Aquatic biodiversity enhances multiple nutritional benefits to humans

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Classification: Biological Sciences/Ecology

Keywords: seafood, biodiversity-ecosystem functioning, ecosystem services

Author contributions: JRB conceived the study, collected and curated the data. JRB analyzed and visualized the data with input from MIO. JRB wrote the original draft of the manuscript, JRB and MIO contributed to writing and editing. MIO supervised the study.

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Abstract

Global food security relies on protein and essential micronutrients provided by seafood (Latham 1997, Golden et al. 2016). The importance of seafood-derived micronutrients to human health suggests that consuming diverse aquatic species could enhance human well-being (Penafiel et al. 2011). Biodiversity provides important ecosystem benefits to humanity (Cardinale et al. 2012), causing concern that declining biodiversity may affect human health (Myers et al. 2013). A key scientific question remains unanswered - does increasing species diversity in seafood diets improve their ability to meet nutritional needs? Here we used biodiversity-ecosystem functioning theory to test whether increasing species diversity allows seafood diets to fulfill multiple nutritional requirements simultaneously, a condition necessary for human health. We found that 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 unify biodiversity-ecosystem functioning theory and human nutrition, demonstrating a direct link between multiple nutritional benefits of biodiversity and an ecosystem service underpinning human wellbeing. Our findings demonstrate that minimizing biodiversity loss at local and global scales will benefit global food and nutrition security.

Significance statement:

Food security is not simply about maintaining yields, it is also the need for a stable supply of nutritionally diverse foods. Obtaining nutritious food is a major challenge facing humanity, and aquatic ecosystems can help meet this goal. From the perspective of human nutrition, how much biodiversity is enough biodiversity? How ecological processes influence the capacity of aquatic ecosystems to provide nutritionally diverse diets is largely unknown. We found that aquatic biodiversity enhanced nutritional benefits, because edible species showed distinct and complementary multi-nutrient profiles. Protein supply was independent of biodiversity, but the supply of micronutrients increased with biodiversity. Extending the multifunctional benefits of biodiversity to human nutrition underscores the need to minimize biodiversity loss for the benefits of humanity.

Introduction

Species losses and range shifts due to climate change, harvesting and other human activities alter aquatic biodiversity locally and globally (6, 7), affecting ecosystem functions and services to humans (8, 9). Seafood, consisting of wild-caught marine and freshwater finfish and invertebrates, not only provides an important source of protein and calories to human consumers, but also provides essential micronutrients, such as vitamins and minerals (1, 2, 10, 11). Though it is appreciated that biodiversity (variety and composition of species) in diets can lead to a more nutritious or beneficial diet overall (3, 12–18), aquatic biodiversity *per se* is only nutritionally valuable if consuming a more diverse seafood diet is more beneficial than simply consuming more seafood biomass. Understanding the value of biodiversity - distinct from total biomass - is a critical challenge as patterns of biodiversity continue to change in the Anthropocene.

Ecological theory predicts that biodiversity can be ecologically and economically important, apart from the importance of total biomass or the presence of particular species (4, 19). Experiments and theory have shown that for a given species pool and ecological context (e.g., prairie grasses, crops or intertidal seaweeds) diversity in ecological communities and agricultural systems enhances ecosystem functioning by two mechanisms: (i) more diverse assemblages may outperform less diverse assemblages of the same biomass because more diverse assemblages are more likely to include high performing species (a *selection effect*), or (ii) more diverse assemblages contain species with complementary functional traits that are not correlated or are correlated negatively among species, allowing them to function more efficiently (a *complementarity effect*) (20, 21). For aquatic animals, increased diversity enhances productivity of fish biomass (22) and also enhances temporal stability of biomass production and total yields

83 (22–24), providing economic and nutritional benefits to humans related to increased stability of
84 harvests and production of biomass for consumption (23). When considering aquatic species
85 from the perspective of human consumers however, functions other than biomass production
86 become relevant. In addition to providing an important source of calories and protein in the
87 human diet, seafood is increasingly recognized for its value in providing micronutrients, which
88 are often scarce in the human diet (25, 26) but critical for human health. Total seafood biomass
89 yields are not predictive of micronutrient benefits, suggesting that micronutrient content does not
90 increase proportionally with community biomass or total seafood intake (26).

91

92 Relationships between biodiversity (broadly defined to include abundance and biomass of
93 species) and ecosystem function have been extended to ecosystem services, which include the
94 cultural, economic or health benefits people derive from nature (5, 8, 27). Though there is clear
95 evidence that certain species, such as salmon, provide important ecosystem services to humans
96 (28), here we are interested in whether aquatic biodiversity *per se* (distinct from the identities
97 and abundance of species) provides ecosystem services in the form of human nutrition, beyond
98 total yields. For biodiversity *per se* (as opposed to increasing total seafood consumption) to
99 enhance nutritional benefits as predicted by biodiversity-ecosystem functioning theory,
100 micronutrient profiles must differ across species and their concentrations must be either
101 uncorrelated or negatively correlated (21). Specifically, a 'biodiversity effect' (sensu (21)) of
102 nutritional benefits requires that some seafood species contain high concentrations of some
103 micronutrients while other species contain high concentrations of different micronutrients (i.e.
104 nutrient concentrations are negatively correlated or uncorrelated across species), creating a
105 complementary distribution of micronutrients across species. In contrast, if key micronutrients

106 are positively correlated across species such that, for example, a species containing high amounts
107 of iron also has a calcium concentration, diversity in the diet would not be important. In the case
108 of positive correlations among micronutrients, the ecosystem service of nutritional benefits
109 would be enhanced by consuming more fish biomass or by selecting a few highly nutritious
110 species, rather than by biodiversity *per se*.

111

112 Differences in species' micronutrient content (29), if complementary and not positively
113 correlated across species, could lead to positive effects of seafood diversity for human nutritional
114 well-being. Furthermore, because micronutrient content does not appear to be correlated with
115 protein or calorie content (26), there is no reason to expect that a positive effect of diversity on
116 biomass or protein would imply a similar relationship between diversity and nutritional benefits.
117 We hypothesized that aquatic biodiversity leads to nutritional complementarity in human diets of
118 seafood, conferring potential benefits for humans via complementarity or selection effects, as
119 predicted by biodiversity-ecosystem functioning theory. We quantified these benefits using
120 recommended dietary allowance (RDA) indices, which are nutrient-based reference values that
121 indicate the average daily dietary intake level that is sufficient to meet the nutrient requirement
122 of nearly all (97 to 98 percent) healthy individuals in a particular life stage and gender group
123 (30). Here we used the RDA for females aged 19-50 (SI Appendix Table S1). We consider
124 nutritional benefits provided by seafood as how much nutrition is provided in a single standard
125 amount of seafood (such as a 100g portion of seafood). We ask whether consuming a more
126 diverse set of species actually increases the nutritional content of a potential seafood diet.
127 Though it is possible to consider alternative ways to increase seafood derived nutrition in a diet,
128 such as increasing total seafood biomass consumed or increasing consumption of certain species,

129 these approaches do not necessarily implicate biodiversity as an important element of the
130 ecosystem service. Furthermore, from an economic or cultural perspective, increasing total
131 seafood consumption is also not always feasible or desirable, especially if seafood is costly or
132 only forms a small part of meals.

