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Predicting nutrient content of ray-finned fishes using phylogenetic information

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Human food and nutrition security is dependent on marine ecosystems threatened by overfishing, climate change, and other processes. The consequences on human nutritional status are uncertain, in part because current methods of analyzing fish nutrient content are expensive. Here, we evaluate the possibility of predicting nutrient content of ray-finned fishes using existing phylogenetic and life history information. We focus on nutrients for which fish are important sources: protein, total fat, omega-3 and omega-6 fatty acids, iron, zinc, vitamin A, vitamin B12, and vitamin D. Our results show that life history traits are weak predictors of species nutrient content, but phylogenetic relatedness is associated with similar nutrient profiles. Further, we develop a method for predicting the nutrient content of 7500+ species based on phylogenetic relationships to species with known nutrient content. Our approach is a cost-effective means for estimating potential changes in human nutrient intake associated with altered access to ray-finned fishes.

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Human activity is rapidly transforming marine ecosystems worldwide. Total catch appears to be declining in fisheries around the world, largely due to intense industrial pressure¹. Climate change-driven increases in sea temperature threaten to alter the abundance and distribution of hundreds of economically and nutritionally important species^{2–5}, and are leading to mass coral bleaching⁶. Ocean acidification, caused by greater absorption of atmospheric carbon dioxide, is inflicting severe damage on biologically rich coral reef habitats⁷. Coastal development, pollution, and other anthropogenic forces are impacting nearly every marine ecosystem in the world⁸.

The consequences of these changes for human health, and especially for nutrient intake, are likely to be severe because fish provide critical nutrients essential to human nutrition, including iron, zinc, vitamin A, vitamin B12, omega-3 and omega-6 fatty acids, and others^{9–11}. In many societies, seafood is the foundation for healthy diets, and its decline presents a significant risk in destabilizing food and nutrition security¹². The consumption of fish is associated with a wide range of health benefits, including the prevention of various non-communicable diseases and the promotion of cognitive development^{13,14}. Ray-finned fish—the class *Actinopterygii*—are particularly important to low-income populations, comprising 80.6% of the total global tonnage of subsistence marine capture fish and seafood in 2010¹⁵.

A lack of information about the nutrient composition of fish species, however, hampers quantification of the nutritional threat to human populations of reduced consumption of wild-harvested fish. Measuring nutrient content is expensive and, as a result, nutrient analyses rarely capture the full breadth of vitamins, minerals, and macronutrients relevant to nutrition. This is exacerbated by the need to collect multiple samples of each species to assess variability across individuals, as well across sub-populations of species. This information gap prevents the design of rational fisheries management strategies and nutritional interventions to optimize public health outcomes in the face of rapidly changing marine conditions.

In this paper, we investigate the possibility that phylogenetic relatedness and life history information explain variation in the nutrient content of key fish species in the most commercially and nutritionally important class, *Actinopterygii* (ray-finned fishes). To our knowledge, this is the first time that such an approach has been explored. We then use the results of this analysis to develop a method for using shared phylogenetic history as a means of predicting the nutrient content of fish whose nutrient information has not yet been assessed. Such predictions are especially critical in regions of the world with known nutrient deficiencies—which are often the same areas where laboratory capacity is often limited. For fish specifically, recent years have seen an emerging desire among policymakers to design fisheries management and aquaculture development interventions with the specific goal of enhancing nutritional security. We note that these methods, if successful, could be used for a broad range of terrestrial animal and plant species as well—wild and domestic—as well as subspecies, varieties, and breeds.

Our results indicate that life history traits predict species nutrient content only weakly; larger datasets and/or use of missing-data imputation techniques may strengthen these models. We find, however, that phylogenetic relatedness is associated with similar nutrient profiles. This finding allows us to create a method for predicting the nutrient content of 7500+ *Actinopterygii* species based on phylogenetic relationships to species with known nutrient content.

Results

Interspecific variability in nutrient content and life history. We sourced nutrient content information for 371 species in the class

Actinopterygii (see Supplementary Table 1 for full list of species, and see Methods section and refs.^{16–28} for data sources). Supplementary Table 2 summarizes the number of species with data, as well as the observed range by nutrient. The dataset includes 26 orders, 126 families, and 279 genera; about 42% of species are in the order *Perciformes* (perch-like fishes). The set of 371 species represents over half of all global capture fisheries by weight, with all 22 of the world's most harvested marine fish species included²⁹.

We used life history traits and phylogenetic relatedness to predict protein, total fat, omega-3 and omega-6 fatty acids, iron, zinc, vitamin A, vitamin B12, and vitamin D content in *Actinopterygii*. These nutrients are critical for human nutrition and are generally present in relatively high concentrations in seafood—although, as we describe below, not all species are rich sources of the all the above nutrients. As predictors of nutrient content, we initially considered six continuous and two categorical life history traits describing body size, trophic level, habitat characteristics, and geographic range (Table 1).

Summaries of nutrient content across species indicate that ray-finned fishes make substantial contributions to human nutrition, particularly for low-income coastal populations (Supplementary Tables 2, 3). Of species with available information for a given nutrient, 98% are sources or rich sources of protein, 94% rich sources of vitamin D, and 81% rich sources of vitamin B12. In addition, 13% of species are either sources or rich sources of iron, 14% sources or rich sources of zinc, and 10% sources or rich sources of Vitamin A (see Supplementary Table 1 for data by species and threshold designations of source and rich source by nutrient).

We see a great deal of variation across ray-finned fish species for which we have nutrient information (Supplementary Table 3). In particular, the ranges of minimum and maximum depth, habitat preferences, and latitudinal range are especially wide. Nearly 40% of fish are demersal, but significant fractions are benthopelagic, pelagic, or reef-associated. The chosen set is divided roughly equally into tropical, subtropical, and temperate species. As calculated by trophic level, the mean *Actinopterygii* species in this dataset is a carnivore, and some are apex predators, but many species are also herbivores, zooplanktivores, detritivores, or omnivores.

Correlations among nutrients and life history variables. We first examined the relationship between nutrient content and life history variables by estimating evolutionary correlations (i.e., the correlations between evolutionary changes inferred using observations among species and their phylogenetic relationships; see Methods section). For this analysis (and all regression models described below), we used the ray-finned fish phylogeny reconstructed in Rabosky et al.³⁰. Due to sample size restrictions, we exclude omega-3 and omega-6 fatty acids from the correlation matrix below; however, correlations with fatty acids included are given in Supplementary Table 4.

