: oceanic	0.53	+		0.24	-0.35	0.82
Trophic position	1.00	0.04	0.08	0.06	-0.17	0.28
Realm: freshwater	1.00	+	+	**-0.95**	**-1.76**	**-0.15**
Realm: freshwater or brackish	1.00	+	+	**-1.32**	**-2.02**	**-0.62**
Realm: freshwater or brackish or marine	1.00	+	+	-0.12	-0.71	0.47
Realm: marine	1.00	+	+	0.03	-0.35	0.41
Climate zone: subtropical	1.00	+	+	0.27	-0.29	0.82
Climate zone: temperate	1.00	+	+	0.36	-0.19	0.90
Climate zone: tropical	1.00	+	+	-0.09	-0.84	0.65
Pagel's λ		0.32	0.53			
R^2		0.42	0.43			
Δ AICc		0.00	0.23			
Akaike weight		0.50	0.45			
Cumulative weight		0.50	0.95			

Table S7. Results from phylogenetic least squares regression model selection and model averaging for models relating DHA concentrations in edible finfish species tissues to finfish species' traits (n = 170 species) (see Supplementary Methods 4 for full model description). Models are ranked in order of increasing AICc differences (Δ AICc). All models in the 95% confidence model set are shown here (cumulative sum of Akaike weights <= 0.95). Akaike weights indicate the relative likelihood of a model, given the set of models being considered. Model-averaged standardized regression coefficients, β_i, with 95% CI, were averaged across all

models in the best set and weighted by each model's Akaike weight. β_i were calculated with β_i = 0 when variable *i* was not included in a model. β_i with 95% confidence intervals not encompassing 0 are shown in bold. Relative variable importance (w_{ip}) is the sum of the relative variable importance across all models including that variable (*10*). Traits for which there is not a coefficient estimate did not appear in any of the models in the top 95% set (with cumulative Akaike weight <= 0.95). Note that different edible portions may come from different species, and not all tissues are available for all species.

Table S8. Dependence of EPA concentrations in edible finfish tissues on ecological traits.

Term	w_{ip}	1	2	β_i	Lower 95% CI	Upper 95% CI
Body part: muscle	1.00	+	+	**-2.48**	**-3.56**	**-1.39**
Body part: muscle & organs (incl. bones)	1.00	+	+	**-1.45**	**-2.76**	**-0.14**
Feeding mode: plankton filtering	1.00	+	+	-0.51	-2.68	1.67
Feeding mode: hunting	1.00	+	+	-0.97	-3.15	1.21
Feeding mode: variable	1.00	+	+	-1.02	-3.17	1.12
Length	1.00	0.03	0.10	0.06	-0.18	0.29
Climate zone: polar	1.00	+	+	0.04	-1.12	1.20
Climate zone: subtropical	1.00	+	+	-0.18	-1.27	0.91
Climate zone: temperate	1.00	+	+	0.16	-0.90	1.22
Climate zone: tropical	1.00	+	+	-0.10	-1.32	1.12
Trophic position	1.00	-0.01	-0.07	-0.03	-0.29	0.22
Realm: freshwater	1.00	+	+	**-1.76**	**-2.65**	**-0.87**
Realm: freshwater or brackish	1.00	+	+	**-1.64**	**-2.42**	**-0.87**
Realm: freshwater or brackish or marine	1.00	+	+	0.06	-0.57	0.70
Realm: marine	1.00	+	+	-0.21	-0.64	0.21
Diet source: demersal	0.33		+	0.19	-0.25	0.62
Diet source: pelagic-neritic	0.33		+	**0.71**	**0.12**	**1.30**
Diet source: oceanic	0.33		+	0.28	-0.38	0.95
Pagel's λ		0.43	0.43			
R^2		0.46	0.48			
Δ AICc		0.00	1.44			
Akaike weight		0.63	0.31			
Cumulative weight		0.63	0.93			

Table S8. Results from phylogenetic least squares regression model selection and model averaging for models relating EPA concentrations in edible finfish species tissues to finfish species' traits (n = 168 species) (see Supplementary Methods 4 for full model description). Models are ranked in order of increasing AICc differences (Δ AICc). All models in the 95% confidence model set are shown here (cumulative sum of Akaike weights <= 0.95). Akaike weights indicate the relative likelihood of a model, given the set of models being considered.

