Aquatic biodiversity enhances multiple nutritional benefits to humans

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Abstract

Global food security relies on protein and essential micronutrients provided by seafood[1–3]. The importance of seafood-derived micronutrients to human health suggests that consuming diverse aquatic species could enhance human well-being[4]. Though biodiversity provides important benefits to humanity[5], it is unclear how changes in species diversity could affect the human health benefits provided by aquatic ecosystems. A key scientific question remains unanswered - does increasing species diversity in seafood diets improve their ability to meet nutritional needs? Here we found that increasing species diversity allows seafood diets to fulfill multiple nutritional requirements simultaneously, a condition necessary for human health. Aquatic species with different ecological traits have distinct and complementary micronutrient profiles. The same complementarity mechanisms that generate positive biodiversity effects on ecosystem functioning in terrestrial ecosystems also operate in seafood assemblages, allowing for more diverse diets to yield increased nutritional benefits. Notably, nutritional metrics that capture multiple micronutrients essential for human well-being depend more strongly on biodiversity than ecological measures of function such as productivity. In contrast to the micronutrients, we found that increasing species diversity did not increase the amount of protein in seafood diets. We provide the first direct link between multiple nutritional benefits of biodiversity and an ecosystem service underpinning human wellbeing, thereby unifying biodiversity ecosystem functioning theory and human health. Our findings demonstrate that minimizing biodiversity loss at local and global scales will benefit global food and nutrition security.

Introduction

Biodiversity enhances ecosystem functions and services because species differ in functional traits or attributes [6–8]. Species losses and range shifts due to climate change, harvesting and other human activities alter aquatic biodiversity locally and globally [9], with consequences for ecosystem functions [6,10]. Wild-caught marine and freshwater finfish and invertebrates (hereafter 'seafood') are rich and unique sources of essential micronutrients, such as vitamins, minerals and fatty acids not found in other foods. Human nutritional benefits from seafood are an important ecosystem service provided by aquatic biodiversity. If aquatic species differ in nutritional profiles as defined by human nutritional needs, the importance of biodiversity for food security depends on exactly how species' multi-nutrient profiles vary. Specifically, a 'biodiversity effect' of nutritional benefits requires that some seafood species contain high concentrations of some micronutrients while other species contain high concentrations of different micronutrients, creating a complementary distribution of micronutrients across species. Ecosystem services that reflect multiple ecosystem functions are believed to be most vulnerable to negative consequences of biodiversity loss [11,12].

We tested the hypothesis that aquatic biodiversity confers nutritional benefits through complementarity in nutrient concentrations among species. We tested whether 1) biodiversity of seafood supply enhances nutritional diversity (N_D) in seafood diets and 2) biodiversity increases the nutritional content of an edible portion of seafood, thereby improving the efficiency (N_E) with which seafood consumers reach nutritional targets (Fig 1). We predicted that increased species richness in seafood diets yields increased nutritional benefits, and that variation in nutrient concentrations among species is related to species' ecological traits. In a global analysis, we considered provision of nutritional benefits to human consumers accessing worldwide seafood markets. We then tested whether seafood biodiversity promotes human health at local scales by providing multiple essential nutrients in fourteen traditional indigenous diets in North America. We quantified variation in nutrient concentrations in edible tissues of 430 commonly consumed aquatic species in the global species pool, and 25 – 57 species in fourteen local dietary species pools. This represents the first extension of biodiversity - ecosystem functioning (BEF) theory to a multivariate ecosystem service that is defined from the perspective of the human beneficiary and is directly relevant to human health.

Results and Discussion

We found that seafood biodiversity not only enhances nutritional benefits for consumers selecting seafood from species included in our global dataset, but it is essential to meeting nutritional targets. Species in the global dataset differed substantially in micronutrient concentrations, but not protein concentrations, relative to dietary reference intake (DRI) targets (Fig 2; ln(protein) geometric coefficient of variation (geometric CV) = 0.03 vs. micronutrient geometric CVs: ln(iron) = 3.97, ln(calcium) = 3.25, ln(EPA) = 2.52, ln(zinc) = 2.10, ln(DHA) = 1.70). When we considered each nutrient separately, we found that fewer than half the species reached an arbitrary single-nutrient threshold of 10% of the daily DRI target [13] for calcium, iron and the essential fatty acid EPA in a standard 100g portion of a single species (Table S1). As species richness of diets increased, 10% DRI for any micronutrient was achieved with less total seafood intake (Fig 3A, $b_E < 0$ for every micronutrient: calcium -0.43 (95% CI -0.47, -0.40), iron -0.40 (95% CI -0.43, -0.36), zinc -0.21 (95% CI -0.21, -0.23), EPA -0.25 (95% CI -0.26, -0.24) and DHA -0.21 (95% CI -0.21, -0.20)), meaning that increasing species richness lead to enhanced nutritional efficiency (N_E). All species reached the protein DRI target, and there was no benefit of seafood diversity for protein (Fig 3A, b_E = 0.0092 95% CI 0.0086, 0.010).

We then considered the effects of seafood species richness on the provisioning of multiple nutrients simultaneously. We treated each nutrient concentration relative to 10% DRI as one ecosystem function. Consistent with biodiversity-ecosystem functioning theory, we found that in the case of a multifunctional metric of an ecosystem service defined from the human perspective (i.e. multiple micronutrient targets reached simultaneously), biodiversity benefits for the multifunctional service are greater than for individual functions (b_E for all five micronutrients simultaneously = -0.49 (95% CI -0.50, -0.48) vs. single nutrients b_E range from -0.43 (95% CI -0.47, -0.40) for calcium to -0.21 for EPA (95% CI -0.21, -0.20)) that comprise the ecosystem service (Fig 3A). Increasing species diversity in a hypothetical diet from one to five species allows consumers to meet 10% of DRI for five essential microelements and fatty acids simultaneously more than twice as efficiently (i.e. a median of 485.83g of tissue required with one species vs. median of 216.96g of tissue required with five species) (Fig 3B, C). We also found positive effects of biodiversity on the number of distinct nutritional functions (10% of DRI reached) in a single 100g portion (Fig 3D): more diverse diets reached more nutritional targets (higher N_D) per serving than diets comprising fewer species (b_D = 0.21 (95% CI: 0.18-0.24) Fig 3D).

Despite recent claims that multifunctionality is not enhanced by biodiversity [14], here we show that when function thresholds are grounded *a priori* in multivariate metrics meaningful for human wellbeing such as DRI, diversity enhances multifunctionality. These findings are robust to multiple DRI threshold levels (Fig S1), and the biodiversity effect is strongest at a threshold of approximately 28% of DRI (Fig S1). More generally, ecosystem service benefits, as defined in metrics of human wellbeing rather than the traits of the species pool under consideration, typically are produced by several underlying ecosystem functions [15]. The strong effects of diversity on multifunctional benefits observed here may also apply to relationships between diversity and other services e.g., desired filtration rates of pollutants in wetlands [16], or desired pest consumption rates in agricultural systems [17].

Consistent with the positive biodiversity effects we observed when assuming consumers have access to global seafood markets, we also found benefits of seafood diversity locally. We analyzed the effects of biodiversity in fourteen traditional indigenous North American diets and found a consistent, positive effect of biodiversity on N_D and N_E, although the magnitude of the biodiversity effect was generally lower at the local scale than the global scale (Fig 3C-D, Fig S2, S5) (global $b_D = 0.21$ (95% CI 0.18, 0.24) vs mean local $b_D = 0.14 \pm 0.0083$ S.E. and global $b_E = -0.50$ (95% CI -0.52, -0.47) vs mean local $b_E = -0.16 \pm 0.0091$ S.E.). This finding is consistent with lower nutritional functional diversity (mean local $FD = 2.77 \pm 0.17$ S.E. vs. global $FD = 3.87 \pm 0.0096$ S.E.) and higher nutritional functional evenness in local diets (mean local $FEve = 0.76 \pm 0.01$ S.E. vs. global $FEve = 0.71 \pm 0.0018$ S.E.) (Fig S2, S5), suggesting that functional consequences of changes to diversity in local seafood diets may be buffered by higher redundancy among species. Given increasing trends towards homogenization of the global food supply [18] including aquaculture [19,20], this local-scale finding highlights the importance of local species diversity in the diets of vulnerable populations [21].