133

134 We tested the hypothesis that aquatic biodiversity confers nutritional benefits through
135 complementarity in nutrient concentrations among species. We quantified nutritional benefits in
136 two ways: 1) the number of distinct nutritional needs met in a single 100g portion (referred to as
137 'nutritional diversity', N_D) and 2) the amount of seafood tissue required to meet a given
138 nutritional threshold (referred to as 'nutritional efficiency', N_E). We tested whether 1) aquatic
139 biodiversity enhances nutritional diversity (N_D) in potential seafood diets and 2) biodiversity
140 increases the nutritional content of an edible portion of seafood, thereby improving the efficiency
141 (N_E) with which seafood consumers reach nutritional targets (Fig 1). We predicted that increased
142 species richness (one measure of biodiversity) in potential seafood diets yields increased
143 nutritional benefits, and that variation in nutrient concentrations among species is related to
144 species' ecological traits. In a global analysis of 430 aquatic species, we considered provision of
145 nutritional benefits to human consumers accessing worldwide seafood markets. To assess the
146 extent to which the relationships between biodiversity and human nutrition benefits depend on
147 spatial scale (8), we tested whether seafood biodiversity is associated with higher nutritional
148 benefits at local scales in fourteen traditional indigenous seafood diets in North America. Fish is
149 critical for indigenous groups, who on average consume fish at a rate of 15 times higher than the
150 global average (31). We quantified variation in nutrient concentrations in edible tissues of 430
151 commonly consumed aquatic species in the global species pool, and 25 – 57 species in fourteen

local dietary species pools. We extend biodiversity-ecosystem functioning theory to a multivariate ecosystem service (32) that is defined from the perspective of the human beneficiary and is directly relevant to human health.

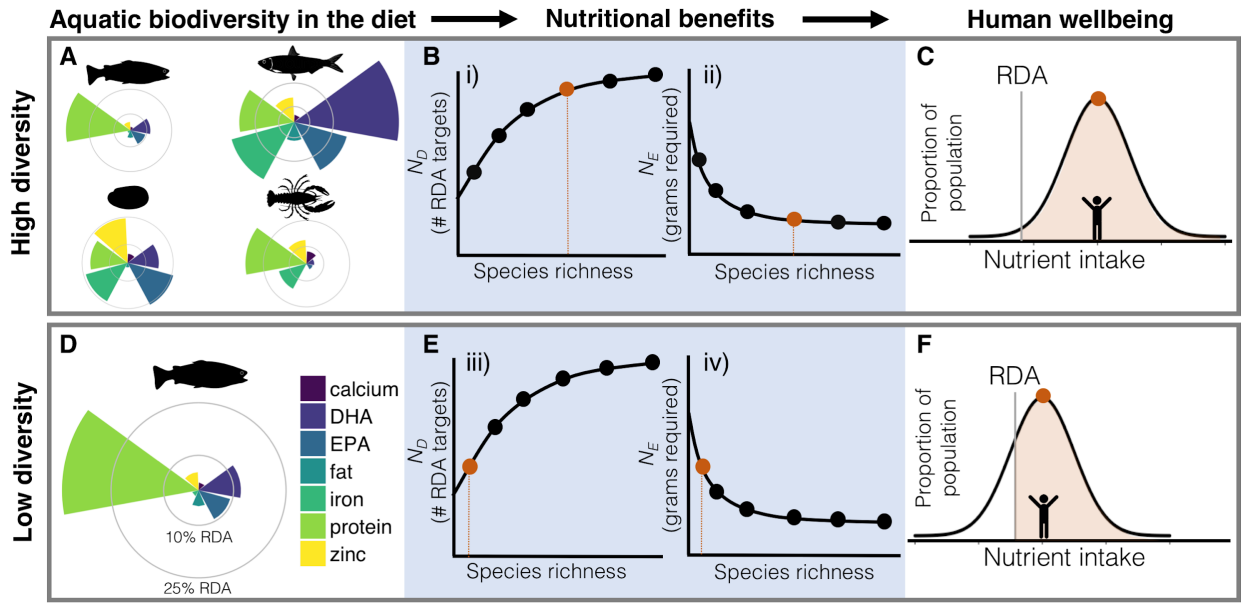

Fig 1. Aquatic biodiversity increases human well-being because edible species have distinct and complementary multi-nutrient profiles (A) and differ in mean micro- and macronutrient content (shown here relative to 10% and 25% thresholds of recommended dietary allowance (RDA) guidelines for representative finfish (*Abramis brama*, *Mullus surmuletus*), mollusc (*Mytilus galloprovincialis*) and crustacean species (*Nephrops norvegicus*). Biodiversity – ecosystem functioning theory predicts that nutritional benefits, including 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 RDA targets if diets are low in diversity (F vs C; orange shading indicates proportion of population that meets nutrient requirements). DHA: docosahexaenoic acid, EPA: eicosapentaenoic acid.