We found the expected associations between pairs of life history variables (top left corner of Fig. 1, lightly shaded). Maximum depth, maximum fish length, and trophic level are moderately associated with each other, suggesting that larger fish tend to live at greater depths and consume a diet higher on the food chain. The *a* and *b* parameters describing species' mass-length scaling relationships are well-correlated to each other, but not to other life history traits.

Patterns are also apparent within the set of nutrients (bottom right corner of Fig. 1, darkly shaded). Fish with more protein tend to contain less Vitamin A and total fat. Fish that are high in total fat also tend to be good sources of Vitamins A, B12, and D. Fish high in iron also tend to be good sources of zinc and all included

Table 1 Nutrient and life history traits used in the analysis*

Nutrients	Description
Protein	"Serves as the major structural component of all cells of the body, and functions as enzymes, in membranes, as transport carriers, and as some hormones"
Total fat	"Energy source and, when found in foods, is a source of n-6 and n-3 polyunsaturated fatty acids"
Omega-6 polyunsaturated fatty acids (linoleic acid)	"Essential component of structural membrane lipids, involved with cell signaling, and precursor of eicosanoids. Required for normal skin function"
Omega-3 polyunsaturated fatty acids (α-linoleic acid)	"Involved with neurological development and growth. Precursor of eicosanoids"
Iron	"Component of hemoglobin and numerous enzymes; prevents microcytic hypochromic anemia"
Zinc	"Component of multiple enzymes and proteins; involved in the regulation of gene expression"
Vitamin A	"Required for normal vision, gene expression, reproduction, embryonic development and immune function"
Vitamin B12	"Coenzyme in nucleic acid metabolism; prevents megaloblastic anemia"
Vitamin D	"Maintains serum calcium and phosphorus concentrations, and, in turn, bone health"
Life history traits	
Maximum length	Largest value ever reported for a given species, in cm (may not correspond to maximum length for subpopulation)
Trophic level	Weighted mean of the trophic level of the organisms that form the diet of the species; primary producers are assigned a value of one
Habitat	Categorical; bathydemersal, benthopelagic, demersal, pelagic, pelagic-neritic, pelagic-oceanic, reef-associated
Latitudinal range	Categorical; tropical, subtropical, temperate, boreal/austral, polar
Minimum depth	Minimum distance (m) below sea surface where species generally live
Maximum depth	Maximum distance (m) below sea surface where species generally live
a length-weight parameter	Empirically determined scalar parameter of the function $W = aL^b$
b length-weight parameter	Empirically determined exponential parameter of the function $W = aL^b$

*Refs. 51–55. All nutrient function descriptions taken from National Academies (2017); see ref. 50 for more details. See FishBase glossary at www.fishbase.org for detailed descriptions of life history traits

vitamins. Vitamin A and Vitamin D are positively associated, and the latter is correlated with Vitamin B12. Overall, this set of correlations suggests that specific sets of nutrients tend to cluster together. Given that nutritional analyses, due to cost considerations, tend to focus on a small set of nutrients, such observed correlations may be important for roughly inferring levels of unmeasured nutrients.

Finally, we see that life history parameters, controlling for phylogeny, vary in their association to key nutrients (top right of Fig. 1, unshaded). Fish living at greater oceanic depths contain more total fat and Vitamin A, but less zinc. Longer fish contain proportionally less zinc and Vitamin B12, but more Vitamin A; smaller fish, often overlooked in conservation, livelihoods, and nutrition programs, may be richer sources of key micronutrients³¹.

These bivariate associations were tested in multiple regression models fit by phylogenetic least squares (PGLS) in a manner that accounts for phylogenetic signal in species residuals^{16,32–34}.

These phylogenetic regressions find that life history parameters are either insignificant predictors of nutrient content or have small effects (Table 2). Longer fish at higher trophic levels but closer to the surface contain more protein, although the coefficient magnitudes are relatively small: 100 cm greater length is associated with 0.69 g more protein; a one-unit higher trophic level is associated with 1.29 g more protein per 100 g of fish weight; and 100 meters greater (i.e., deeper) maximum depth is associated with 0.14 g less protein. Maximum depth is also a significant predictor for total fat, omega-3 and omega-6 fatty acids, and vitamin A, but regression coefficients are small in these cases as well. Other relationships are insignificant. Overall, regression models suggest that life history variables are generally poor predictors of fish nutrient content when accounting for phylogenetic dependence in the data.

Predicting nutrient content of unmeasured species. All nutrients exhibit significant phylogenetic signal; that is, covariance

among species in nutrient content tends to be moderately to strongly associated with phylogenetic relatedness. Estimates of Pagel's λ vary^{17,18} are highest (indicating strong phylogenetic signal) in zinc, vitamin D, and vitamin A, intermediate in total fat, omega-3 and omega-6 fatty acids, and vitamin B12, and weaker in protein and iron (Table 3).

The phylogenetic structuring of nutrient content can be seen in the heatmap of Fig. 2, which shows some clustering of nutrient values among closely related species, although the location of these clusters varies depending on nutrient. For example, various species of the genus *Thunnus* contain high levels of protein, as indicated by the dark red region near the top of the phylogeny in the first column of the heatmap. We also observe such clustering at close phylogenetic distance but across genera; for example, *Engraulis encrasicolus*, *Tribolodon hakoensis*, *Misgurnus anguillicaudatus*, and *Anguilla japonicus* all fall within the top 10% of zinc levels in the database, as indicated by the dark red region near the bottom of the phylogeny in the fourth column of the heatmap; other nearby species also contain relatively large amounts of zinc.

Given our findings that nutrient content is weakly predicted by life history but tends to be phylogenetically structured, we developed a procedure for predicting nutrient content in unmeasured species based on their phylogenetic relationships to measured species and empirical estimates of phylogenetic signal (see Methods for details). We used a jackknifing procedure to determine that this method has acceptable accuracy. Observed nutrient values fell within the prediction 95% confidence intervals for at least 89.7% of cases across all variables (see Fig. 3, as well as Supplementary Fig. 1 for residual plots) and median deviations between predicted and observed values were within 40% of the among-species standard deviation. We note that the method can lead to wide confidence intervals when long phylogenetic branches separate unmeasured from measured species. This prediction method also compares favorably to predictions based on life history regression models; average accuracy and median