Substantial variation in nutrient concentrations in edible portions among species can be explained partly by major ecological attributes and traits: taxonomic group, latitude, body size, diet breadth and feeding habits (Tables S2-S6). Finfish, crustaceans and molluscs differed significantly in their multi-nutrient profiles (PERMANOVA, $F_{2,103} = 3.429$, $p = 0.006$). Among finfish, concentrations of calcium, iron and zinc in edible tissue decreased with increasing body size (Fig 4, negative slopes, $p < 0.01$, Tables S2-S6). Variation in protein and fat was poorly explained by species' ecological traits (Marginal $R^2 = 0.023, 0.09$, for protein and fat). In addition to ecological traits, finfish species that are eaten whole, or whose edible portions include organs such as skin, liver or bones, have higher nutrient concentrations in the edible portion than those whose edible portions are restricted to muscle tissue ($R^2 = 0.60$, $F_{5, 251} = 76.24$, $p < 0.01$; Fig S3). Nutrient concentrations were typically weakly negatively correlated or uncorrelated with each other among species (Fig S4), allowing complementarity among species to increase nutritional benefits.

Maintaining the diversity of global fisheries is important for ensuring food and nutrition security. A diverse seafood species pool feeds not only local communities but also seafood markets worldwide, and aquatic species contain micronutrients not found in other foods. Many of the most nutritionally vulnerable populations – those that are deficient in essential micronutrients during particularly sensitive stages of life (i.e. pregnancy, breastfeeding and childhood) may rely on local ecosystems to meet their nutritional demands [3,22,23]. These populations may have access to a limited amount of locally available fish tissue each day or to fish from a subset of habitat types, suggesting that for these populations nutritional efficiency may be particularly important. In tropical regions, fish diversity in coastal regions has plummeted in recent decades [24] characterized by two-fold declines in body sizes of fish [25,26]. These regions are also regions of high nutritional vulnerability and reliance on locally harvested seafood [27]. However, as the seafood trade becomes increasingly global [28,29], seafood-derived nutrition available to consumers participating in the global market may be related to globally harvested seafood biodiversity. As a result, changes to local biodiversity and resultant impacts on human nutrition may be buffered by access to global seafood markets. Together, our results suggest that in the context of global change, understanding and protecting the potential for nature to support diverse and productive aquatic ecosystems has direct and immediate benefits to humanity.

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Figures

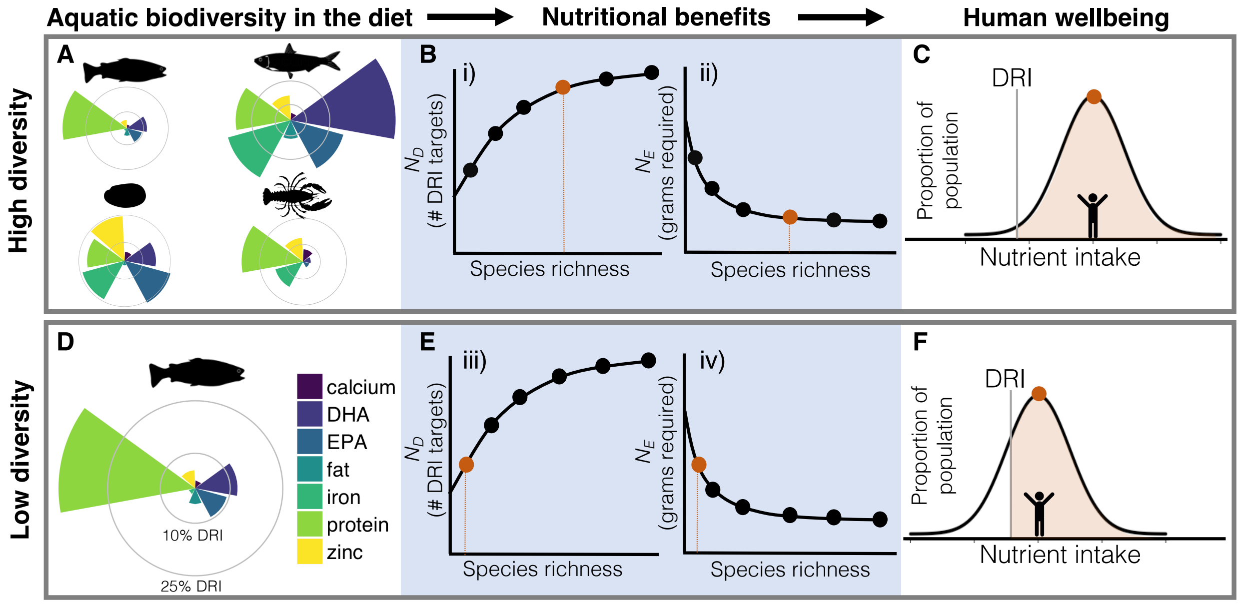


Fig 1. Aquatic biodiversity increases human well-being because edible species have distinct and complementary multi-nutrient profiles (A) and differ in mean micro- and macronutrient content (shown here relative to 10% and 25% thresholds of dietary reference intake (DRI) guidelines for representative finfish (*Abramis brama, Mullus surmuletus*), mollusc (*Mytilus galloprovincialis*) and crustacean species (*Nephrops norvegicus*). Biodiversity – ecosystem functioning theory predicts that nutritional benefits, including nutritional diversity (N_D; i, iii) and nutritional efficiency (N_E; ii, iv) (B, E), are enhanced with increasing dietary species richness. Seafood consumers with limited access to seafood each day may not reach DRI targets if diets are low in diversity (F vs C; orange shading indicates proportion of population that meets nutrient requirements).