Results and Discussion

Biodiversity and nutritional benefits of edible aquatic species

171 We found that for a given amount of seafood, biodiversity not only enhances nutritional benefits
172 for consumers selecting seafood from our global species dataset, but that biodiversity *per se* is
173 essential to meeting nutritional targets. To assess the contribution of species diversity and traits
174 to the ecosystem service of promoting human well-being, we assessed species' protein, fat, and
175 micronutrient concentrations in edible tissues of a standard amount - 100g - relative to a measure
176 of requirements for these nutritional elements set by public health organizations - the
177 recommended dietary allowance (RDA) targets ((30); Methods). The global species pool was
178 highly diverse with regard to concentrations of the micronutrients iron, zinc, calcium, and two
179 fatty acids DHA and EPA in edible fish tissue relative to RDA targets for those micronutrients
180 (Fig 2; micronutrient geometric CVs: ln(iron) = 3.97, ln(calcium) = 3.25, ln(EPA) = 2.52,
181 ln(zinc) = 2.10, ln(DHA) = 1.70). There was very little diversity in species' protein
182 concentrations relative to RDA targets (Fig 2; ln(protein) geometric coefficient of variation
183 (geometric CV) = 0.03). Most species did not meet a single micronutrient RDA threshold: when
184 we considered each micronutrient separately we found that fewer than half of the 430 species
185 reached a single-nutrient threshold of 10% of the daily RDA target (30) for calcium, iron and the
186 essential fatty acid EPA in a standard 100g portion of a single species (Table S2).
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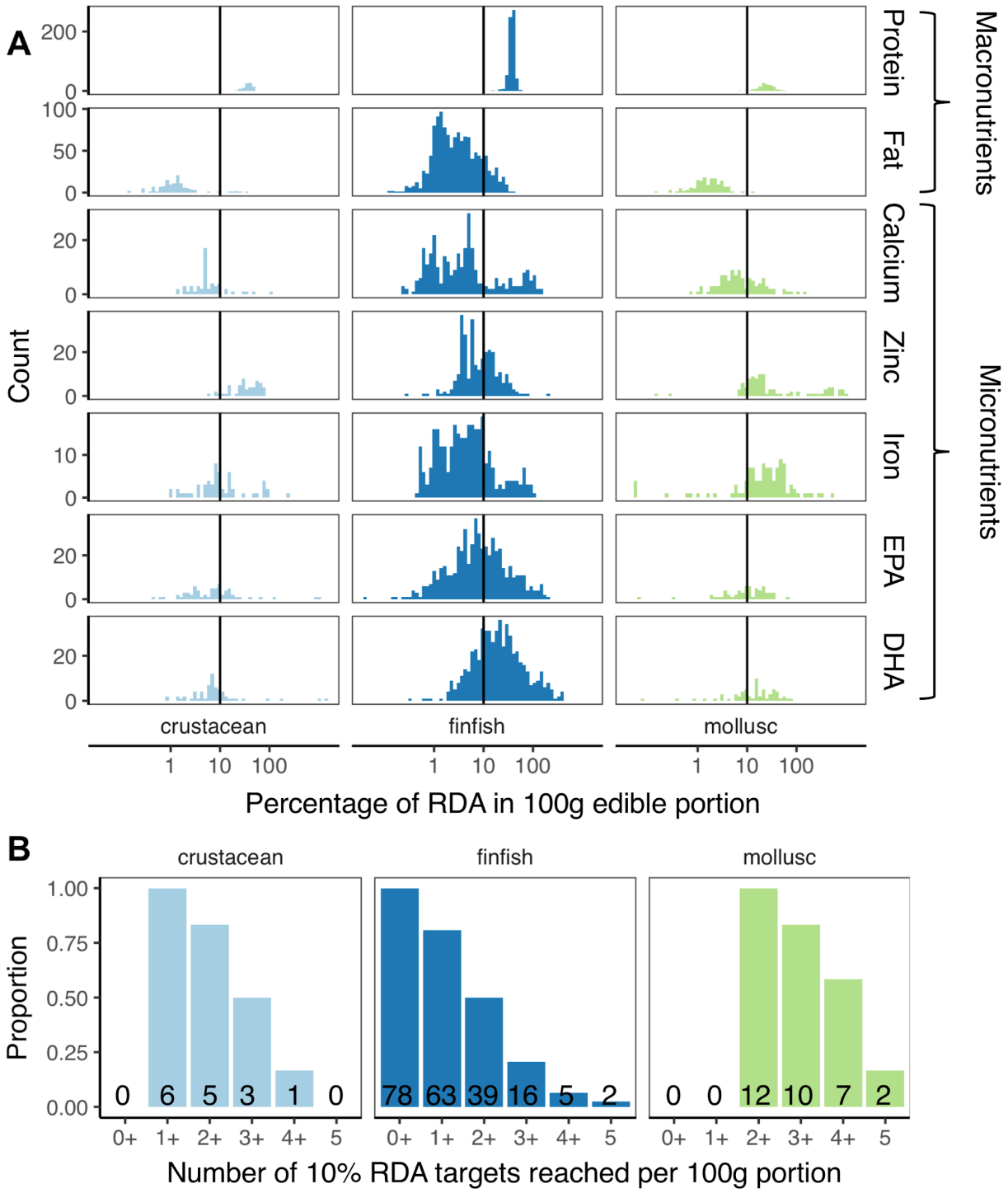

Fig 2. Variation in nutrient concentrations differs among taxonomic groups. (A) Frequency of reported protein, fat and micronutrient (including eicosapentaenoic acid (EPA), docosahexaenoic acid (DHA)) content in 100 g of the edible portion of 430 seafood species (references in Dataset S1). (B) Proportion 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.

195 ***Nutritional traits covary with ecological traits***

196 Substantial variation in nutrient concentrations in edible portions among species can be
197 explained partly by major ecological attributes and traits: taxonomic group, latitude, body size,
198 diet breadth and feeding habits (Tables S3-S7). Finfish, crustaceans and molluscs differed
199 significantly in their multi-nutrient profiles (PERMANOVA, $F_{2,103} = 3.429$, $p = 0.006$). Among
200 finfish, concentrations of calcium, iron and zinc in edible tissue decreased with increasing body
201 size (Fig 3, negative slopes, $p < 0.05$). Variation in protein and fat was poorly explained by
202 species' ecological traits ($R^2 = 0.023$, 0.09, for protein and fat). In addition to ecological traits,
203 finfish species that are eaten whole, or whose edible portions include organs such as skin, liver or
204 bones, have higher nutrient concentrations in the edible portion than those whose edible portions
205 are restricted to muscle tissue ($R^2 = 0.60$, $F_{5, 251} = 76.24$, $p < 0.01$; Fig S3). Nutrient
206 concentrations were typically weakly negatively correlated or uncorrelated with each other
207 among species (Fig S4), allowing complementarity among species to increase nutritional
208 benefits.