Model-averaged standardized regression coefficients, β_i, with 95% CI, were averaged across all models in the best set and weighted by each model's Akaike weight. β_i were calculated with β_i = 0 when variable *i* was not included in a model. β_i with 95% confidence intervals not encompassing 0 are shown in bold. Relative variable importance (w_{ip}) is the sum of the relative variable importance across all models including that variable (*10*). Traits for which there is not a coefficient estimate did not appear in any of the models in the top 95% set (with cumulative Akaike weight <= 0.95). Note that different edible portions may come from different species, and not all tissues are available for all species.

Table S9. Dependence of calcium (Ca) concentrations in edible tissues of small finfish on ecological traits.

Term	w_{ip}	1	2	3	β_i	Lower 95% CI	Upper 95% CI
Body part: muscle	1.00	+	+	+	0.97	-0.30	2.25
Body part: muscle & organs (incl. bones)	1.00	+	+	+	2.75	1.42	4.08
Length	0.67	-0.29		-0.34	-0.30	-1.20	0.60
Trophic position	0.83	0.50	0.75		0.60	-0.52	1.73
Feeding mode: hunting	0.50		+	+	-0.12	-1.18	0.95
Feeding mode: variable	0.50		+	+	0.54	-0.62	1.69
Diet source							
Climate zone							
Realm							
R^2		0.54	0.56	0.55			
Δ AICc		0.00	0.84	2.09			
Akaike weight		0.46	0.30	0.16			
Cumulative weight		0.46	0.76	0.92			

Table S9. Results from ordinary least squares regression model selection and model averaging for models relating calcium concentrations in edible finfish species tissues to finfish species' traits (n = 39 species) for species with maximum length less than 50cm and mean length less than 25 cm (see Supplementary Methods 4 for full model description). Models are ranked in order of increasing AICc differences (Δ AICc). All models in the 95% confidence model set are shown here (cumulative sum of Akaike weights <= 0.95). Akaike weights indicate the relative likelihood of a model, given the set of models being considered. Model-averaged standardized regression coefficients, β_i, with 95% CI, were averaged across all models in the best set and weighted by each model's Akaike weight. β_i were calculated with β_i = 0 when variable i was not included in a model. β_i with 95% confidence intervals not encompassing 0 are shown in bold. Relative variable importance (w_{ip}) is the sum of the relative variable importance across all

models including that variable (*10*). Traits for which there is not a coefficient estimate did not appear in any of the models in the top 95% set (with cumulative Akaike weight <= 0.95). Note that different edible portions may come from different species, and not all tissues are available for all species.

Table S10. Dependence of iron (Fe) concentrations in edible tissues of small finfish on ecological traits.

Term	w_{ip}	1	2	3	4	5	β_i	Lower 95% CI	Upper 95% CI
Trophic position	0.46	0.66			0.47		0.59	-0.26	1.43
Climate zone: polar	1.00	+	+	+	+	+	**-2.66**	**-4.34**	**-0.98**
Climate zone: subtropical	1.00	+	+	+	+	+	0.24	-1.35	1.84
Climate zone: temperate	1.00	+	+	+	+	+	-1.30	-2.63	0.03
Climate zone: tropical	1.00	+	+	+	+	+	**-1.57**	**-2.87**	**-0.28**
Length	0.53		-0.60		-0.75	-0.53	-0.64	-1.40	0.12
Feeding mode: hunting	0.36			+	+		0.71	-0.11	1.53
Feeding mode: variable	0.36			+	+		**0.96**	**0.07**	**1.86**
Body part: muscle	0.11					+	-0.12	-1.22	0.99
Body part: muscle & organs (incl. bones)	0.11					+	0.55	-0.63	1.74
Diet source realm									
R^2		0.49	0.49	0.53	0.62	0.56			
Δ AICc		0.00	0.26	0.85	0.94	1.85			
Akaike weight		0.25	0.22	0.16	0.16	0.10			
Cumulative weight		0.25	0.47	0.63	0.79	0.89			