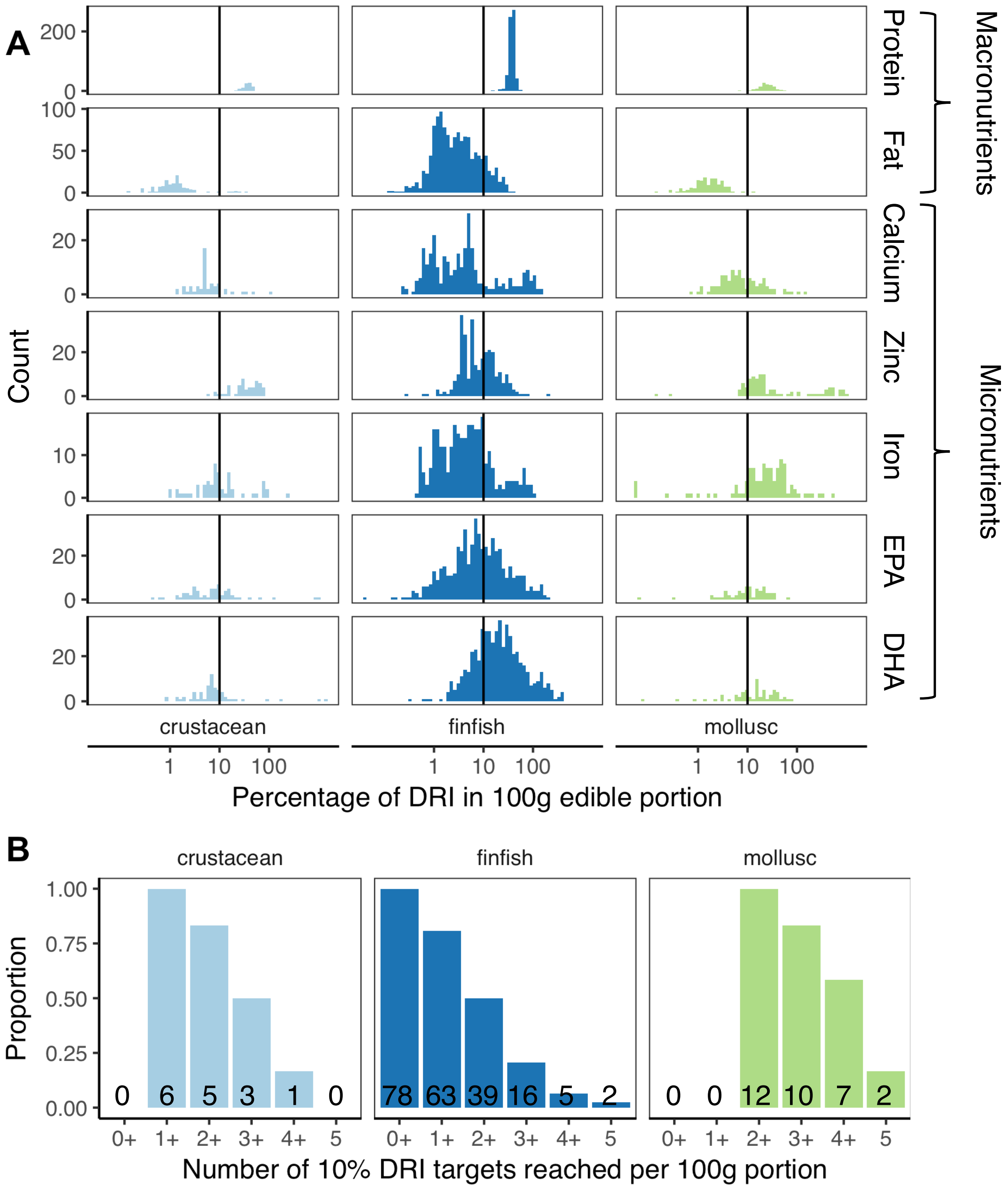


Fig 2. Variation in nutrient concentrations differs among taxonomic groups. (A) Frequency of reported protein, fat and micronutrient (including eicosapentaenoic acid (EPA), docosahexaenoic acid (DHA)) content in 100 g of the edible portion of 430 seafood species (references in Dataset S1). (B) Proportion of species, and number shown on each bar, with available data that reach 10% of RDI targets for any one, two or up to five of the micronutrients examined here.

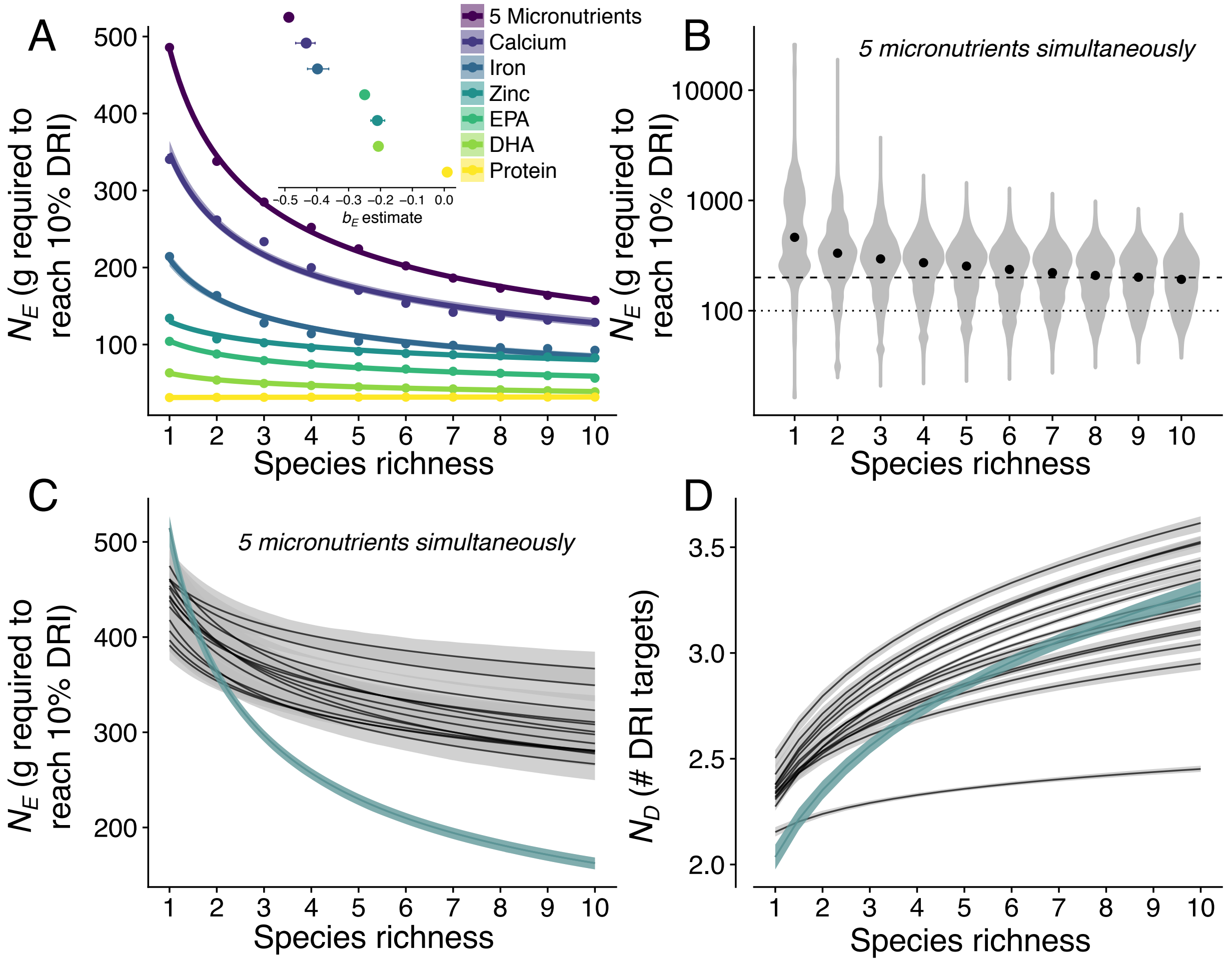


Fig 3. A) Seafood species richness improves the efficiency with which human diets can meet 10% of DRI by reducing the grams of seafood required to meet nutritional thresholds. Nutritional efficiency (N_E) is shown for five micronutrients and protein separately (points are median values for calcium, iron, zinc, EPA, DHA and protein, lines show the fit of Equation 1 to the data and shading refers to 95% CI) as well as for five micronutrients simultaneously (purple line labeled '5 Micronutrients'); estimates for the b_E parameter (± standard error, inset) describe the strength of the biodiversity effect. B) Increasing dietary species richness sourced from global seafood markets increases the efficiency with which five micronutrient nutritional targets are reached; solid circles are median values, as plotted in the purple line in A. C) Increasing species richness increases the efficiency with which five micronutrient nutritional targets are reached at local and

global scales; shaded areas are 95% confidence intervals about the mean; black lines are the fit of Equation 1 for each of fourteen traditional diets in North America, green line is for a diet sourced from the global seafood market. D) Species richness increases the number of distinct DRI targets met in a 100g seafood portion (nutritional diversity, N_D) in local and global seafood diets; lines are the fit of Equation 2, color coding as in C.