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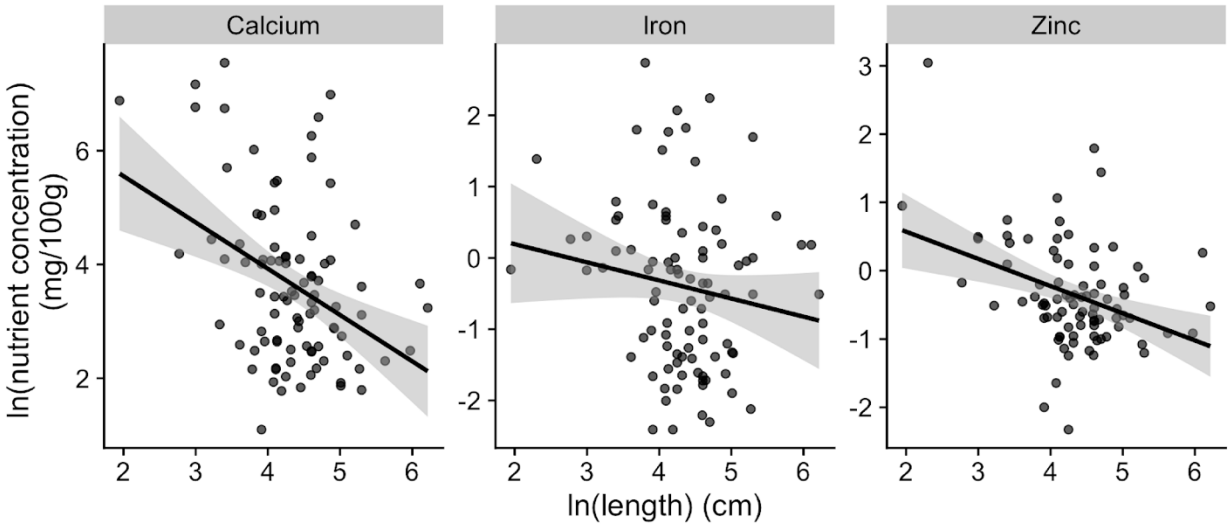

Fig 3. Micronutrient concentrations are significantly negatively related to body size (length, cm) in finfish. Negative slopes from phylogenetic least squares: calcium: -0.63 (95% CI -0.94, -0.33, n = 89), iron: -0.31 (95% CI -0.61, -0.0075, n = 92), zinc: -0.33 (95% CI -0.52, -0.13, n = 86).

Aquatic biodiversity effects on nutritional benefits to humans

To quantify the effect of biodiversity on nutritional benefits, we first quantified the amount of seafood, in grams, that would be required to reach a given nutrient intake target (10% of RDA, Table S1) at each of ten levels of species richness (nutritional efficiency, $N_{E,}$ for which lower values signify higher nutrition benefits to consumers). We then estimated the biodiversity effect using Equation 1, in which b_E is the scaling coefficient that describes how function (i.e. N_E) varies with species richness. As species richness increased in potential diets, 10% RDA for any micronutrient was achieved with less total seafood intake (Fig 4A, $b_E < 0$ 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)). This indicates that increasing species richness enhanced nutritional efficiency (N_E) in our sample diets, independent of any changes in the identity of species included, since the diets were assembled using a random sample of the species pool. All species reached the 10% protein RDA

target, so that there was no benefit of seafood diversity for protein (Fig 4A, b_E = 0.0092 95% CI 0.0086, 0.010). In other words, the ecosystem service of protein provision to diets is adequately provided by seafood edible biomass, and not by diversity or even species identity.

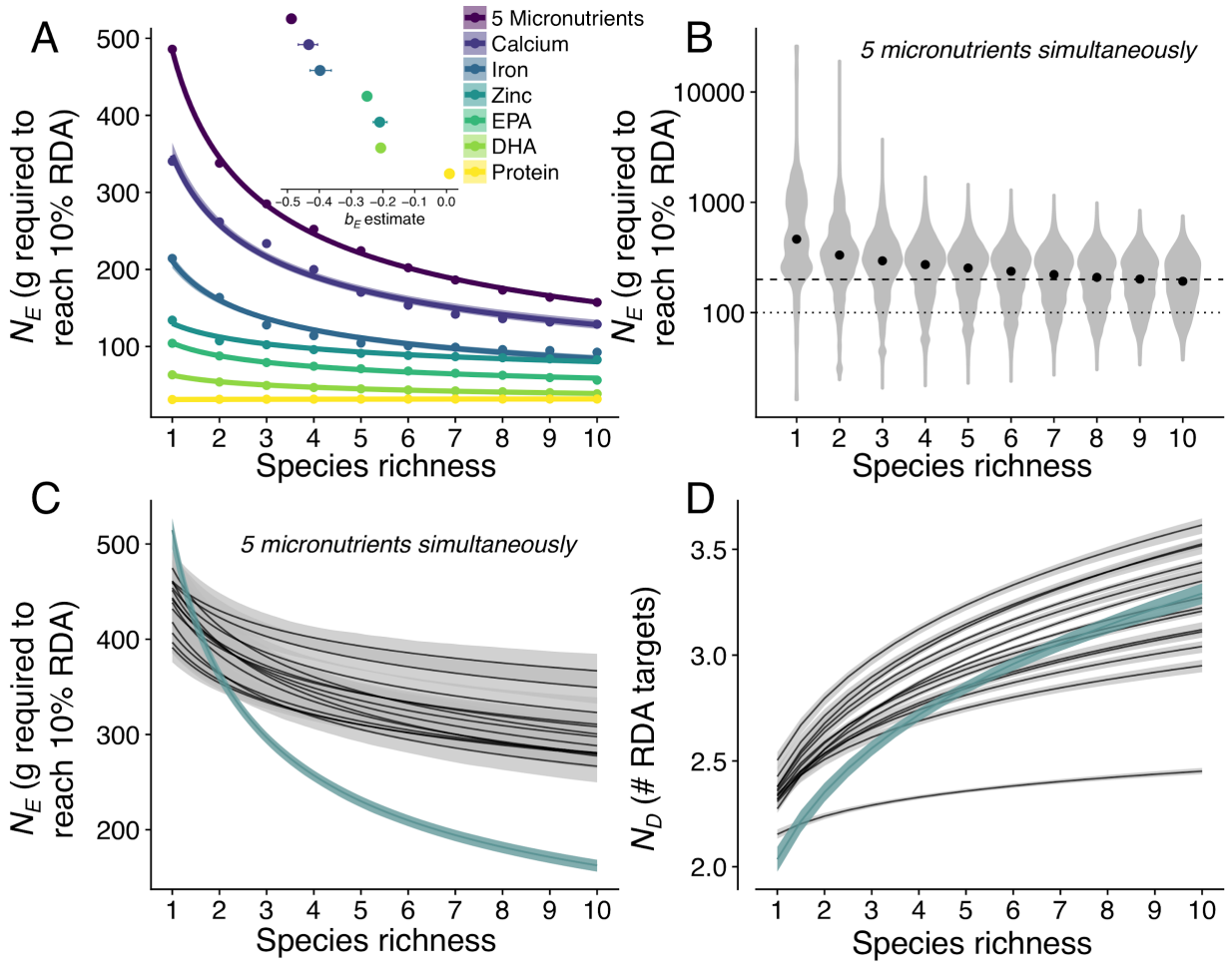

Fig 4. Aquatic biodiversity enhances nutritional benefits at global and local scales. A) Seafood species richness improves the efficiency with which human diets can meet 10% of RDA by reducing the grams of seafood required to meet nutritional thresholds. Nutritional efficiency (N_E) is shown for five 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

244 increases the efficiency with which five micronutrient nutritional targets are reached at local and
245 global scales; shaded areas are 95% confidence intervals about the mean; black lines are the fit of
246 Equation 1 for each of fourteen traditional indigenous diets in North America, green line is for a
247 diet sourced from the global seafood market. D) Species richness increases the number of
248 distinct RDA targets met in a 100g seafood portion (nutritional diversity, N_D) in local and global
249 seafood diets; lines are the fit of Equation 2, color coding as in C.