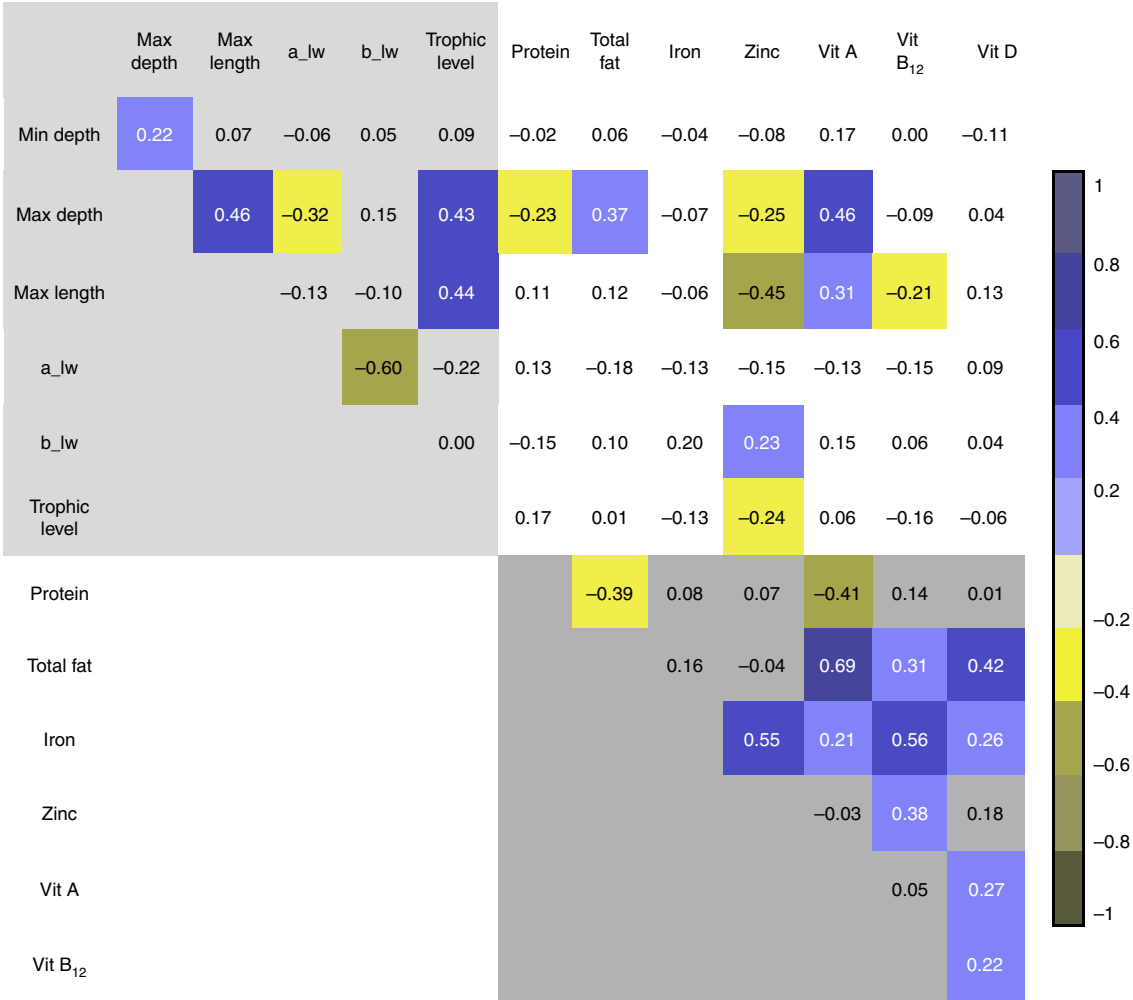


Fig. 1 Evolutionary correlation matrix of key variables, log-transformed. Colored cells indicate correlations significant at $p < 0.1$ (Pearson's r). Lightly shaded top left corner shows correlations between life history variables; darkly shaded bottom right corner shows correlations between nutrient variables. Unshaded top right corner shows correlations between life history and nutrient variables. The variables 'min depth' and 'max depth' refer to habitat preferences. 'Max length' refers to maximum reported length of the species. The variables 'a_lw' and 'b_lw' refer to the scalar and exponential parameters in the length-weight relationship equation $W = aL^b$, wherein W is weight and L is length. 'Trophic level' refers to the weighted mean of the trophic level of the diet of the species. See Table 1 for more details

differences are lower in the phylogenetic signal-only method (Table 4). Moreover, the phylogenetic prediction method can be readily applied to any species whose phylogenetic relationship to measured species has been estimated. Regression-based prediction requires this information in addition to information on species life history, although imputation methods may help to predict missing observations from a combination of other life history predictors and phylogenetic information¹⁹. Because our phylogenetic method performed well in validation tests, we used it to estimate missing nutrient values for all commercially valuable species in our original 371 species, as well as for all 7500+ unmeasured species in the *Actinopterygii* phylogeny (see Supplementary Data Files 2–10)¹⁴. Moreover, we used this approach to identify ray-finned fish families representing promising sources of key nutrients (Table 5). Some of the families we identify contain no or relatively few measured species, but our phylogenetic method predicts their potential to contain species rich in specific nutrients.

Discussion

At least one-tenth of the global population is vulnerable to future deficiencies in micronutrient intake linked to the degradation of

marine ecosystems⁷. Unsustainable fishing practices, the effects of climate change on sea temperature and dissolved oxygen content, and pollution are all major threats to a wide range of commonly consumed fish stocks. Quantifying the exact magnitude of these risks depends on knowing the nutrient content of key species—information that is extremely expensive to obtain, given the cost of directly evaluating nutrient composition data in a laboratory setting. In this study, we develop a modeling framework for using phylogenetic and life history information to predict nutrient content in fish species of the economically and nutritionally important class *Actinopterygii* (ray-finned fishes). We focus on nine nutrients—protein, total fat, omega-3 and omega-6 fatty acids, iron, zinc, vitamin A, vitamin D, and vitamin B12. Fish can be important sources of each of these, especially among coastal populations in the developing world. We find that most nutrients exhibit substantial phylogenetic signal—i.e., covariance among species in nutrient values is proportional to their shared evolutionary history—and a model based solely on phylogenetic relationships and empirical estimates of phylogenetic signal provide reasonable predictions of species nutrient content. This phylogenetic signal-based model provides better predictive ability than the multiple regression

Table 2 Phylogenetic generalized least squares models predicting nutrient content