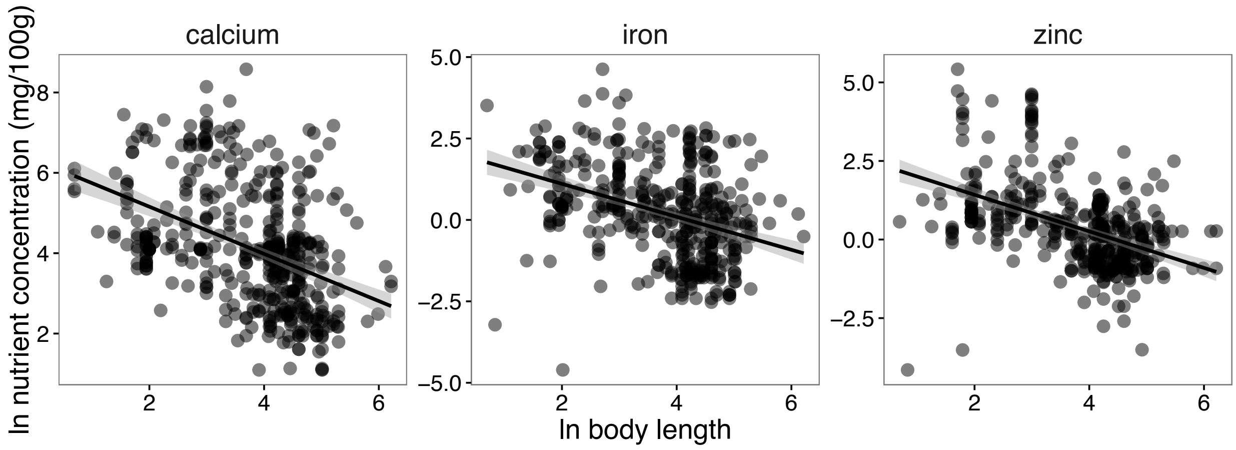


Fig 4. Micronutrient concentrations are significantly negatively related to body size (length, cm) in finfish. Negative slopes: calcium: -0.26 (95% CI -0.38, -0.14, *n* = 174), iron: -0.16 (95% CI -0.30, -0.02, *n* = 181), zinc: -0.16 (95% CI -0.30, -0.03, *n* = 161).

Supplementary Materials:

Materials and Methods
Figs. S1 to S5
Tables S1 to S9

Other Supplementary Materials for this manuscript includes the following:

Database S1: Seafood nutrient data sources.

Materials and Methods

Quantifying nutritional value in terms of human health benefits

We characterized an aquatic species' nutritional profile by drawing on two well-established nutritional metrics: nutrient concentration (nutrient content/100g edible portion) and Dietary Reference Intake (DRI). DRIs are developed following health guidelines, and quantify the recommended amount of a particular nutrient required to maintain health [13]. The DRI used here is the Recommended Dietary Allowance, established by the Food and Nutrition Board of the United States Institute of Medicine, which is daily intake level of a nutrient needed to meet the requirements of 97–98% of healthy adults (males and females above age 19) [13]. We defined the nutritional value of a fish species for each nutrient in terms of the nutrient content in an edible portion relative to DRI. For some aquatic species, micronutrients are in such high concentrations in edible tissues that a single 100g portion contains the entire dietary reference intake (DRI) for that nutrient, while edible tissues from other species provide only small fractions of the DRI. We considered thresholds of nutritional benefit (function) between 1% and 100% of DRI, although we focus on 10% of DRI since it is a minimum threshold for a food to be considered of nutritional benefit [13]. We defined a nutritional function as providing ≥10% of DRI for a given nutrient. Using this definition, a particular species provides a nutritional function if it reaches 10% or more of DRI for a given nutrient in a single 100g portion. For example, if a species provides 7% of DRI for zinc, 12% of DRI for iron, 30% of DRI for calcium, and 15% of DRI for each of EPA and DHA in a single 100g portion, then it provides four nutritional functions. We characterized nutritional profiles in two ways: first, in terms of concentrations of each nutrient (single nutrient profile), and secondly, in terms of multiple nutrients simultaneously (i.e. multi-nutrient profile).

Defining nutritional benefits

We quantified the effect of biodiversity on nutritional benefits in two ways (Fig 1): 1) *nutritional efficiency*, $N_{E,}$ which quantifies that amount of tissue, in grams, required to reach a given number of nutritional functions (10% DRI targets) simultaneously and 2) *nutritional diversity*, $N_{D,}$ which quantifies the number of distinct nutritional functions (10% DRI thresholds reached) in a standard 100g edible portion. Nutritional benefit increases with decreasing values of N_E, since N_E quantifies the grams required to provide a nutritional function, and fewer grams required is better from the perspective of human nutrition. We quantified N_D in an arbitrary daily diet, assuming that the seafood diet contains 100g of seafood per day.

Literature search and data collection

We assembled a dataset of published nutrient concentrations in edible portions of 430 aquatic species. We analyzed tissue concentrations of nutrients for which DRI standards exist and that are implicated in a range of biologically important processes that affect organismal growth and reproduction, and therefore may potentially relate ecological function with human nutritional wellbeing. We examined macronutrients including protein and fat, as well as five micronutrients: the polyunsaturated fatty acids eicosapentaenoic acid (EPA) and docosahexaenoic acid (DHA), metals beneficial at low concentrations but toxic at high concentrations (zinc and iron), and one beneficial mineral (calcium). 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 [30]. For finfish, we restricted our analysis to include only edible portions of wild, raw fish (excluding prepared or farmed seafood items). We included both farmed and wild mollusc species because mollusc farming does not typically involve additional food inputs, which could influence tissue nutrient composition. For each species, we noted which body parts are included in the edible portion and season of collection. For each sample, we noted the location of origin (e.g. latitude and longitude). To address inconsistencies in fatty acid data reporting, we standardized fatty acid measurements using the fatty acid conversion factors proposed by Nowak et al. 2014 [31]. When there were multiple observations available for a single species, we averaged nutrient concentrations across the observations. We did not include data from national food composition tables because these data usually report seafood data with a generic food description, which does not allow for a clear description of which fish tissues are included in the edible portion. For each species with nutritional data, we collected ecological trait information from FishBase [32] and SeaLifeBase [33]. We included body size (maximum length), fractional trophic position, temperature preference (using latitude as a proxy), habitat preference, and feeding mode (Table S9).

Statistical analyses and hypothesis testing

Hypothesis 1: Biodiversity enhances nutritional benefits

We tested the effect of species diversity (quantified as the number of species, or *species richness, S*) on nutritional diversity and efficiency by randomly assembling diets from the global seafood species pool. When estimating nutritional diversity, we kept the portion size constant (100 grams) across all levels of diversity. In analyses using the global dataset (430 species), we assumed that human populations have access to the entire global species pool and choose species at random. Though this assumption certainly ignores economic, social and cultural factors that affect which species people consume, in the absence of detailed, species-specific diet information for the majority of the world's populations this is a necessary assumption. To assess potential effects of biodiversity on nutritional benefits for populations that consume seafood locally and not as part of the global seafood market, we analyzed traditional diets in fourteen indigenous cultures in North America. We used species lists for local diets that were obtained from an ethnographic database of traditional animal foods of indigenous peoples of northern North America, and only included species that were harvested wild and whose nutrient compositions where analyzed when raw (Table S7, [34]). To avoid confounding differences in biodiversity effects at global and local scales with the sizes of the species pools at each of these scales when comparing local and global biodiversity effects, we matched the size of the global species pool to the average size of the local species pools by first randomly subsampling 40 species, the average size of the local species pools, from the global species pool.