250

251 ***Multi-functional biodiversity benefits of aquatic species***

252 We then considered the effects of seafood species richness on the provisioning of multiple
253 nutrients simultaneously. This is referred to as a multifunctional benefit of biodiversity (32–34),
254 and takes into account possible trade-offs or correlations among functions, in this case,
255 concentrations of micronutrients. For some ecosystem services (e.g. water quality or
256 ecotourism), benefits of biodiversity accumulate when multiple ecosystem functions are
257 considered simultaneously (32, 35, 36). We treated each micronutrient concentration (relative to
258 10% RDA for that micronutrient, Table S1) as one ecosystem function. Consistent with
259 biodiversity-ecosystem functioning theory (37), we found that in the case of a multifunctional
260 metric of an ecosystem service defined from the human perspective (i.e. multiple micronutrient
261 targets reached simultaneously), biodiversity benefits for the multifunctional service are greater
262 than for individual functions (b_E for all five micronutrients simultaneously = -0.49 (95% CI -
263 0.50, -0.48) vs. single nutrients b_E range from -0.43 (95% CI -0.47, -0.40) for calcium to -0.21
264 for EPA (95% CI -0.21, -0.20)) that comprise the ecosystem service (Fig 4A). Increasing species
265 diversity from one to five species in 1000 simulated, resampled hypothetical diets drawing from
266 our global species pool allowed consumers to meet 10% of RDA for five essential microelements
267 and fatty acids simultaneously more than twice as efficiently (i.e. a median of 485.83g of tissue
268 required with one species vs. median of 216.96g of tissue required with five species) (Fig 4B, C).
269 Then, we assessed the effects of biodiversity when the total seafood biomass is held constant, at

100g, by counting the number of distinct RDA thresholds in a 100g portion (N_D). We also found positive effects of biodiversity on the number of distinct nutritional functions (10% of RDA reached) in a single 100g portion (Fig 4D): more diverse diets reached more nutritional targets (higher N_D) per 100g serving than diets of the same fish biomass comprising fewer species (b_D = 0.21 (95% CI: 0.18-0.24) Fig 4D). These results 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.

Our analysis provides new and 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 (37), but rather a statistical artifact of how multifunctionality was commonly estimated. Our findings are robust to multiple RDA threshold levels (Fig S1), and the biodiversity effect is strongest at a threshold of approximately 28% of RDA (Fig S1). In this case, the positive effects of biodiversity are greatest at levels of nutritional benefit that are significant for human nutrition, highlighting the importance of species diversity in seafood diets. More generally, ecosystem service benefits, as defined in metrics of human wellbeing 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 (32). 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 (38), or desired pest consumption rates in agricultural systems (39).

293 ***Biodiversity benefits are consistent from local to global scales***

294 Consistent with the positive biodiversity effects we observed when assuming consumers have
295 access to global seafood markets, we also found benefits of seafood diversity in a local context.
296 We analyzed the effects of biodiversity in fourteen traditional indigenous North American diets
297 of seafood harvested locally, and found a consistent, positive effect of biodiversity on N_D and N_E,
298 although the magnitude of the biodiversity effect was generally lower at the local scale than the
299 global scale (Fig 4C-D, Fig S2, S5) (global b_D = 0.21 (95% CI 0.18, 0.24) vs mean local b_D =
300 0.14 ± 0.0083 S.E. and global b_E = -0.50 (95% CI -0.52, -0.47) vs mean local b_E = -0.16 ± 0.0091
301 S.E.). This finding is consistent with lower nutritional functional diversity (mean local *FD* = 2.77
302 ± 0.17 S.E. vs. global *FD* = 3.87 ± 0.0096 S.E.) and higher nutritional functional evenness in
303 local diets (mean local *FEve* = 0.76 ± 0.01 S.E. vs. global *FEve* = 0.71 ± 0.0018 S.E.) (Fig S2,
304 S5), suggesting that functional consequences of changes to diversity in local seafood diets may
305 be buffered by higher redundancy among species. Given increasing trends towards
306 homogenization of the global food supply (40) including aquaculture (41, 42), this local-scale
307 finding highlights the importance of local species diversity in the diets of vulnerable populations
308 (26).

309

310 ***Potential benefits of aquatic biodiversity for human well being***

311 The problem of 'hidden hunger', in which people have access to sufficient calories but
312 insufficient essential micronutrients, is becoming increasingly recognized as a major contributor
313 to the burden of disease in developing countries (43, 44). Indeed, more than two billion people
314 suffer from micronutrient deficiencies, and it is the aim of the United Nations Sustainable
315 Development Goals (SDGs) to end all forms of malnutrition (44). Micronutrients in fish lead to a

316 variety of health benefits, including lowered risk of cardiovascular disease, improved maternal
317 health and pregnancy outcomes, increased early childhood physical and cognitive development.
318 Polyunsaturated fatty acids such as EPA and DHA are important for cardiovascular and brain
319 health. The amount of seafood in the human diet is often limited, either by costs or because
320 traditionally harvested species are being replaced by other 'junk foods' (45). In light of this, we
321 have focused here on the nutritional benefits potentially provided by seafood biodiversity over
322 and above the services provided by consuming seafood in general, and by consuming particular
323 highly nutritious species. Seafood consumption is influenced by many factors including cultural
324 preferences, social status, and economic pressures, none of which are considered here. Still, our
325 study adds to our knowledge of seafood and nutrition by quantifying the contribution of
326 biodiversity *per se* to meeting nutritional needs, and this biodiversity effect occurs in addition to
327 how diversity enhances and stabilizes total yields (22). This finding bridges the growing
328 understanding of hidden hunger and food security with the large theoretical and empirical
329 understanding of relationships between biodiversity, ecosystem function and benefits to people.