Table S10. Results from ordinary least squares regression model selection and model averaging for models relating iron concentrations in edible finfish species tissues to finfish species' traits (n = 35 species) for species with maximum length less than 50cm and mean length less than 25 cm (see Supplementary Methods 4 for full model description). Models are ranked in order of increasing AICc differences (Δ AICc). All models in the 95% confidence model set are shown here (cumulative sum of Akaike weights <= 0.95). Akaike weights indicate the relative likelihood of a model, given the set of models being considered. Model-averaged standardized regression coefficients, β_i, with 95% CI, were averaged across all models in the best set and

weighted by each model's Akaike weight. β_i were calculated with $\beta_i = 0$ when variable *i* was not included in a model. β_i with 95% confidence intervals not encompassing 0 are shown in bold. Relative variable importance (w_{ip}) is the sum of the relative variable importance across all models including that variable (*10*). Traits for which there is not a coefficient estimate did not appear in any of the models in the top 95% set (with cumulative Akaike weight <= 0.95). Note that different edible portions may come from different species, and not all tissues are available for all species.

Table S11. Dependence of zinc (Zn) concentrations in edible tissues of small finfish on ecological traits.

Term	w_{ip}	1	2	3	4	5	6	β_i	Lower 95% CI	Upper 95% CI
Length	0.47	-0.36			-0.37			-0.36	-0.93	0.21
Feeding mode: hunting	1	+	+	+	+	+	+	0.3	-0.35	0.94
Feeding mode: variable	1	+	+	+	+	+	+	**0.93**	**0.25**	**1.61**
Trophic position	0.44		0.38			0.38	0.4	0.38	-0.28	1.03
Diet source: demersal	0.12			+			+	-0.22	-0.82	0.38
Diet source: pelagic-neritic	0.12			+			+	0.26	-0.44	0.97
Diet source: pelagic-oceanic	0.12			+			+	0.53	-0.24	1.31
Body part: muscle & organs (incl. bones)	0.15				+	+		-0.04	-0.54	0.46
Climate zone										
Realm										
R^2		0.33	0.32	0.41	0.33	0.32	0.46			
Δ AIC		0	0.31	3.07	3.21	3.57	4.85			
Akaike weight		0.36	0.31	0.08	0.07	0.06	0.03			
Cumulative weight		0.36	0.68	0.75	0.83	0.89	0.92			

Table S11. Results from ordinary least squares regression model selection and model averaging for models relating zinc concentrations in edible finfish species tissues to finfish species' traits (n = 28 species) for species with maximum length less than 50cm and mean length less than 25 cm (see Supplementary Methods 4 for full model description). Models are ranked in order of increasing AICc differences (Δ AICc). All models in the 95% confidence model set are shown here (cumulative sum of Akaike weights <= 0.95). Akaike weights indicate the relative likelihood of a model, given the set of models being considered. Model-averaged standardized regression coefficients, β_i, with 95% CI, were averaged across all models in the best set and

weighted by each model's Akaike weight. β_i were calculated with $\beta_i = 0$ when variable *i* was not included in a model. β_i with 95% confidence intervals not encompassing 0 are shown in bold. Relative variable importance (w_{ip}) is the sum of the relative variable importance across all models including that variable (*10*). Traits for which there is not a coefficient estimate did not appear in any of the models in the top 95% set (with cumulative Akaike weight <= 0.95). Note that different edible portions may come from different species, and not all tissues are available for all species.

Table S12. Seafood consumed by North America Indigenous communities.