We calculated two metrics of nutritional benefits for hypothetical diets comprising species drawn randomly from either the global dataset (global diet) or local datasets (local diets):

1) Nutritional efficiency (N_E). We tested the hypothesis that complementarity in nutrient concentrations among species enhances N_E by estimating the effect of species richness, S, on N_E (the 'biodiversity effect'). To estimate the 'biodiversity effect' on N_E, we took an approach to modeling dietary species composition that is analogous to a biodiversity-ecosystem function experiment with a replacement design, where species abundances (i.e. portion size) decline proportionally as species richness increases. From the global species pool, 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). We repeated this process of sampling ten species from the global species pool and then assembling all possible diets 1000 times. For each combination of species in each dietary diversity level (1-10 species), we calculated the number of grams required to reach a given nutritional function (either: one of six possible 10% DRI targets individually, considering five micronutrients: calcium, iron, zinc, EPA and DHA and one macronutrient, protein, or all five micronutrient targets simultaneously). We quantified the effect of species richness in a diet on nutritional efficiency, N_E, by fitting a power function to these bootstrapped nutritional efficiency estimates:

$$N_E = a_E S^{b_E} \tag{1}$$

where the parameter b_E describes the relationship between a change in species richness, S, and a change in N_E, and a_E is a scaling factor (in grams) that determines the value of N_E when $S = 1$. Since N_E is measured in grams required to reach a given nutritional function (10% DRI target), and fewer grams required is better from the perspective of human nutrition, then a benefit of biodiversity would be reflected in a negative b_E (i.e. N_E, measured in grams of tissue required, decreases with species richness). For each nutrient individually, and for all five micronutrients together, we estimated the exponent parameter, b_E, using non-linear regression using the *nls.LM* function in the *minpack.lm* package in R [35]. To quantify uncertainty in parameter estimates associated with sampling from the pool of observed nutrient content values, we calculated bootstrapped confidence intervals using non-parametric bootstrapping of mean centered-residuals using the *nlsBoot* function in the R package *nlstools* [36].

2) Nutritional diversity (N_D). To test the hypothesis that complementarity in nutrient concentrations among species increases nutritional benefits by increasing the number of distinct nutritional functions (10% DRI targets) in a 100g portion, we constructed nutrient function accumulation curves. These are analogous to species accumulation curves used in ecological studies to assess patterns of beta-diversity, or species turnover, in ecological community composition data. We assessed turnover of nutrient content in edible tissues among seafood species. Each seafood species is associated with a set of 0s and 1s corresponding to whether or not it provides a nutritional function (achieves a threshold of 10% DRI) for each of five micronutrients (equivalent to a species presence-absence matrix in community composition data), sampled with replacement 1000 times. This approach allowed us to explore how likely it would be for human diets containing different numbers of seafood species to provide a given number of nutritional functions for micronutrients (N_D ranges between 0 and 5), assuming that species were included in the human diet at random. We quantified the effect of biodiversity on nutritional diversity, N_D, by fitting a power function,

$$N_D = a_D S^{b_D} \tag{2}$$

where the parameter b_D describes the relationship between a change in species richness, S, and a change in N_D (i.e. the number of nutritional functions (distinct 10% DRI targets) reached per average 100g portion), and a_D is a scaling factor (in units of number of DRI targets) that determines the value of N_D when $S = 1$.

For both N_E and N_D, we tested the hypothesis that biodiversity enhances nutritional benefits by assessing whether the estimate of the scaling exponent, b, had confidence intervals not overlapping zero. We concluded that biodiversity enhanced nutritional benefits if b_E was negative and b_D was positive.

We hypothesized that nutritional functional diversity would be higher at the global scale than the local scale, because the global species pool contains more ecological and biogeographic diversity. To assess levels of nutritional functional diversity among species, we calculated functional diversity (FD) [37]. FD is based on an assessment of the entire functional diversity of a group represented as a functional dendrogram, and FD allows estimation of complementarity among species' nutrient concentrations (i.e. nutritional functional traits) using the dendrogram. We treated the concentration of each micronutrient (calcium, iron, zinc, EPA and DHA) as a functional trait. We also quantified a functional evenness metric (*FEve*) using the *FD* package in R, which normally quantifies the evenness of abundance in a functional trait space. Here, we used *FEve* to quantify the evenness in concentration of nutrients across species [38]. To compare *FD* and *FEve* 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' *FD* and *FEve* 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 (Fig S5). The purposed of calculating 'expected' *FD* and *FEve* values is to test whether local diets are different from random subsets of the global species pool.

Hypothesis 2: Diversity in nutrient concentrations of the edible portion is related to ecological diversity estimated as species' ecological traits.

We tested the hypothesis that nutrient concentrations are related to species' ecological traits in two ways: 1) testing whether multi-nutrient profiles (i.e. concentrations of all five micronutrients) differ among major phylogenetic groups and 2) whether differences in single nutrient concentrations differ with species ecological traits. We examined variation in multi-nutrient profiles among seafood species using the *vegan* package in R [39]. We ln transformed nutrient concentration data to achieve normality. We tested the hypothesis that major phylogenetic groups (i.e. finfish, mollusc, and crustacean) correlated with functional differences in life history, resource use and ecology differ in their multi-nutrient profiles via permutational multivariate ANOVA (PERMANOVA) using the *adonis* function (999 permutations) based on Bray-Curtis dissimilarity matrices. We used an overall (three-way) PERMANOVA to investigate phylogenetic group effects on nutrient profile of a species' edible tissue.

To test for associations between species' ecological functional traits and their nutrient concentrations, we modeled the relationship between traits and ln(nutrient concentration) with linear regression. The full model included the entire set of trait predictors as fixed effects and a random effect term for each study j, μ_j, capturing systematic variation among studies in terms of how nutrient concentrations were estimated:

$$ln(nutrient) = \beta_0 + \beta_1 * ln(body\ size) + \beta_2 * latitude + \beta_3 * trophic\ position + \beta_4 * habitat + \beta_5 * feeding\ mode + \beta_6 * diet\ breadth + \mu_j + \varepsilon_i$$

We created models from subsets of the full model that represented hypotheses based on the known physiological roles of micronutrients and their relationships to our set of predictors (Tables S2-S6, S9). 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, ∂aic and Akaike weights (w) to compare models. We ranked models based on w, 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 [40]. In cases where we could not obtain measurements of all traits for all species, we performed model selection on reduced datasets without missing values.

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 [41]). Still, tissue concentrations may vary depending on analytical techniques, labs, 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 labs. 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 430 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 [42], species with capture production of 150 000 tonnes or more, after removing species for which the majority of production volume is diverted to fish meal and oil [43], Table S8). 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. For the nutritional diversity and nutritional efficiency analyses, these uncertainties were not modeled. For the ecological trait analyses, the uncertainty in observation precision was modeled as normally distributed error term, ε_i, at the species level.

To account for model uncertainty in the ecological trait correlation analyses, we performed model averaging of coefficients in all models with ∂aic <2 (∂aic = $AIC_i - AIC_{min}$), and included zeros as coefficients when variables did not enter a given model [40]. We conducted our model selection and averaging analyses with the *MuMIn* package [44] and all other analyses in R version 3.3.2 [45].