330

331 ***Aquatic biodiversity and food security in a changing world***

332 Maintaining the diversity of global fisheries is important for ensuring food and nutrition security.
333 A diverse seafood species pool feeds not only local communities but also seafood markets
334 worldwide, and aquatic species contain micronutrients not found in other foods. Many of the
335 most nutritionally vulnerable populations – those that are deficient in essential micronutrients
336 during particularly sensitive stages of life (i.e. pregnancy, breastfeeding and childhood) may rely
337 on local ecosystems to meet their nutritional demands (2, 25, 29). These populations may have
338 access to a limited amount of locally available fish tissue each day or to fish from a subset of

339 habitat types, suggesting that for these populations nutritional efficiency may be particularly
340 important. In tropical regions, fish diversity in coastal regions has plummeted in recent decades
341 (46) characterized by two-fold declines in body sizes of fish (47, 48). These regions are also
342 regions of high nutritional vulnerability and reliance on locally harvested seafood (49). However,
343 as the seafood trade becomes increasingly global (50, 51), seafood-derived nutrition available to
344 consumers participating in the global market may be related to globally harvested seafood
345 biodiversity. As a result, changes to local biodiversity and resultant impacts on human nutrition
346 may be buffered by access to global seafood markets. Together, our results suggest that in the
347 context of global change, understanding and protecting the potential for nature to support diverse
348 and productive aquatic ecosystems has direct and immediate benefits to humanity.

349

350 Conclusions

351 Nutritional diversity appears to be derived from ecological diversity, suggesting links between
352 the complexity of aquatic ecosystems and their capacity to produce nutritional benefits. While
353 the role of seafood is well recognized as an important source of protein in the human diet, the
354 role of seafood as a source of essential micronutrients is often overlooked. This study provides
355 the first global assessment of patterns in the macro- and micronutrient content of aquatic species.
356 Our results reveal that not all fish species are equally nutritionally valuable to humans and that
357 aspects of ecological structure, including species and trait diversity enhance nutritional diversity,
358 thereby linking the processes that structure ecosystems with the benefits they provide.

359 **Methods**

360 *Quantifying nutritional value in terms of human health benefits*

361 We characterized an aquatic species' nutritional profile by drawing on two well-established
362 nutritional metrics: nutrient concentration (nutrient content/100g edible portion) and
363 Recommended Dietary Allowances (RDA). RDAs are developed following health guidelines,
364 and quantify the recommended amount of a particular nutrient required to maintain health (30).
365 The RDAs used here were established by the Food and Nutrition Board of the United States
366 Institute of Medicine, and quantify the daily intake level of a nutrient needed to meet the
367 requirements of 97–98% of healthy adults (females aged 19-50) (30). We defined the nutritional
368 value of a fish species for each nutrient in terms of the nutrient content in an edible portion
369 relative to the RDA for that nutrient. For some aquatic species, micronutrients are in such high
370 concentrations in edible tissues that a single 100g portion contains the entire RDA for that
371 nutrient, while edible tissues from other species provide only small fractions of the RDA. We
372 considered thresholds of nutritional benefit (function) between 1% and 100% of the RDA,
373 although we focus on 10% of RDA since it is a minimum threshold for a food to be considered
374 of nutritional benefit (30). We defined an RDA target as 10% of RDA for a given nutrient. We
375 characterized nutritional profiles in two ways: first, in terms of concentrations of each nutrient
376 (single nutrient profile), and secondly, in terms of multiple nutrients simultaneously (i.e. multi-
377 nutrient profile).

378

379

380 *Defining nutritional benefits*

381 We quantified the effect of biodiversity on nutritional benefits in two ways (Fig 1): 1) nutritional
382 efficiency, N_E, which quantifies the amount of tissue, in grams, required to reach a given number
383 of RDA targets for different nutrients simultaneously and 2) nutritional diversity, N_D, which
384 quantifies the number of distinct RDA thresholds for different nutrients met in a standard 100g
385 edible portion. Nutritional benefit increases with decreasing values of N_E, since N_E quantifies the
386 grams required to reach RDA targets, and fewer grams required is better from the perspective of
387 human nutrition. We quantified N_D in an arbitrary daily diet, assuming that the seafood diet
388 contains 100g of seafood per day.

389

390 *Literature search and data collection*

391 We assembled a dataset of published nutrient concentrations in edible portions of 430 aquatic
392 species. We analyzed tissue concentrations of nutrients for which RDA standards exist and that
393 are implicated in a range of biologically important processes that affect organismal growth and
394 reproduction, and therefore may potentially relate ecological function with human nutritional
395 wellbeing. We examined macronutrients including protein and fat, as well as five micronutrients:
396 metals beneficial at low concentrations but toxic at high concentrations (zinc and iron), one
397 beneficial mineral (calcium) and the polyunsaturated fatty acids eicosapentaenoic acid (EPA)
398 and docosahexaenoic acid (DHA). We aimed to include as many marine and freshwater species
399 as possible covering a wide geographic extent. We searched peer-reviewed literature for
400 analytical food composition values as well as the Food and Agriculture Organization's Global
401 Food Composition Database for Fish and Shellfish (52). For finfish, we restricted our analysis to
402 include only edible portions of wild, raw fish (excluding prepared or farmed seafood items). We

403 included both farmed and wild mollusc species because mollusc farming does not typically
404 involve additional food inputs, which could influence tissue nutrient composition. For each
405 species, we noted which body parts are included in the edible portion and season of collection.
406 For each sample, we noted the location of origin (e.g. latitude and longitude). To address
407 inconsistencies in fatty acid data reporting, we standardized fatty acid measurements using the
408 fatty acid conversion factors proposed by Nowak et al. 2014 (53). When there were multiple
409 observations available for a single species, we averaged nutrient concentrations across the
410 observations. We did not include data from national food composition tables because these data
411 usually report seafood data with a generic food description, which does not allow for a clear
412 description of which fish tissues are included in the edible portion. For each species with
413 nutritional data, we collected ecological trait information from FishBase (54) and SeaLifeBase
414 (55). We included body size (maximum length), fractional trophic position, temperature
415 preference (using latitude as a proxy), diet breadth and feeding mode.

416

417 *Statistical analyses and hypothesis testing*

418 **Hypothesis 1: Biodiversity enhances nutritional benefits**

419 We tested the effect of species diversity (quantified as the number of species, or species richness,
420 *S*), on nutritional diversity and efficiency by randomly assembling diets from the global seafood
421 species pool, keeping the portion size constant (100 grams) across all levels of diversity. In
422 analyses using the global dataset (430 species), we assumed that human populations have access
423 to the entire global species pool and choose species at random. Though this assumption certainly
424 ignores economic, social and cultural factors that affect which species people consume, in the
425 absence of detailed diet information for the majority of the world's populations this is a

426 necessary assumption. To assess potential effects of biodiversity on nutritional benefits for
427 populations that consume seafood locally and not as part of the global seafood market, we
428 sampled diets from species contained within traditional diets in fourteen indigenous cultures in
429 North America. We used species lists for local diets that were obtained from an ethnographic
430 database of traditional animal foods of indigenous peoples of northern North America, and only
431 included species that were harvested wild and whose nutrient compositions were analyzed when
432 raw (Table S7, (56)). To avoid confounding differences in biodiversity effects at global and local
433 scales with the sizes of the species pools at each of these scales, we matched the size of the
434 global species pool to the average size of the local species pools (40 species).