	(1) Protein	(2) Total fat	(3) Omega-3	(4) Omega-6	(5) Iron	(6) Zinc	(7) Vitamin A	(8) Vitamin B12	(9) Vitamin D
Intercept	14.27*** (11.06)	1.98*** (4.22)	0.70 (1.80)	0.21 (1.83)	0.90*** (4.67)	0.71*** (3.92)	4.11*** (3.47)	2.60*** (4.81)	2.48*** (3.59)
Max length	0.0069* (2.52)	−0.0003 (−0.36)	−0.0006 (−1.04)	−0.0001 (−0.76)	0.0002 (0.63)	−0.0006 (−1.82)	0.0016 (0.90)	−0.0004 (−0.52)	0.0018 (1.79)
Trophic level	1.29*** (3.44)	−0.17 (−1.54)	−0.0262 (−0.25)	0.0196 (−0.62)	−0.07 (−1.21)	0.01 (−0.16)	−0.43 (−1.39)	−0.24 (−1.59)	−0.21 (−1.19)
Max depth	−0.0014*** (−3.99)	0.0004*** (4.30)	0.0002** (3.21)	0.0001** (2.87)	−0.0001 (−1.67)	−0.0001 (−1.30)	0.0011*** (5.22)	−0.0001 (−1.32)	0.0001 (−0.61)
N	183	183	81	81	175	111	101	89	93
Pagel's λ	0.000	0.627	0.672	0.637	0.165	0.607	0.725	0.480	0.784
Log-likelihood	34.99	53.89	15.31	9.83	9.34	19.82	33.82	25.86	32.29
p-Value	<0.0001	<0.0001	0.0018	0.0180	0.0219	0.0002	<0.0001	<0.0001	<0.0001

T-statistics in parentheses. All outcome variables except protein are logged

*** $p < 0.001$ ** $p < 0.01$ * $p < 0.05$ **Table 3 Unconditional phylogenetic signal (Pagel's λ) of each nutrient across subsets of Actinopterygii**

Nutrient	N	λ	p ($\lambda = 0$, likelihood ratio test)
Protein	270	0.4188	<0.0001
Total fat	267	0.6627	<0.0001
Omega-3 fatty acids	89	0.6036	0.0014
Omega-6 fatty acids	89	0.5366	0.1782
Iron	254	0.3461	0.0008
Zinc	146	0.8538	<0.0001
Vitamin A	122	0.7444	1.0000
Vitamin B12	102	0.5080	0.0008
Vitamin D	103	0.7640	<0.0001

model (Table 4), although the latter accounts for both phylogenetic signal and life history trait values. This seemingly counterintuitive result can be explained by two factors. First, the sample size for estimating parameters of phylogenetic signal-based model is greater than that of phylogenetic regression model for all nutrients (see Tables 2, 3). Some of the increased predictive capacity of the phylogenetic signal model may be a consequence of better parameter estimation associated with a larger sample of species. Second, even though some life history variables (such as maximum depth) are significant predictors of some nutrients, the magnitude of effect is relatively small (Table 2). Therefore, inclusion of life history variables in nutrient predictions, as in the phylogenetic regression models, does not seem to offset the loss of sample size imposed by the additional requirement of having data on species life history. Note that we do not intend for our results to suggest that life history is unimportant in determining fish nutrient content, but rather that based on available data, incorporation of life history information does not improve predictions of species nutrient values. With the addition of more life history data and/or use of missing-data imputation techniques, phylogenetic regression models may ultimately yield better predictions than the phylogenetic signal model.

In addition, the method developed in this paper provides the basis for targeting new potential sources of key nutrients. The tendency for variation in nutrients to be phylogenetically structured means that groups of species that are closely related to nutrient-rich species are also reasonably likely to be nutrient-rich. As noted above, we explored this possibility by looking across predicted and observed nutrient values for more than 7000 ray-finned fish species, and identified families that are likely to contain species rich in key nutrients. The nutritional quality of the

members of some of these families is well known; scombrids, carangids, salmonids, and clupeids make large contributions to existing fisheries. However, we also identify as potentially nutrient-rich several fish families for which species nutrient content of their species is mostly unknown (Table 5). For example, our predictions suggest that exocoetids (flying fish), sphyraenids (barracuda), and centropomids (snook) may be high in protein even though protein content has been measured for no more than one species in any of these families. In addition, even though no species of muraenid, ophichthid, congrid, or chanichthyid has been assayed for total fat content, their close phylogenetic relationships to species high in fats lead us to suggest that they may be good sources of this nutrient. To be clear, we recommend that our predictions be used to inform the selection of potentially nutrient-rich species for nutrient content measurement, and we caution against use of our predictions as strong statements on which species should be exploited for nutrition.

Moreover, our identification of nutrient-rich families is limited in some important ways. First, we could only predict nutrient content in species represented in the Rabosky et al. phylogeny, and so some families may be over- or under-represented in our predictions¹⁴. For example, some nutrient-rich families may not appear in Table 5 if they have relatively few species in the phylogeny. Conversely, some families may appear to contain a large number of nutrient-rich species because they are well sampled in the phylogeny and because they contain one or more species known to be high in particular nutrients or are closely related to species of high nutritional quality. In fact, our phylogenetic prediction method is unable to make distinctions between unmeasured species of the same phylogenetic distance from measured relatives, though new nutritional data would likely help resolve this issue. Finally, we acknowledge that our predictions are contingent on Rabosky et al.'s estimation of phylogenetic relationships among these ray-finned fishes¹⁴, whose relation to the true phylogeny is unknown. Future work will refine these predictions as increasing phylogenetic information becomes available. Despite these limitations, we view our approach as a first step toward more precise estimates of the consequences of marine ecosystem transformation.

We identify several priorities in taking the conclusions of this research forward. First, improving the phylogenies of other classes important for human nutrition, including other marine seafood species as well as freshwater fish, is essential. Second, increasing the size of the nutrient validation sample—that is,