Supplemental figures and tables

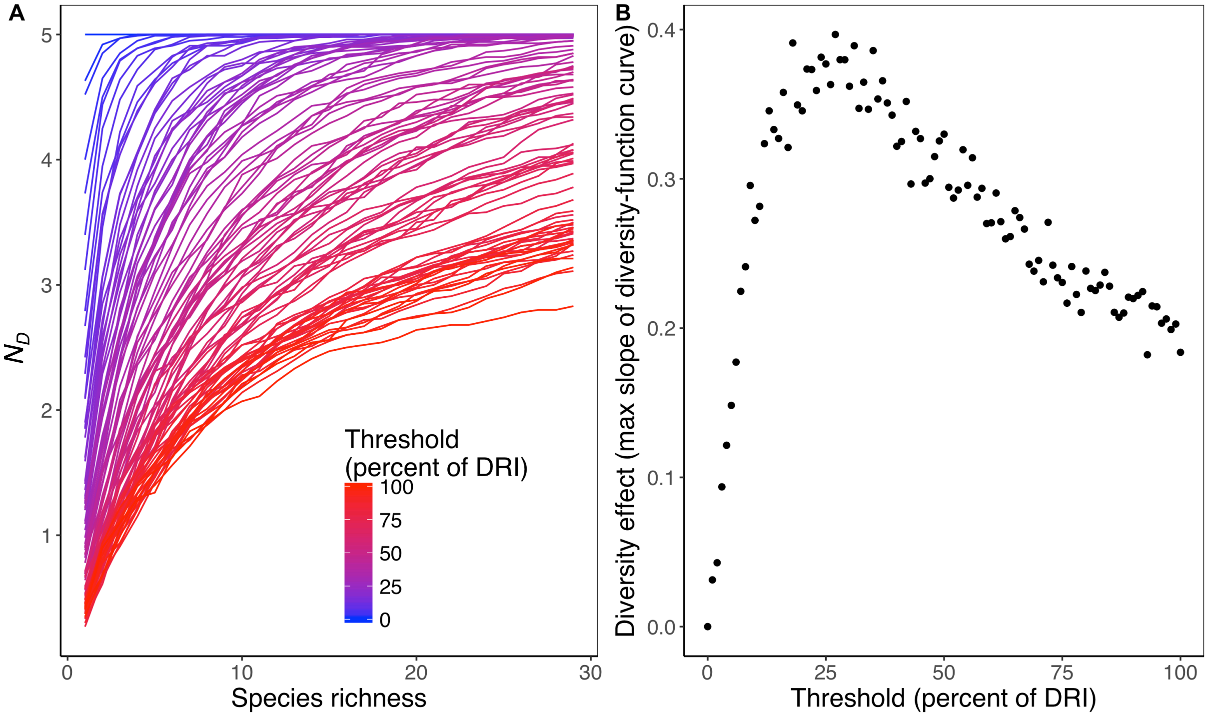


Fig S1. The effect of biodiversity on nutritional diversity (N_D) depends on the DRI threshold. A) Number of nutritional functions (distinct DRI targets), estimated as $N_{D,}$ provided per 100g edible portion increases with species richness. B) The effect of biodiversity on nutritional diversity (N_D) is strongest at a threshold of approximately 28% of DRI.

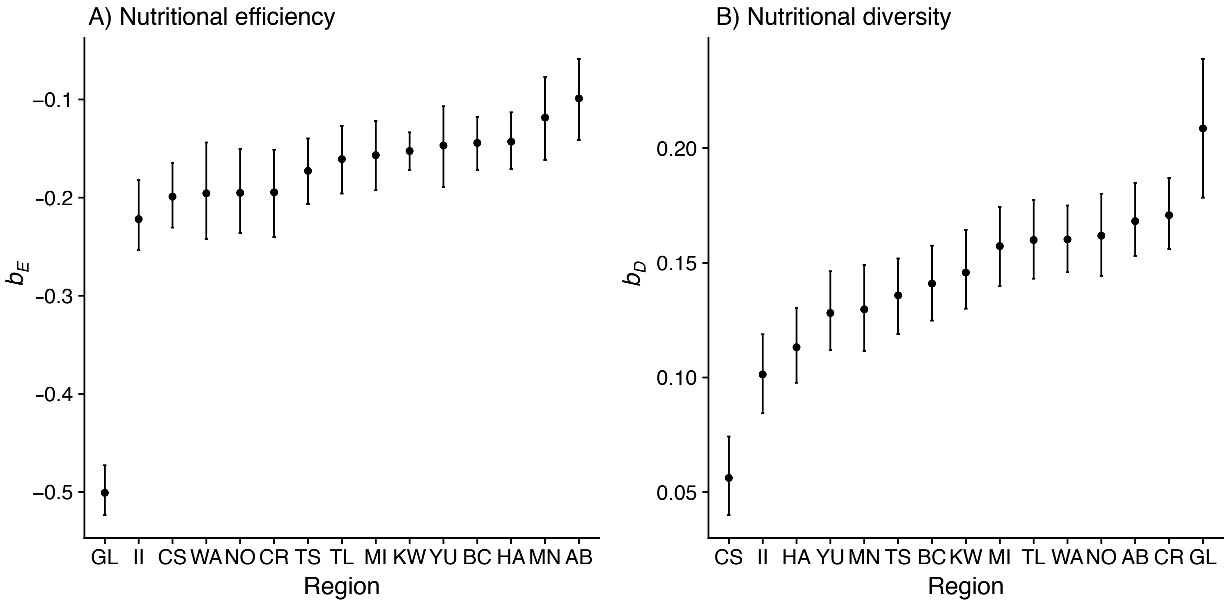


Fig S2. Biodiversity enhances nutritional benefits in terms of two metrics of nutritional benefit: nutritional efficiency (N_E) (A) and nutritional diversity (N_D) (B). Each point corresponds to the *b* parameter estimate from $y = aS^b$, where y = nutritional benefit (N_E or N_D) and each point corresponds to one of fourteen local indigenous diets and the global diet (GL; standardized to 40 species). Points are means ± 95% CI from non-parametric bootstrapping of the fit of Equations 1 (panel A) and 2 (panel B) to randomly assembled diets. Names of regions for each local diet are represented in two-letter abbreviations which are listed in Table S7.

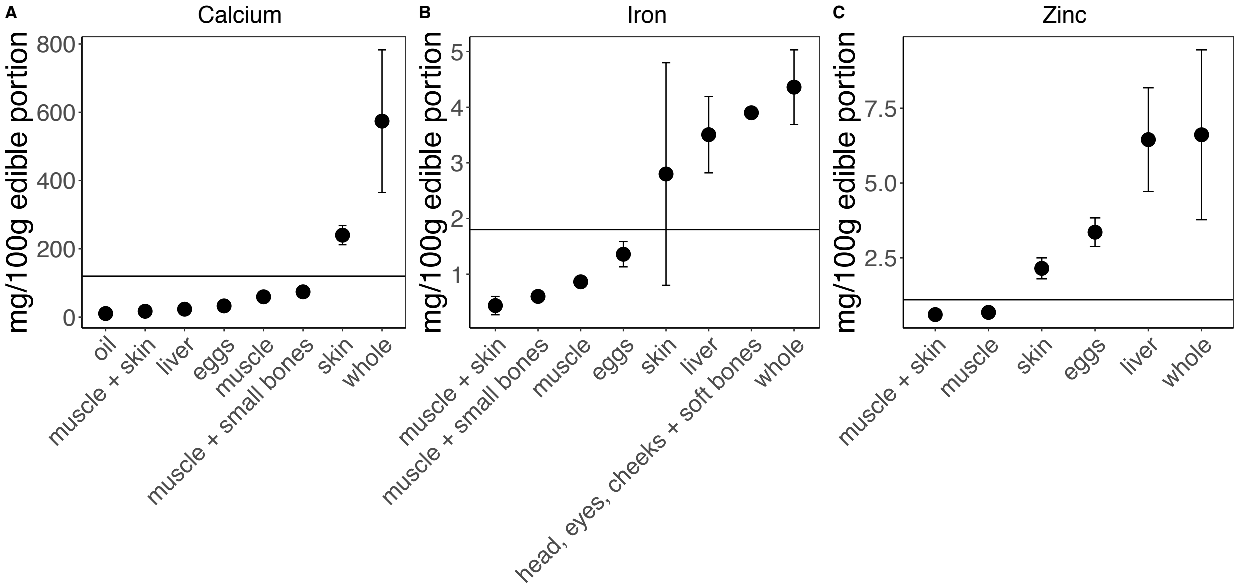


Fig S3. Nutrient variation associated with human dietary practices. Among finfish species, nutrient concentration varies by body part in the edible portion. Fish species that are eaten whole, or whose edible portions include organs such as skin, liver or bones have higher nutrient concentrations than those whose edible portions are restricted to muscle tissue. Points are means ± standard error.