435

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

438

439 1) Nutritional efficiency (N_E). We tested the hypothesis that complementarity in nutrient
440 concentrations among species enhances N_E by estimating the effect of species richness on N_E (the
441 'biodiversity effect'). To estimate the 'biodiversity effect' on N_E, we took an approach to
442 modeling dietary species composition that is analogous to a biodiversity-ecosystem function
443 experiment with a replacement design, where species abundances decline proportionally as
444 species richness increases. From the global species pool, we sampled ten species at random and
445 then assembled seafood diets from all possible combinations of these ten randomly chosen
446 species at 10 levels of species richness (1-10). We repeated this process of sampling ten species
447 from the global species pool and then assembling all possible diets 1000 times. For each
448 combination of species in each dietary diversity level (1-10 species), we calculated the number

449 of grams required to reach a given RDA target (either: one of six possible nutrient targets
450 individually, or five micronutrient (calcium, iron, zinc, EPA and DHA) targets simultaneously).
451 We quantified the effect of species richness in a diet on nutritional efficiency, N_E, by fitting a
452 power function to these bootstrapped nutritional efficiency estimates:
453

454 $$N_E = aS^{b_E} \quad (1)$$

455 where the parameter b_E describes the relationship between a change in species richness, S, and a
456 change in N_E, and a is a constant (in units of grams). Since N_E is measured in grams required to
457 reach a given RDA target, and fewer grams required is better from the perspective of human
458 nutrition, then a benefit of biodiversity would be reflected in a negative b_E (i.e. N_E, measured in
459 grams of tissue required, decreases with species richness). For each nutrient individually, and for
460 all five micronutrients together, we estimated the exponent parameter, b_E, using non-linear
461 regression using the *nls.LM* function in the *minpack.lm* package in R (57). To quantify
462 uncertainty in parameter estimates associated with sampling from the pool of observed nutrient
463 content values, we calculated bootstrapped confidence intervals using non-parametric
464 bootstrapping of mean centered-residuals using the *nlsBoot* function in the R package *nlstools*
465 (58).
466

467 2) Nutritional diversity (N_D). To test the hypothesis that complementarity in nutrient
468 concentrations among species increases nutritional benefits by increasing the number of distinct
469 RDA targets in a 100g portion, we constructed recommended dietary allowance (RDA) target
470 accumulation curves. These are analogous to species accumulation curves used in ecological
471 studies to assess patterns of beta-diversity, or species turnover, in ecological community

472 composition data. We assessed turnover of nutrients content in edible tissues among fish species.
473 Each fish species is associated with a set of 0s and 1s corresponding to whether or not it achieves
474 10% of RDA for each of five micronutrients (equivalent to a species presence-absence matrix in
475 community composition data), sampled with replacement 1000 times. This approach allowed us
476 to explore how likely it would be for human diets containing different numbers of fish species to
477 reach a given number of micronutrient RDA targets (N_D ranges between 0 and 5), assuming that
478 fish species were included in the human diet at random. We quantified the effect of biodiversity
479 on nutritional diversity, N_D, by fitting a power function,
480
481 $$N_D = aS^{b_D} \quad (2)$$
482 where the parameter b_D describes the relationship between a change in species richness, S, and a
483 change in N_D (i.e. the number of RDA targets reached per average 100g portion), and a is a
484 constant.
485
486 For both N_E and N_D, we tested the hypothesis that biodiversity enhances nutritional benefits by
487 assessing whether the estimate of the scaling exponent, b, had confidence intervals not
488 overlapping zero. We concluded that biodiversity enhanced nutritional benefits if b_E was
489 negative and b_D was positive.
490
491 We tested the hypothesis that nutritional functional diversity drives positive biodiversity effects
492 by testing for a positive association between nutritional functional diversity and the biodiversity
493 scaling exponent, b. We hypothesized that nutritional functional diversity would be higher at the

494 global scale than the local scale, because the global species pool contains more ecological and
495 biogeographic diversity. To assess levels of nutritional functional diversity among species, we
496 calculated functional diversity (*FD*) (59). *FD* is based on an assessment of the entire functional
497 diversity of a group represented as a functional dendrogram, and *FD* allows estimation of
498 complementarity among species' nutrient concentrations (i.e. nutritional functional traits) using
499 the dendrogram. We treated the concentration of each micronutrient (calcium, iron, zinc, EPA
500 and DHA) as a functional trait. We also quantified functional evenness metric (*FEve*) using the
501 *FD* package in R, which normally quantifies the evenness of abundance in a functional trait
502 space. Here, we used *FEve* to quantify the evenness in concentration of nutrients across species
503 (60). To compare *FD* and *FEve* at the global and local scales, we first subsampled 40 species
504 (the average species pool at the local scale) from the global pool, then calculated the functional
505 diversity metrics on the subsample, and repeated this process 1000 times. Using this same
506 approach, we calculated levels of 'expected' *FD* and *FEve* for each local diet by choosing
507 random subsets of the global pool with sample size equal to the species pool in each local diet,
508 and repeated this process 1000 times (Fig S5).

509

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

512

513 We tested the hypothesis that nutrient concentrations are related to species' ecological traits in
514 two ways: 1) testing whether multi-nutrient profiles (i.e. concentrations of all five
515 micronutrients) differ among major phylogenetic groups and 2) whether differences in single
516 nutrient concentrations differ with species ecological traits. We examined variation in multi-

517 nutrient profiles among seafood species using the *vegan* package in R (61). We ln transformed
518 nutrient concentration data to achieve normality. Differences in multi-nutrient profiles were
519 visualized through non-metric dimensional scaling (NMDS) using the *metaMDS* function. The
520 ordination ran for 1000 iterations, and the stress score of 0.032 for the final solution was
521 sufficiently low to enable reliable interpretation in the two dimensions (62). First, we tested the
522 hypothesis that major phylogenetic groups correlated with functional differences in life history,
523 resource use and ecology (i.e. finfish, mollusc, and crustacean) differ in their multi-nutrient
524 profiles via permutational multivariate ANOVA (PERMANOVA) using the *adonis* function (999
525 permutations) based on Bray-Curtis dissimilarity matrices. We used an overall (three-way)
526 PERMANOVA first to investigate phylogenetic group effects on nutrient profile of a species'
527 edible tissue.