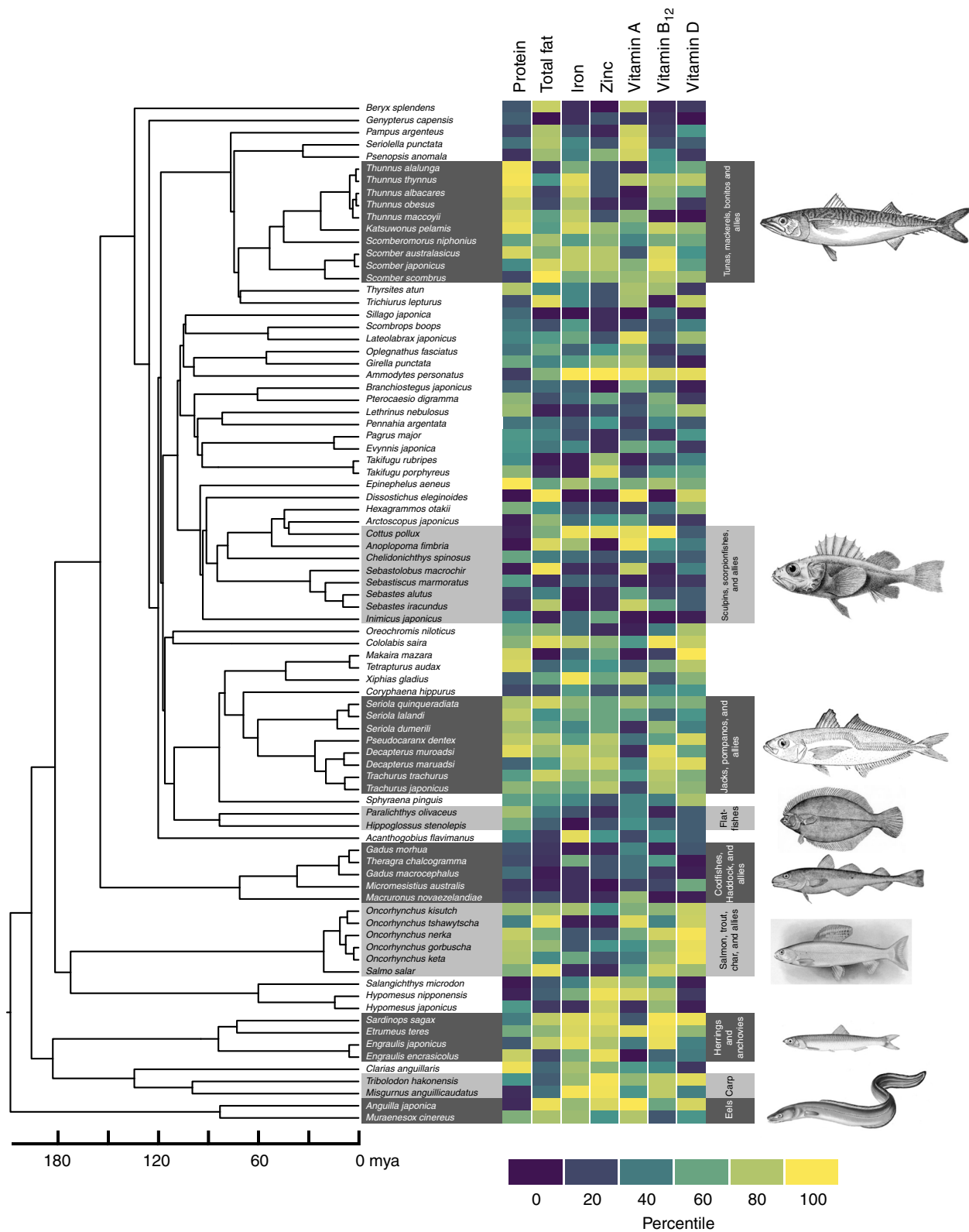


Fig. 2 Phylogenetic relationships and nutrient content, expressed in percentiles. Eighty-four of the most commercially and nutritionally important of the 371 species in the database described above are shown. The time-scale is shown as millions of years ago (mya). The color scales indicate percentiles of nutrient content; see Supplementary Table 1 for ranges of each variable. Common names and pictorial representations of select groups of fishes are shown. All images are taken from Wikipedia, and are Public Domain images

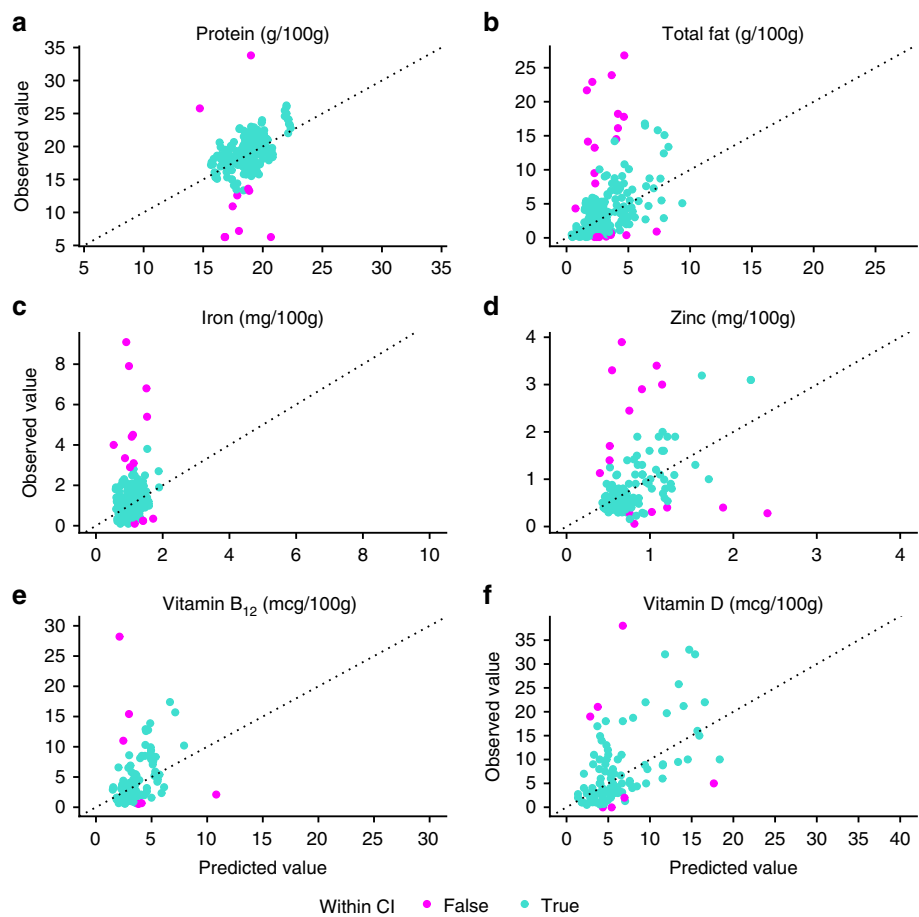


Fig. 3 Predicted versus observed values for selected nutrients using phylogenetic signal only. Points in green fall within the 95% prediction interval; points in red are outside the interval. The diagonal represents points where predictions are equal to observed values

Table 4 Confidence interval coverage and median deviation of nutrient prediction using phylogenetic signal only and phylogenetic signal plus life history information				
	Phylogenetic signal only		Phylogenetic signal + life history variables	
	95% confidence interval coverage	Median difference (proportion of SD)	95% confidence interval coverage	Median difference (proportion of SD)
Protein	95.9	0.366	95.1	0.448
Total fat	92.1	0.304	91.8	0.316
Iron	94.5	0.395	97.1	0.473
Zinc	89.7	0.289	91.9	0.310
Vitamin A	91.0	0.036	88.1	0.034
Vitamin B12	94.1	0.364	92.1	0.338
Vitamin D	93.2	0.346	91.4	0.347
Mean	92.9	0.300	92.5	0.323

Confidence interval coverage is the proportion of measured values falling inside the 95% prediction interval. Median percent difference is calculated as (measured value – predicted value)/sample standard deviation of species values

measuring the nutrient content of more species directly—would enable a better utilization of the large amount of life history information available. It is possible, perhaps even likely, that the weak associations between life history variables and nutrient content in this study is due to an overly restrictive validation sample. We recommend expanding the sample by prioritizing

nutrient assays in species that belong to families identified as potentially nutrient-rich, as presented in Table 5. Third—approaching the small sample problem from the opposite direction—use of techniques like that of Thorson et al. (2017) to predict life history parameters would allow more existing nutrient information to be utilized¹⁹.