Culture	Abbreviation	Region	Location	Taxa
Abenaki	AB	Northeast	Quebec, Maine	29
Bella Coola	BC	Northwest Coast	British Columbia	40
Central Salish	CS	Northwest Coast	British Columbia, Washington	42
Cree	CR	Subarctic	Labrador, Quebec, Ontario, Manitoba, Saskatchewan, Alberta	27
Haida	HC	Northwest Coast	British Columbia, Alaska	36
Inuit-Inupiaq	II	Arctic	Alaska, Northwest Territories, Nunavut, Nunavik, Quebec, Labrador	52
Kwakiutl	KW	Northwest Coast	British Columbia	40
Mi'kmaq	MI	Northeast	Nova Scotia, New Brunswick, Quebec, Newfoundland	57
Montagnais-Naskapi	MN	Subarctic	Labrador, Quebec	25
Nootkan	NO	Northwest Coast	British Columbia, Washington	49
Tlingit	TL	Northwest Coast	British Columbia, Yukon, Alaska	51
Tsimshian	TS	Northwest Coast	British Columbia, Alaska	41
Wampanoag	WA	Northeast	Massachusetts	35
Yupik	YU	Arctic	Alaska	38

Table S12. North American Indigenous cultures, and numbers of seafood species in traditional diets used in the local scale nutritional benefits analysis (**Figure S4**; Supplementary Methods 1.4 and 3).

Table S13. Top fourteen of 41 most commonly consumed species as per FAO production volumes in the nutrient dataset. Data from (9).

Genus species
Theragra chalcogramma
Gadus morhua
Gadus macrocephalus
Tenualosa ilisha
Rastrelliger kanagurta
Merluccius productus
Oncorhynchus gorbuscha
Pollachius virens
Melanogrammus aeglefinus
Thunnus alalunga
Oreochromis niloticus
Panaeus monodon
Portunus pelagicus
Trachurus trachurus

Table S14. Predictors used in phylogenetic generalized least squares models used to predict nutrient content as a function of ecological traits.

Predictor	*Categories*
Feeding mode	Filtering plankton, grazing, hunting, selective plankton feeding, variable
Diet source and habitat	Reef associated, Pelagic, Oceanic, Neritic, Demersal, Benthopelagic, Bathypelagic
Realm	Freshwater, Freshwater or brackish, Freshwater or brackish or marine, marine
Climate zone	Temperate, subtropical, polar, tropical, boreal
Maximum body length	continuous
Trophic position	continuous
Body part	Muscle, muscle + organs (including bones, skin etc.), eggs or liver

Appendix A: References

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Part B: Supplementary Methods

This file includes:

Supplementary Methods
Part B: References

Other supplementary materials for this manuscript include the following:

Part A: Supplementary Figures and Tables

Supplementary Methods

1. Literature search and data collection

1.1 Nutrient concentration data

We assembled a dataset of published nutrient concentrations in edible portions of 547 aquatic species (**Figure S1A**). We aimed to include as many marine and freshwater species as possible covering a wide geographic extent. We searched peer-reviewed literature for analytical food composition values as well as the Food and Agriculture Organization's Global Food Composition Database for Fish and Shellfish (INFOODS) (1). We extracted data from peer-reviewed literature by downloading datasets directly when available, or extracting data from tables using the 'Tabula' software, from figures using 'WebPlotDigitizer', or manually when none of these options was available. We searched the peer-reviewed literature using Google Scholar for papers published between 1970 and 2017, using search terms including (but not limited to): "seafood AND micronutrient", or "fish AND zinc", "fish AND calcium", "fish AND iron", or "fish AND essential fatty acids", "fish AND nutrient composition" or species-specific searches such as "*Mya arenaria* AND zinc" to find published papers on edible tissue nutrient concentrations that met the following criteria. First, for finfish, we restricted our search and analysis to include only edible portions of wild caught, raw fish (excluding prepared or farmed finfish samples). We included both farmed and wild caught mollusc species because mollusc farming does not typically involve additional food inputs, which could influence tissue nutrient composition. Second, we only included data for which the body part contained in the edible portion was made explicit (i.e. muscle tissue, whole body, eggs). For each sample, we noted which body parts are included in the edible portion and season of collection. We did not include data from national food composition tables because these data usually report seafood data with a

generic food description (for example ‘salmon’), which does not allow for a clear description of which fish tissues are included in the edible portion or the species. We excluded samples that were of mixed species groups, or not identified to genus and species. We only included data that were available in terms of concentrations per fresh wet weight. We standardized all measurements to mg (for calcium, iron and zinc) or g (for DHA, EPA, fat and protein) per 100g edible tissue. To address inconsistencies in fatty acid data reporting, consistent with fatty acid data in the INFOODS database, we standardized fatty acid measurements using the fatty acid conversion factors proposed by Nowak et al. 2014 (2). When there were multiple observations available for a single species and given body part, we averaged nutrient concentrations across the observations. For each sample, we noted the location of collection (e.g. latitude and longitude). We standardized species’ Latin names (i.e. genus and species) using the *taxize* package in R (3). In total, we assembled 5041 observations of nutrient concentrations.