528

529 To test for associations between species' ecological functional traits and their nutrient
530 concentrations, we modeled the relationship between traits and ln(nutrient concentration) with
531 phylogenetic least squares regression (PGLS). The full model included the entire set of trait
532 predictors as fixed effects:

533

534 $ln(nutrient) = \beta_0 + \beta_1 \times ln(body\ size) + \beta_2 \times latitude + \beta_3 \times trophic\ position + \beta_4 \times feeding\ mode +$
535 $\beta_5 \times diet\ breadth + \varepsilon$

536

537 Unlike in ordinary least squares (OLS), which assumes there is no covariance structure in the
538 error term, ε, (all species are independent from one another, and residuals from closely related
539 species are not more similar on average than residuals from distantly related species), PGLS

540 assumes that the residuals are non-independent, and that the expected covariance is related to the
541 shared evolutionary history between the species. To assess whether the relationships between
542 species' traits and their nutritional profiles were associated, we fit multiple regression models
543 using PGLS using the *gls* function in the *nlme* package in R using the Brownian motion model of
544 evolution. This approach allowed us to account for phylogenetic non-independence by using
545 shared ancestry as weights on the elements of the residual variance-covariance matrix used in the
546 model. We created a supertree by combining phylogenies that included the species of finfish,
547 molluscs and crustaceans in our nutrient dataset using the *rotl* package in R (63), which is an
548 interface to the Open Tree of Life (64). We computed branch lengths according to taxonomic
549 depth (65) using the *compute.brlen* function in the *ape* package in R (66).

550

551 We created models from subsets of the full model that represented hypotheses based on the
552 known physiological roles of micronutrients and their relationships to our set of predictors
553 (Tables S3-S7, S10). To avoid issues associated with multicollinearity of predictor variables, we
554 excluded other possible variables if they were highly correlated (i.e. correlation coefficient >
555 0.6). We identified the best subset of models using the Akaike Information Criterion, adjusted
556 for small sample sizes (AICc). We used AICc, ∂aic and Akaike weights (w) to compare models.
557 We ranked models based on w, and selected the set of models that produced a cumulative w >
558 0.95, meaning that we are 95% confident that the chosen set includes the best model (67). In
559 cases where we could not obtain measurements of all traits for all species, we performed model
560 selection on reduced datasets without missing values.

561

562 To account for model uncertainty in the ecological trait correlation analyses, we performed
563 model averaging of coefficients in all models that produced a cumulative $w > 0.95$, and included
564 zeros as coefficients when variables did not enter a given model (67). We conducted our model
565 selection and averaging analyses with the *MuMIn* package (68) and all other analyses in R
566 version 3.3.2 (69).

567

568 *Uncertainties:*

569 There are several sources of uncertainty in our analyses. First, there are substantial sources of
570 uncertainty in food composition estimates. The data in our dataset meet international standards
571 for data quality and standardization, meaning that we followed guidelines for checking food
572 composition data and converting units, denominators and expressions (70). Still, tissue
573 concentrations may vary depending on analytical techniques, labs, season, diet of the animal, life
574 stage etc. Some of these sources of uncertainty (e.g. differences in analytical techniques) are
575 unavoidable consequences of synthesizing previously published data collected across many labs.
576 We assumed that these uncertainties in the data were randomly distributed over our
577 geographically and taxonomically diverse dataset. Further uncertainty is associated with how
578 well our set of 430 species represents the global pool of seafood consumed. We do not know
579 whether our sample is random or biased, though we can say that our dataset includes 41 of the 67
580 most consumed species worldwide (as determined by FAO production volumes (71), species
581 with capture production of 150 000 tonnes or more, after removing species for which the
582 majority of production volume is diverted to fish meal and oil (72), Table S9). A remaining
583 source of variation among samples is likely due to natural sources of variation associated with

584 seasonal and other sources of temporal variability, which we consider to be an important

585 component of biodiversity.

586

Acknowledgments: We thank P. Thompson, A. Gehman, W. Cheung, M. Ruckelshaus and C. Harley and M. Deith for helpful comments on previous versions of this manuscript.

Funding: Funding was provided by a Vanier Canada Graduate Scholarship to JRB.

Competing interests: We declare no competing interests.

Data and materials availability: All data and code will be archived at the Dryad digital repository.

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743

744

745 **Figure legends**

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

756

757 **Fig 2.** Variation in nutrient concentrations differs among taxonomic groups. (A) Frequency of
758 reported protein, fat and micronutrient (including eicosapentaenoic acid (EPA), docosahexaenoic
759 acid (DHA)) content in 100 g of the edible portion of 430 seafood species (references in Dataset
760 S1). (B) Proportion of species, and number shown on each bar, with available data that reach
761 10% of RDI targets for any one, two or up to five of the micronutrients examined here.

762

763 **Fig 3.** Micronutrient concentrations are significantly negatively related to body size (length, cm)
764 in finfish. Negative slopes from phylogenetic least squares: calcium: -0.63 (95% CI -0.94, -0.33,
765 n = 89), iron: -0.31 (95% CI -0.61, -0.0075, n = 92), zinc: -0.33 (95% CI -0.52, -0.13, n = 86).

766

767 **Fig 4**. Aquatic biodiversity enhances nutritional benefits at global and local scales. A) Seafood
768 species richness improves the efficiency with which human diets can meet 10% of RDA by
769 reducing the grams of seafood required to meet nutritional thresholds. Nutritional efficiency (N_E)
770 is shown for five micronutrients and protein separately (points are median values for calcium,
771 iron, zinc, EPA, DHA and protein, lines show the fit of Equation 1 to the data and shading refers
772 to 95% CI) as well as for five micronutrients simultaneously (purple line labeled '5
773 Micronutrients'); estimates for the b_E parameter (± standard error, inset) describe the strength of
774 the biodiversity effect. B) Increasing dietary species richness sourced from global seafood
775 markets increases the efficiency with which five micronutrient nutritional targets are reached;
776 solid circles are median values, as plotted in the purple line in A. C) Increasing species richness
777 increases the efficiency with which five micronutrient nutritional targets are reached at local and
778 global scales; shaded areas are 95% confidence intervals about the mean; black lines are the fit of
779 Equation 1 for each of fourteen traditional indigenous diets in North America, green line is for a
780 diet sourced from the global seafood market. D) Species richness increases the number of
781 distinct RDA targets met in a 100g seafood portion (nutritional diversity, N_D) in local and global
782 seafood diets; lines are the fit of Equation 2, color coding as in C.
783
784