We utilize several methods in this paper: evolutionary correlations, Brownian-motion models of trait evolution, and phylogenetic least squares regression. We believe that the availability of data is the key determinant of which of these methods is preferable in predicting fish nutrient content. In the absence of life history information, evolutionary correlations and phylogenetic signal-based models provide a rough sense of which nutrients are likely to be found together in *Actinopterygii*. As phylogenies expand and nutrient and life history datasets grow, life history regression models will likely improve on the predictive power of these methods. Overall, we believe that the combination of phylogenetic and life history information holds great potential for inexpensively inferring the nutrient content of a wide range of wild foods, and thereby quantifying the impacts of ecosystem transformation on human food and nutrition security.

Methods

Data sources. We utilized fish nutrient information from food composition tables from Argentina, Bangladesh, Cambodia, Canada, Chile, Denmark, Japan, Finland, Gambia, Greece, Italy, Japan, Malaysia, South Korea, Peru, Turkey, and the United States; 89% of the species we examined have entries in either the Korea, Japan, Bangladesh, or Argentina tables^{20–28,35–38}. The life history data come from

Table 5 Ray-finned fish families identified as potentially nutrient-rich based on phylogenetic prediction and observation of nutrient content

Nutrient	Family name	Types of fishes	Number of total species in family	Number of measured species in family	Number of nutrient-rich measured species in family
Protein	Serranidae	Sea basses	111	7	2
	Carangidae	Jacks, pompanos	80	12	10
	Scombridae	Tunas, mackerels	37	22	18
	Exocoetidae	Flying fishes	32	1	1
	Sphyrnidae	Barracudas	14	1	1
	Centropomidae	Snooks	12	0	0
	Salmonidae	Salmon, trout	12	12	7
	Istiophoridae	Billfishes	8	1	1
Total fat	Muraenidae	Moray eels	56	0	0
	Clupeidae	Herrings	49	10	8
	Nototheniidae	Cod icefishes	28	1	1
	Engraulidae	Anchovies	22	6	4
	Ophichthidae	Snake eels	20	0	0
	Scombridae	Tunas, mackerels	19	21	10
	Anguillidae	Freshwater eels	15	1	1
	Carangidae	Jacks, pompano	14	12	6
	Channichthyidae	Crocodile icefishes	13	0	0
	Congridae	Garden eels	13	0	0
	Salmonidae	Salmon, trout	12	12	5
	Centrolophidae	Medusafishes	10	2	2
	Cyprinidae	Minnows, carp	118	20	9
	Cobitidae	Loaches	102	2	2
Iron	Nemacheilidae	Stone loaches	36	0	0
	Balitoridae	River loaches	34	0	0
	Catostomidae	Suckers	10	0	0
	Scombridae	Tunas, mackerels	10	19	10
	Cyprinidae	Minnows, carp	162	14	6
	Cobitidae	Loaches	102	1	1
Zinc	Nemacheilidae	Stone loaches	36	0	0
	Balitoridae	River loaches	34	0	0
	Muraenidae	Moray eels	56	0	0
	Cyprinidae	Minnows, carp	44	6	1
Vitamin A	Cottidae	Sculpins	32	1	1
	Nototheniidae	Cod icefishes	28	1	1
	Mastacembelidae	Spiny eels	21	1	1
	Ophichthidae	Snake eels	20	0	0
	Anguillidae	Freshwater eels	15	1	1
	Abyssocottidae	Deep water sculpins	14	0	0
	Channidae	Snakeheads	14	1	1
	Channichthyidae	Crocodile icefishes	13	0	0
	Congridae	Garden eels	13	0	0
	Centrolophidae	Medusafishes	10	2	2
	Cyprinidae	Minnows, carp	136	4	2
	Cobitidae	Loaches	57	1	1
	Clupeidae	Herrings	54	4	4
	Carangidae	Jacks, pompanos	25	8	5
Vitamin B12	Engraulidae	Anchovies	23	2	1
	Salmonidae	Salmon, trout	21	6	4
	Osmeridae	Smelts	13	2	2
	Carangidae	Jacks, pompanos	60	8	5
	Muraenidae	Moray eels	56	0	0
	Clupeidae	Herrings	54	6	6
	Salmonidae	Salmon, trout	30	8	7
	Nototheniidae	Cod icefishes	28	1	1
	Cyprinidae	Minnows, carp	20	3	1
	Anguillidae	Freshwater eels	15	1	1
	Channichthyidae	Crocodile icefishes	13	0	0
	Sphyrnidae	Barracudas	11	1	1

Final column lists number of species in each family identified as potentially nutrient-rich, based on phylogenetic prediction and observation of nutrient content. Species are considered nutrient-rich if their nutrient content rank within the 500 largest values out of more than 7000 species from the Rabosky et al. phylogeny with predicted or known nutrient content¹⁴. Values in parentheses indicate the number of measured species that are nutrient-rich over the total number of species measured for that family

FishBase, a publicly accessible database containing taxonomic, biological, ecological, life history, and human use information on finfishes³⁹. We utilized the species-level, time-calibrated, multi-gene phylogeny for *Actinopterygii* assembled by Rabosky et al.¹⁴. Although other large-scale species-level phylogenetic trees are also available for this group^{40,41}, we chose the Rabosky et al. phylogeny because it maximizes overlap with nutrient content data. Rabosky et al.'s reconstruction of the phylogeny was based on maximum likelihood phylogenetic analysis of 13 genes with subsequent smoothing of among-lineage substitution rate heterogeneity and divergence date estimation using fossil calibrations. The original phylogeny includes over 7500 ray-finned fish species. As described in more detail further below, we used this phylogeny in combination with life history predictor variables and estimates of phylogenetic signal (i.e., the tendency for phenotypic similarity among species to be proportional to their time of shared evolution) to predict nutrient content in species lacking such information.