1.2 Ecological trait data

To test our hypothesis that nutritional benefits may depend on biodiversity because they are correlated with ecological functional trait diversity among aquatic species, we collected ecological trait information from FishBase (4) and SeaLifeBase (5) (**Figure S1E**). We selected a range of ecological functional traits that relate to species’ ecological roles (6): body size (maximum length), fractional trophic position, habitat and diet source (e.g. oceanic, reef-associated, neritic) and feeding mode (e.g. filter-feeding vs hunting), realm (freshwater, brackish, marine), and climate zone (e.g. tropical, temperate) (Table S14). We focused on this set of functional traits because these traits are related to species’ diets, morphology, energetic demands and habitats, all of which may influence the concentration of biologically essential elements and

fatty acids in their tissues (7, 8), and which determine the functional roles that organisms play in ecosystems (6). We extracted these data directly from FishBase or SeaLifeBase data using the R package *rfishbase (9)*. If multiple observations were available for a single ecological functional trait for a single species, we took an average across multiple observations. This approach allowed us to characterize traits at the species' level, although it does not allow investigation of intraspecific variation in traits across different regions or times.

1.3 Contaminant data from North American seafood species

We drew on existing, published datasets for heavy metals that can be toxic to human health if they are consumed in high enough quantities (contaminants). We synthesized contaminant concentrations in North American finfish and invertebrate species including mercury, cadmium, arsenic and lead (10, 11) (**Figure S1A**). These datasets contain data from the peer-reviewed literature, as well as US federal and state government reports. From these datasets, we extracted data for samples which were identifiable to species, and which consisted of raw, wild muscle tissue only (thus excluding farmed, cooked, tinned or otherwise prepared samples), and which were wild-caught in North America (i.e. thus excluding samples that were sourced from markets and for location of origin may be unknown). In total, we extracted 2209 observations of contaminant concentrations: 322 observations for each of lead, arsenic and cadmium, and 1243 observations for mercury, which resulted in mercury concentrations for 353 species, and lead, arsenic and cadmium concentrations for 200 species. These observations were of total metal concentrations, and did not account for metal fractions in different forms. For mercury, because approximately 95% of total mercury burden in finfish is methylmercury (12, 13), and methylmercury is the form of mercury that poses most risk to human health, we calculated

methylmercury concentrations assuming that 95% of total mercury is methylmercury (following (10, 13, 14)). However, because molluscs tend to have much lower methylmercury fractions, we assumed methylmercury was 35% of total mercury (based on (14–16)). For arsenic, we considered total arsenic, and did not address ratios between total and inorganic forms of arsenic. A source of error in this analysis is the percentage of total mercury that is methylmercury, which may vary across species (15, 17). Because we still do not know what drives variation in methylmercury to total mercury ratios across species, and methylmercury data are not widely available, this was a necessary assumption in this analysis, and deserves further study.

1.4 Biodiversity in North American Indigenous diets

To assess the effects of biodiversity in seafood diets sourced from local or regional species pools, we determined species lists for species included in traditional animal food diets (past or present) in North America. We focused on traditional Indigenous diets in North America because many of these communities rely on locally harvested aquatic species to meet their nutritional needs (18–20). We compiled lists of seafood species contained in traditional diets from an ethnographic database of traditional animal foods of Indigenous peoples of North America (21). This database represents a compilation of hundreds of ethnographic sources, and includes data collected with a range of methods, including interviews, 24-hour recall surveys, food questionnaires, and archaeological records. From this database, we extracted information on seafood species associated with Indigenous cultures' traditional diets, how these species are traditionally prepared (e.g. smoked, raw, steamed), and which body parts are included in the edible portion (e.g. eggs, muscle, liver). The information available was not quantitative estimates of amounts or frequencies of foods consumed, rather just the lists of species traditionally included in diets