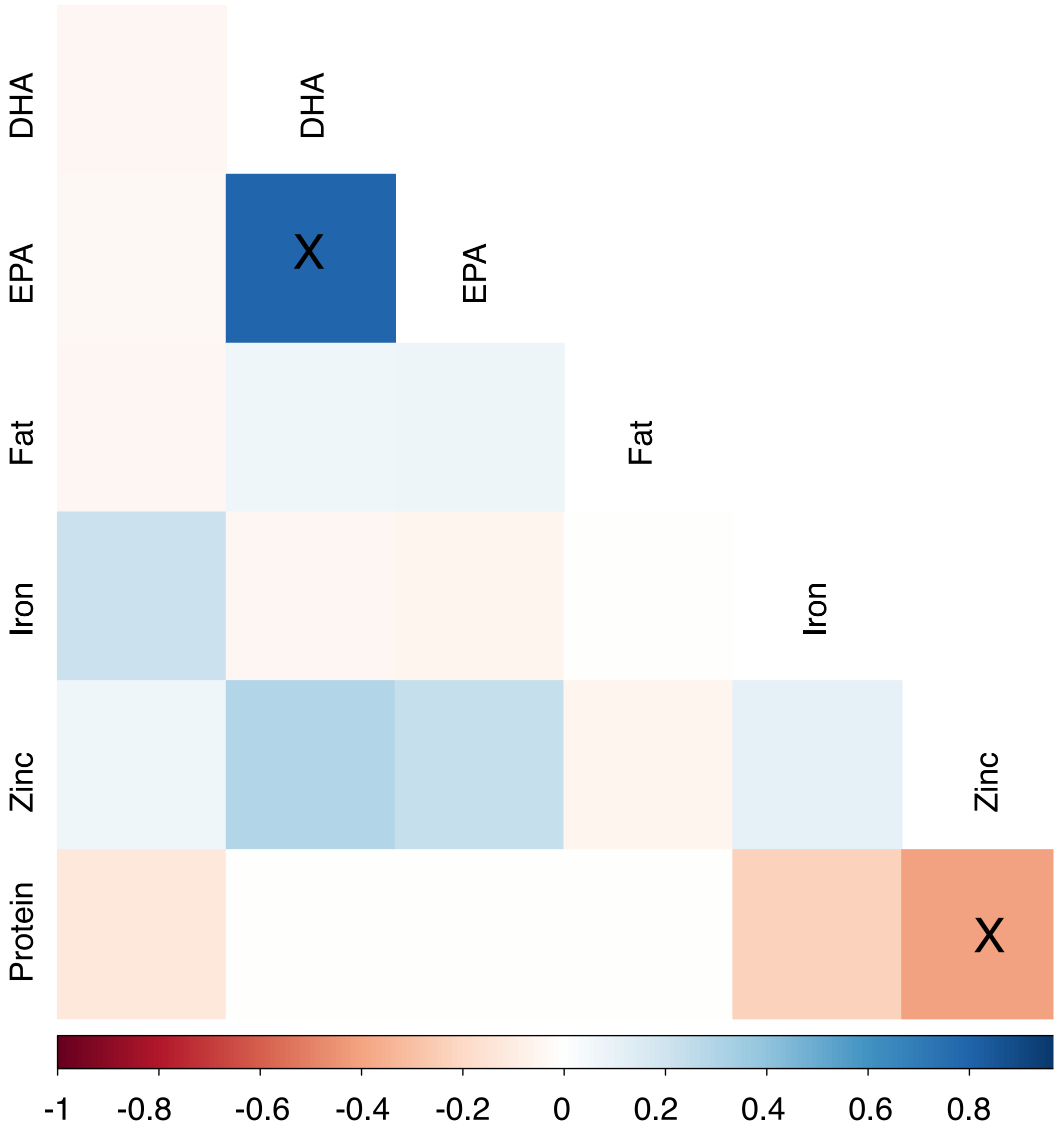
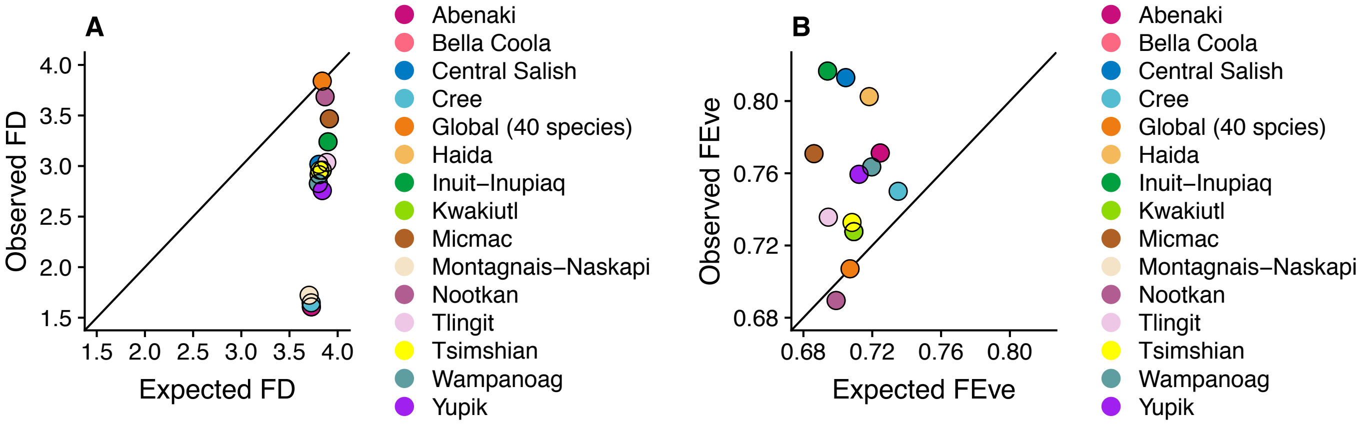


Fig S4. Correlations among nutrient concentrations among species. Nutrient concentrations are typically weakly correlated or uncorrelated among species. Shading corresponds to correlation coefficients, squares covered with an 'X' are significantly correlated; $p < 0.05$.



580
581 **Fig S5**. Observed vs Expected functional diversity (*FD*) and functional evenness (*FEve*) in local
582 and global diets.
583

Nutrient	Crustacean	Crustacean n	Finfish	Finfish n	Mollusc	Mollusc n	All species	All species n
Calcium	25	20	31.03	174	35.29	34	31.14	228
DHA	30	30	72.47	287	62.5	24	68.04	341
EPA	34.38	32	43.75	288	70.83	24	44.77	344
Fat	4	50	11.59	509	0	53	9.97	612
Iron	50	22	18.78	181	91.89	37	32.92	240
Protein	100	34	100	351	100	45	100	430
Zinc	94.12	17	44.72	161	88.24	34	55.66	212

Table S1. Percentage of species that reach 10% of DRI, and total number of species (n) grouped by taxonomic group.

Iron	Model rank						Model average	
Trait	1	2	3	4	5	6	β	95% CI
ln(body size)	●		●		●	●	0.099	-0.11 to 0.30
Trophic position	●	●	●	●	●		**-0.46**	-0.74 to -0.20
Herbivore grazer	●			●	●	●	-0.051	-1.03 to 0.91
Omnivore	●			●	●	●	-0.27	-0.69 to 0.14
Latitude	●	●	●	●		●	-0.022	-0.041 to -0.034
Feeding mode grazer		●	●	●		●	0.039	-0.70 to 0.77
Feeding mode active predator		●	●	●		●	0.26	-0.75 to 1.27
Feeding mode filter feeder		●	●	●		●	0.57	-0.49 to 1.63
Feeding mode variable		●	●	●		●	-0.13	-1.24 to 0.98
Marginal R^2	0.12	0.12	0.12	0.12	0.039	0.12		
Conditional R^2	0.80	0.79	0.79	0.79	0.80	0.77		
δaic	0.00	0.14	1.79	2.77	2.93	14.20		
w	0.35	0.33	0.14	0.0089	0.0081	0.00029		

Table S2. Results of model averaging and model selection for iron. The variables included in each model are shown with the symbol •. Models are ranked in order of increasing ∂aic. Akaike weights (*w*) indicate the relative likelihood of a model, given the particular set of best models being considered [40]. Model-averaged regression coefficients (β) are averages of β across all models with ∂aic < 2, weighted by each model's Akaike weight *w*. Calculations for β include β = 0 when variables are not in a given model. β whose 95% confidence intervals do not encompass zero are given in bold.