Evolutionary correlations. We first explored bivariate evolutionary correlations between all pairwise combinations of life history and nutrient variables. Here, evolutionary correlations are the Pearson correlation coefficients describing associations between evolutionary changes in pairs of variables^{42,43}. We estimated these correlations for log-transformed species values given the Rabosky et al. phylogeny and a Brownian motion model with Pagel's λ correction for the degree of phylogenetic signal using the *ratematrix* function of the *geiger* package⁴⁴ for R⁴⁵.

Multivariable regression models. To evaluate the capacity to predict nutrient content from life history information, we fit multiple regression models using phylogenetic least squares (PGLS) as implemented in the R package *phylolm*⁴⁶. Because species with a recent common ancestor are expected to have more similar trait values, the assumptions of ordinary least squares (OLS) are violated⁴⁷. PGLS accounts for phylogenetic non-independence using shared ancestry as inverse weights on the elements of the residual variance-covariance matrix used in the model^{15,29–31}. Thus, in matrix notation, a coefficient β is estimated as follows:

$$\beta = (\mathbf{X}'\mathbf{V}^{-1}\mathbf{X})^{-1}\mathbf{X}'\mathbf{V}^{-1}\mathbf{y} \quad (1)$$

where \mathbf{X} is a matrix of n species and $m+1$ life history trait values (with an intercept column); \mathbf{X}' is the transpose of \mathbf{X} ; \mathbf{y} is a vector of values for a given nutrient; and \mathbf{V} is the residual variance-covariance matrix. Under OLS assumptions, the diagonal elements of \mathbf{V} are the variance of the residuals; the residuals are expected to be normally distributed with mean zero. Under PGLS, the residual covariances are computed using branch lengths from each member of a species pair to their common ancestor. Instead of assuming covariance among species to be proportional to their time of shared evolution, we used a maximum likelihood procedure to identify a scalar of \mathbf{V}^{-1} , called Pagel's λ , that best fits the observed data; $\lambda = 0$, the OLS approximation, would indicate trait evolution completely independent of phylogeny, $\lambda = 1$ would indicate that shared evolutionary history (i.e., shared phylogenetic branch length) predicts phenotypic similarity among species, and intermediate λ ($0 < \lambda < 1$) discounts the phylogenetic dependence of trait values among species^{30,32,33}. The best-fit inverse matrix \mathbf{V}^{-1} is then used to estimate the predictor coefficient β ^{30,31,48}.

Phylogenetic prediction. The objective of the PGLS modeling exercise is to advance towards methods for predicting the nutrient content of species for which information is not available. Although our analysis shows that life history parameters are generally weak predictors of all nutrients, phylogeny is more promising. We thus predict nutrient content of unmeasured *Actinopterygii* fish species using nutrient data for measured species and the Rabosky et al. phylogenetic tree relating both measured and unmeasured species¹⁴, assuming a λ -corrected Brownian motion model of evolution. Under this model, character change along any branch of the phylogeny is a normally distributed random variate with expected value equal to zero and variance proportional to the length of the branch²⁴. Because the character has no tendency to increase or decrease under the model, the predicted value for an unmeasured species is equal to the estimated state for the most recent common ancestor (MRCA) between that species and the measured species most closely related to it. The state of this ancestor is evaluated as the branch length-weighted mean of the estimated character states in the next node deeper and the next more recent node that connect measured species (though, in some cases, the more recent node is a tip species). We estimated the states of these nodes using the *phytools* function *fastAnc*⁴⁹.

Although the expectation under the Brownian model is that the character will remain unchanged in the unmeasured species from the time of its split from the measured species most closely related to it, the uncertainty in the predicted value increases with time since this split. Therefore, the variance around each predicted value incorporates the branch length (t) subtending the unmeasured species, and is evaluated as

$$t \times \sigma^2 \quad (2)$$

where σ^2 is the time-independent variance of the Brownian motion process²⁴. The parameter σ^2 was estimated from the data and phylogeny using methods described

in the next paragraph. We constructed 95% confidence intervals around each predicted value as $\pm 1.96 \times \sqrt{t \times \sigma^2}$.

Our predictions also incorporate empirical estimates of the degree of phylogenetic signal in measured species nutrient values. We fit Pagel's λ separately for each nutrient using the *phylosig* function of the *phytools* package for R^{22,32,33,44}, which returns the maximum likelihood estimates for both σ^2 and λ . We then transformed branch lengths of the phylogeny by the empirical estimates for λ using the *rescale* function of the R package *geiger*²¹; $\lambda = 1$ recovers the original phylogeny, $\lambda < 1$ compresses internal branches relative to terminals, and $\lambda = 0$ is a star phylogeny. We then estimated ancestral character states, predicted states for unmeasured species, and their confidence intervals on this branch length-transformed tree.

Validation. We used a jackknifing approach to validate the method for phylogenetic prediction of nutrient content. For each nutrient, we removed one measured species from the dataset and applied the method to predict the species' nutrient value and calculate its prediction interval. We then determined whether the prediction interval contained the measured value. If it does not, we label that trial as an error, and then calculated the error rate for each nutrient over all measured species. We also calculated the median percent deviation between predicted and measured values as a proportion of the standard deviation of the sample of all species nutrient values. We then compared error rates and accuracy of phylogeny-only predictions to predictions based on the best-fit multiple regression models. These latter predictions were obtained following the method of Garland and Ives⁵⁰, and were restricted to the sample of species for which life history data were available.

Code availability. All code used in the analysis is made available as Supplementary Data 11–15. SD11 is the script for evolutionary correlations. SD12 is the script for phylogenetic least squares. SD13 is the script for estimating the phylogenetic signal of nutrient variables. SD14 is the script for validating the predictions under the lambda model. SD15 is the script for validating predictions under the lambda plus phylogenetic regression model.

Data availability

We declare all data used in the above analysis, tables, and figures to be available within the paper and in the supplementary information files. Supplementary Data 1 is the fish life history and nutrient content database. Phylogenetically predicted nutrient values are labeled as Supplementary Data 2–10.

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Author contributions

B.V. led writing of the manuscript and contributed to the analysis. D.C. led analysis. M.R. S. and S.S.M. created the underlying fish nutrient database. B.L.R. contributed to draft revisions and designed Fig. 2. C.D.G. conceptualized the research idea and overall study design, and all authors contributed to writing and draft revision.

Additional information

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Supplementary Tables

Supplementary Table 1. List of included species and sources and rich sources of key nutrients. See below for units and thresholds for “source” and “rich source” as designated by FAO.¹ Values above the source threshold are highlighted in blue, values above the rich source threshold are highlighted in dark blue.