(currently or historically), which allowed us to quantify the role of biodiversity theoretically. From this dataset of more than 70 Indigenous diets, we focused on Indigenous cultures which included more than 25 seafood species in their traditional diet. This resulted in a dataset of the seafood species included in the traditional diets of fourteen Indigenous cultures, including Abenaki, Bella Coola, Central Salish, Cree, Haida, Inuit-Inupiaq, Kwakiutl, Mi'kmaq, Montagnais-Naskapi, Nootkan, Tlingit, Tsimshian, Wampanoag and Yupik (Table S12).

2. Quantifying the effects of seafood biodiversity on contaminant exposure

We quantified effects of biodiversity on contaminant exposure using methods analogous to those described for nutritional benefits, using two metrics: *NC* and P_{max}. Contaminant exposure risks were estimated for species sampled from the North American seafood contaminant dataset (Supplementary Methods 1.3) (**Figure S1C**).

1) Number of contaminants, *NC* (Table S1, Equation A4): We quantified the effects of seafood species richness on contaminant exposure using methods analogous to those we used for the nutrients. We assembled diets from the North American species pool (Supplementary Methods 1.3) at random, with a replacement design, as described in Methods 2.2. To test the hypothesis that complementarity in contaminant concentrations among species increases health risks by increasing the number of distinct Provisional Tolerable Daily Intake (PTDI; Table S1) limits exceeded in a 100g portion, we quantified, for all possible combinations of species at each level of species richness (from 1 - 10 species, n = 1023), the number of distinct contaminant PTDIs exceeded by assigning each combination of species a set of 0's or 1's according to whether that

combination exceeded the PTDI for each contaminant (see Table S1, Equation A4) (**Figure S1B, C**). Our approach allowed us to explore how likely it would be for human diets containing different numbers of fish species to exceed a given number of contaminant PTDI limits (*NC* ranges between 0 and 4), assuming that fish species were included in the human diet at random. At level of species richness, we took an average of *NC*, and then repeated this process of assembling diets, and estimating *NC* 1000 times. This process yielded 1000 estimates of *NC* (**Figure S1B, C**). We quantified the effect of biodiversity on *NC* (*n* = 1000 estimates of *NC* per richness level) by fitting a power function,

$$NC = aS^{b_{NC}} \qquad (B1)$$

where the parameter b_{NC} describes the relationship between a change in species richness, *S*, and a change in *NC* (i.e. the number of distinct PTDI limits exceeded per average 100g portion), and *a* is a constant (**Figure S1D**).

2) Maximum portion size, P_{max} (Table S1 Equation A3): We assessed the effect of increasing seafood species richness on the average contaminant concentrations in seafood diets, and therefore the maximum portion size before upper tolerable limits are exceeded. Following similar methods as described above for minimum portion size, P_{min} (Main text Methods): from the North American species pool (Supplementary Methods 1.3), we sampled ten species at random and then assembled seafood diets from all possible combinations of these ten randomly chosen species at 10 levels of species richness (1-10). For each combination of species at each level of species richness (1-10 species), we calculated the number of grams required to exceed a given contaminant tolerable upper intake (100% of PTDI), P_{max} (see Table S1 Equation A3). At each level of species richness, we took an average P_{max}. We repeated this process of sampling ten

species from the North American species pool, assembling all possible diets at each richness level, and estimating P_{max} 1000 times, yielding 1000 estimates of P_{max} per richness level. We quantified the effect of species richness in a diet on maximum portion size, P_{max} (n = 1000 estimates of P_{max} per richness level), by fitting a power function to these P_{max} estimates:

$$P_{max} = aS^{b_{Pmax}} \quad (B2)$$

where the parameter b_{Pmax} describes the relationship between a change in species richness, S, and a change in P_{max}, and a is a constant (in units of grams) (**Figure S1D**). Since P_{max} is measured in grams required to exceed a given PTDI threshold, and fewer grams required is worse from the perspective of human nutrition, then a negative effect of biodiversity would be reflected in a negative b_{Pmax} (i.e. P_{max}, measured in grams of tissue required, decreases with species richness).