Calcium	Model rank						Model average	
Trait	1	2	3	4	5	6	β	95% CI
ln(body size)	●	●	●			●	**-0.37**	-0.63 to -0.12
Trophic position	●	●		●	●	●	-0.17	-0.49 to 0.16
Herbivore grazer	●		●		●	●	-0.21	-1.11 to 0.28
Omnivore	●		●		●	●	-0.18	-0.83 to 0.42
Latitude	●	●	●	●	●		**-0.040**	-0.058 to -0.022
Feeding mode grazer	●	●	●			●	-0.063	-0.80 to 0.92
Feeding mode active predator	●	●	●			●	0.33	-0.54 to 1.20
Feeding mode filter feeder	●	●	●			●	-0.049	-1.02 to 0.92
Feeding mode variable	●	●	●			●	0.088	-0.96 to 1.14
Marginal R^2	0.30	0.29	0.29	0.26	0.26	0.032		
Conditional R^2	0.74	0.74	0.75	0.74	0.74	0.78		
δaic	0.00	2.23	5.32	8.83	11.07	13.20		
w	0.71	0.23	0.050	0.0086	0.0028	0.00096		

Table S3. Results of model averaging and model selection for calcium. The variables included in each model are shown with the symbol ●. Models are ranked in order of increasing ∂aic. Akaike weights (*w*) indicate the relative likelihood of a model, given the particular set of best models being considered [40]. Model-averaged regression coefficients (β) are averages of β across all models with ∂aic < 2, weighted by each model's Akaike weight *w*. Calculations for β include β = 0 when variables are not in a given model. β whose 95% confidence intervals do not encompass zero are given in bold.

Zinc	Model rank						Model average	
Trait	1	2	3	4	5	6	β	95% CI
ln(body size)		●	●	●		●	-0.091	-0.28 to 0.097
Trophic position	●	●	●		●		-0.16	-0.39 to 0.067
Herbivore grazer		●		●	●	●	-0.22	-0.95 to 0.52
Omnivore		●		●	●	●	0.057	-0.32 to 0.44
Latitude	●	●	●	●	●		**-0.023**	-0.037 to -0.0074
Feeding mode grazer	●			●	●		-0.30	-1.02 to 0.41
Feeding mode active predator	●			●	●		-0.21	-1.12 to 0.70
Feeding mode filter feeder	●			●	●		0.12	-0.82 to 1.07
Feeding mode variable	●			●	●		-0.43	-1.43 to 0.58
Marginal R^2	0.15	0.14	0.16	0.17	0.16	0.014		
Conditional R^2	0.70	0.72	0.79	0.68	0.69	0.74		
δaic	0.00	0.62	0.19	2.63	3.35	5.20		
w	0.355	0.261	0.196	0.095	0.067	0.026		

Table S4. Results of model averaging and model selection for zinc. The variables included in each model are shown with the symbol ●. Models are ranked in order of increasing ∂aic. Akaike weights (w) indicate the relative likelihood of a model, given the particular set of best models being considered [40]. Model-averaged regression coefficients (β) are averages of β across all models with ∂aic < 2, weighted by each model's Akaike weight w. Calculations for β include β = 0 when variables are not in a given model. β whose 95% confidence intervals do not encompass zero are given in bold.

EPA	Model rank						Model average	
Trait	1	2	3	4	5	6	β	95% CI
ln(body size)	●	●	●	●	●		**-0.21**	-0.40 to -0.015
Trophic position	●	●	●	●		●	-0.26	-0.57 to 0.057
Herbivore grazer	●	●			●	●	-0.069	-0.59 to 0.45
Omnivore	●	●			●	●	-0.23	-0.72 to 0.26
Latitude		●	●	●	●	●	0.0093	-0.0085 to 0.027
Marginal R^2	0.015	0.020	0.022	0.020	0.021	0.022		
Conditional R^2	0.82	0.82	0.82	0.82	0.82	0.82		
δaic	0.00	1.02	6.32	6.82	9.48	10.24		
w	0.591	0.356	0.025	0.020	0.005	0.004		

Table S5. Results of model averaging and model selection for EPA. The variables included in each model are shown with the symbol •. Models are ranked in order of increasing ∂aic. Akaike weights (*w*) indicate the relative likelihood of a model, given the particular set of best models being considered [40]. Model-averaged regression coefficients (β) are averages of β across all models with ∂aic < 2, weighted by each model's Akaike weight *w*. Calculations for β include β = 0 when variables are not in a given model. β whose 95% confidence intervals do not encompass zero are given in bold.

DHA	Model rank						Model average	
Trait	1	2	3	4	5	6	β	95% CI
ln(body size)	●	●	●	●			**-0.21**	-0.40 to -0.023
Trophic position	●	●		●	●	●	0.10	-0.19 to 0.39
Herbivore grazer		●	●	●	●	●	-0.27	-0.85 to 0.31
Omnivore		●	●	●	●	●	-0.31	-0.76 to 0.15
Latitude			●	●	●	●	0.0071	-0.0090 to 0.023
Feeding mode grazer	●		●		●	●	0.38	-0.27 to 1.02
Feeding mode active predator	●		●		●	●	0.072	-0.57 to 0.72
Feeding mode filter feeder	●		●		●	●	0.70	-0.21 to 1.61
Feeding mode variable	●		●		●	●	-0.18	-0.86 to 0.51
Marginal R^2	0.022	0.010	0.024	0.016	0.018	0.020		
Conditional R^2	0.81	0.80	0.81	0.80	0.81	0.81		
δaic	0.00	0.45	1.62	1.82	2.26	5.35		
w	0.329	0.263	0.146	0.133	0.106	0.023		

Table S6. Results of model averaging and model selection for DHA. The variables included in each model are shown with the symbol •. Models are ranked in order of increasing ∂aic. Akaike weights (*w*) indicate the relative likelihood of a model, given the particular set of best models being considered [40]. Model-averaged regression coefficients (β) are averages of β across all models with ∂aic < 2, weighted by each model's Akaike weight *w*. Calculations for β include β = 0 when variables are not in a given model. β whose 95% confidence intervals do not encompass zero are given in bold.

Culture	Abbreviation	Region	Location	Species in diet
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	HA	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
Micmac	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 S7. Names and locations of North American indigenous cultures used in the local scale nutritional diversity analysis.

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

Table S8. Top fourteen of 41 most commonly consumed species as per FAO production volumes in the nutrient dataset. Data source: [42].

Categorical predictors	**Levels**		
Feeding mode	browsing on substrate		
	feeding on the prey of a host (commensal)		
	filtering plankton		
	grazing on aquatic plants		
	hunting macrofauna (predator)		
	other		
	selective plankton feeding		
	sucking food-containing material		
	variable		
Diet breadth	mainly animals		
	mainly plants/detritus		
	plants/detritus+animals		
Continuous predictors	Min	Mean	Max
ln(body size)	1.95	4.22	6.68
absolute latitude	0.03	38.06	82.86
fractional trophic position	2	3.55	4.55

Table S9. Predictors used in linear mixed effects models.

Dataset S1. (separate file)

List of species and data sources for nutrient concentration in the global seafood nutrient dataset.