3. Comparing local scale biodiversity effects to global scale biodiversity effects

We assessed biodiversity effects on nutritional benefits in local scale Indigenous diets as described in the Main text Methods ("Statistical Analysis and Hypothesis Testing") for global seafood diets. Instead of sampling from the global species pool, we sampled diets from species contained within traditional diets in fourteen Indigenous cultures in North America (Supplementary Methods 1.4, Table S12). For each of these diets, we repeated the replacement design randomization process described above, and calculated NT and P_{min} (Main text Methods). We compared estimates of the 'biodiversity effect', the slope parameter, b, at global and local scales, by comparing the b estimates from the 14 traditional Indigenous diets to global diets standardized to 40 species (the average number of species in the Indigenous diets, Main text Methods), indicated as 'GL' in **Figure S4**.

We tested the hypothesis that biodiversity effects at local and global scales are associated with differences in the diversity of nutritional profiles of species available at local and global scales. We used a metric called 'nutritional functional diversity', *NFD* (22, 23). *NFD* is based on an assessment of the entire functional diversity of a group represented as a functional dendrogram, and *NFD* allows estimation of complementarity among species' nutrient concentrations (i.e. nutritional functional traits) using the dendrogram. We hypothesized that *NFD* would be higher at the global scale than the local scale, because the global species pool contains more ecological and biogeographic diversity. We treated the concentration of each micronutrient or fatty acid (calcium, iron, zinc, EPA and DHA) as a nutritional functional trait. We also quantified a metric of nutritional functional evenness metric (*NFEve*) using the *dbFD* function in the *FD* package in R (24), which normally quantifies the evenness of abundance in a functional trait space. Here, we used *NFEve* to quantify the evenness in concentration of nutrients across species (25). To compare *NFD* and *NFEve* at the global and local scales, we first subsampled 40 species (the average species pool at the local scale) from the global pool, then calculated the functional diversity metrics on the subsample, and repeated this process 1000 times. Using this same approach, we calculated levels of 'expected' *NFD* and *NFEve* for each local diet by choosing random subsets of the global pool with sample size equal to the species pool in each local diet, and repeated this process 1000 times (**Figure S5**).

4. Assessing the relationship between species' ecological traits and nutrient concentrations

We tested for complementarity in nutrient concentrations among species by calculating Pearson correlation coefficients among nutrient concentrations across species (i.e. pairwise correlations

across all species). We identified correlations between multiple nutrients in seafood tissues using principal components analysis, using the '*rda*' function in *vegan* (94). We tested the hypothesis that major phylogenetic groups correlated with functional differences in life history, resource use and ecology (i.e. finfish, mollusc, and crustacean) differ in their multi-nutrient profiles via permutational multivariate ANOVA (PERMANOVA) using the *adonis* function (999 permutations) based on Bray-Curtis dissimilarity matrices.

To test for associations between species' ecological functional traits and their nutrient concentrations, we modeled the relationship between traits and ln(nutrient concentration) with phylogenetic least squares regression (PGLS). To assess whether the relationships between species' traits and their nutrient concentrations were associated, we fit multiple regression models using PGLS using the *gls* function in the *nlme* package in R (26). Unlike in ordinary least squares (OLS), which assumes there is no covariance structure in the error term, ε, (all species are independent from one another, and residuals from closely related species are not more similar on average than residuals from distantly related species), PGLS assumes that the residuals are non-independent, and that the expected covariance is related to the shared evolutionary history between the species.

The full model included the entire set of trait predictors (Table S14) as fixed effects:

$$ln(concentration) = \beta_0 + \beta_1 \times ln(body\ length) + \beta_2 \times trophic\ position + \beta_3 \times feeding\ mode + \beta_4 \times diet\ source + \beta_5 \times realm + \beta_6 \times climate\ zone + \beta_7 \times body\ part + \varepsilon$$

This approach allowed us to account for phylogenetic non-independence by using shared ancestry as weights on the elements of the residual variance-covariance matrix used in the model. We created a supertree by combining phylogenies that included the species of finfish, molluscs and crustaceans in our nutrient dataset using the *rotl* package in R (27), which is an interface to the Open Tree of Life (28). We computed branch lengths according to taxonomic depth (29) using the *compute.brlen* function in the *ape* package in R (30). We incorporated phylogenetic information into the models using Pagel's λ correlation structure (31) constructed with the *corPagel* function in the *ape* package and estimated the amount of phylogenetic signal in the data estimated using maximum likelihood. When $\lambda = 0$, this suggests that the relationship between predictor and response variables is unrelated to phylogeny, and when $\lambda = 1$, this indicates that traits have evolved under Brownian motion on the given phylogeny such that variation among species in traits may reflect evolutionary history rather than contemporary predictor variables. Where λ was negative, suggesting closely related species have negatively correlated phenotypes under the Brownian model of evolution, we fixed λ at 0. To assess whether the relationships between species' traits and their nutrient concentrations were associated, we fit multiple regression models using PGLS using the *gls* function in the *nlme* package in R (26).

We created models from subsets of the full model that represented hypotheses based on the known physiological roles of micronutrients and fatty acids and their relationships to our set of predictors. To avoid issues associated with multicollinearity of predictor variables, we excluded other possible variables if they were highly correlated (i.e. correlation coefficient > 0.6). We identified the best subset of models using the Akaike Information Criterion, adjusted for small

sample sizes (AICc). We used AICc, Δ AICc and Akaike weights (*w*) to compare models. We ranked models based on AICc, and selected the set of models that produced a cumulative *w* >= 0.95, meaning that we are 95% confident that the chosen set includes the best model (32). We limited our analyses to species for which we had complete trait data (Table S14), identified to the species level; we did not impute missing trait data using phylogenetic or taxonomic relationships. To account for model uncertainty in the ecological trait correlation analyses, we performed model averaging of coefficients in all models in the 95% confidence set, and included zeros as coefficients when variables did not enter a given model (32). We conducted our model selection and averaging analyses with the *MuMIn* package (33) and all other analyses in R version 3.3.2 (*18*).

The nutrient concentration of different seafood tissues varies according to which body parts are included in the edible portion (e.g. muscle tissues, eggs, liver). To control for these effects of body part in our analyses of ecological traits, we included 'body part' as a covariate, and in a subset of analyses, we included data for muscle tissues only. We also tested for associations between nutrient concentrations (calcium, iron and zinc) and ecological traits among small finfish species (mean length < 25 cm; maximum length < 50 cm), whose edible portions more often include tissues other than muscle only, using ordinary least squares regression (noting that the strength of the phylogenetic signal for calcium, iron and zinc, $\lambda = 0$).

5. Quantifying the relationship between ecological functional diversity and nutritional benefits

To quantify the relationship between ecological functional diversity and nutritional benefits, we created simulated diets from the global species as described above (Main text Methods). To isolate the effects of ecological functional diversity from species richness, we focus on diets of ten species only, thereby capturing the effect of changes in ecological functional diversity independent from changes in species richness. For each of these diets, we quantified the ecological functional diversity, minimum portion size required, P_{min}, and the number of nutrient RDA targets per 100g, *NT* (Main text Methods). We estimated ecological functional diversity using a metric of trait dispersion in multidimensional ecological trait space: functional dispersion (34) (**Figure S1F**). Hereafter, when we refer to ecological functional diversity, we mean functional dispersion. This metric measures the distance of each species from the mean coordinates of the assemblage, weighted by abundance. However, in our simulated diets, since abundance of all species was equal, this metric is simply the mean distance, in multidimensional trait space, of each individual species from the centroid of all species. Here, we constructed the multidimensional trait space using a set of the ecological functional traits (body size, trophic position, diet source and feeding mode). We chose to focus on these traits because they are strongly related to the ecological roles that species play in ecological communities. We estimated the relationship between ecological functional diversity and *NT* (which ranges from 0-5) using ordinal logistic regression. We estimated the relationship between ecological functional diversity and minimum portion size, P_{min}, (in grams) using reduced major axis regression.

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