Nutrient	Source threshold (/100g)	Rich source threshold (/100g)
Protein	7.65 g	15.3 g
Iron	1.95 mg	3.9 mg
Zinc	1.425 mg	2.85 mg
Vitamin A	120 mcg	240 mcg
Vitamin B12	0.75 mcg	1.5 mcg
Vitamin D	0.36 mcg	0.72 mcg

Summary	Protein	Iron	Zinc	Vitamin A	Vitamin B12	Vitamin D
Valid species, n	372	345	178	143	122	122
# Source	17	33	15	7	15	4
# Rich Source	348	11	10	7	99	115
# Source or Rich Source	365	44	25	14	114	119
% Source	4.57	9.57	8.43	4.90	12.30	3.28
% Rich Source	93.55	3.19	5.62	4.90	81.15	94.26
% Source or Rich Source	98.12	12.75	14.04	9.79	93.44	97.54

Species	Common name	Order	Family	Protein	Iron	Zinc	Vit A	Vit B12	Vit D
<i>Acanthistius brasilianus</i>	Argentine Seabass	Perciformes	Serranidae	17.90					
<i>Acanthogobius flavimanus</i>	Goby	Gobioidei	Gobiidae	18.90	2.10	0.60	7	2.70	3.00
<i>Acanthogobius hasta</i>	Javelin goby	Gobioidei	Gobiidae	16.40	0.90				
<i>Acanthopagrus schlegelii</i>	Black sea bream	Perciformes	Sparidae	19.60	0.75	0.80	12	3.70	4.00
<i>Acheilognathus rhombeus</i>	Flat bitterling	Cypriniformes	Cyprinidae	17.50	1.20				
<i>Ailia coila</i>	Gangetic Ailia	Siluriformes	Schilbeidae	15.30	0.90				
<i>Alcichthys alcornis</i>	Elkhorn sculpin	Scorpaeniformes	Cottidae	17.10	0.80				
<i>Allothunnus fallai</i>	Slender Tuna	Perciformes	Scombridae	19.80	1.30	1.10	227	0.70	
<i>Amblypharyngodon mola</i>	Mola Carplet	Cypriniformes	Cyprinidae	17.10	3.80	3.19	2680		
<i>Ammodytes personatus</i>	Sandlance	Perciformes	Ammodytidae	16.60	7.90	3.90	200	11.00	21.00
<i>Anabas testudineus</i>	Climbing Perch	Perciformes	Abantidae	17.50	1.20	1.13	215		
<i>Anchoa compressa</i>	Deep-bodied anchovy	Clupeiformes	Engraulidae	16.90	1.40				
<i>Anguilla japonica</i>	Eel	Anguilliformes	Anguillidae	15.75	1.05	1.40	2400	3.50	18.00
<i>Anoplopoma fimbria</i>	Sablefish	Scorpaeniformes	Anoplopomatidae	13.35	1.25	0.30	1500	2.80	3.50
<i>Arctoscopus japonicus</i>	Saifin Sandfish/Sandfish	Perciformes	Trichodontidae	14.10	0.50	0.60	20	1.70	2.00
<i>Argyrops bleekeri</i>	Taiwan tai	Perciformes	Sparidae	17.80	9.10				
<i>Auxis rochei</i>	Frigate mackerel	Perciformes	Scombridae	24.10	1.70				
<i>Auxis thazard</i>	Bullet mackerel	Perciformes	Scombridae	23.40	1.90				
<i>Bagrus bajad</i>	Bayad	Siluriformes	Bagridae	27.50	1.10	0.73	9	2.80	0.80
<i>Banjós banjos</i>	Banjo fish	Perciformes	Banjosidae	20.80	1.40				

Species	Common name	Order	Family	Protein	Iron	Zinc	Vit A	Vit B12	Vit D
<i>Barbonymus gonionotus</i>	Silver Barb	Cypriniformes	Cyprinidae	6.25				2.00	
<i>Belone belone</i>	Needle fish Gar fish Pacific	Beloniformes	Belonidae	19.80	0.50				
<i>Bero elegans</i>	Elegant sculpin	Scorpaeniformes	Cottidae	19.50	0.90				
<i>Beryx decadactylus</i>	Broad alfonsino	Beryciformes	Berycidae	18.50	2.00				
<i>Beryx splendens</i>	Splended Alfonsino	Beryciformes	Berycidae	17.80	0.30	0.30	63	1.10	2.00
<i>Bodianus bilunulatus</i>	Crescent-banded wrasse	Perciformes	Labridae	20.30	1.50				
<i>Boreogadus saida</i>	Polar Cod	Gadiformes	Gadidae		0.25	0.37	24		
<i>Brama japonica</i>	Pacific pomfret	Perciformes	Bramidae	18.90	0.40				
<i>Branchiostegus japonicus</i>	Blanquillo	Perciformes	Branchiostegidae	18.45	0.45	0.30	27	2.10	1.00
<i>Caesio xanthonota</i>	Yellowback Fusilier	Perciformes	Caesionidae	21.10	0.40	0.40	19	0.41	
<i>Callanthias japonicus</i>	Yellowtail red bass	Perciformes	Callanthiidae	17.30	0.70				
<i>Callionymus lunatus</i>	Moon dragonet	Perciformes	Callionymidae	18.50	0.80				
<i>Calliurichthys japonicus</i>	Dragonet	Perciformes	Callionymidae	16.50	1.30				
<i>Carangoides equula</i>	Whitefin trevally	Perciformes	Carangidae	19.60	1.00				
<i>Caranx sexfasciatus</i>	Six-bed jack	Perciformes	Carangidae	24.00	1.70				
<i>Carassius auratus</i>	Crucian carp	Cypriniformes	Cyprinidae	18.15	1.95	1.90	12	5.50	4.00
<i>Catla catla</i>	Catla	Cypriniformes	Cyprinidae	19.90	0.60	0.48	3		0.00
<i>Cephalopholis miniata</i>	Coral Hind	Perciformes	Serranidae	18.40	0.40	0.40	0	1.00	
<i>Channa punctata</i>	Spotted Snakehead	Perciformes	Channidae	17.30	1.50	1.08	191		
<i>Channa striata</i>	Striped Snakehead	Perciformes	Channidae	17.70	1.00	0.31			
<i>Chanodichthys dabryi</i>	Humpback	Cypriniformes	Cyprinidae	18.70	1.10				
<i>Cheilodactylus quadricornis</i>	Black-barred morwong	Perciformes	Cheilodactylidae	19.20	1.30				
<i>Cheilodactylus zonatus</i>	Spottedtail morwong	Scorpaeniformes	Scorpaenidae	19.80	1.30				
<i>Cheilopogon agoo</i>	Japanese flying fish	Beloniformes	Exocoetidae	22.20	0.90				
<i>Chelidonichthys spinosus</i>	Bluefin searobin	Scorpaeniformes	Triglidae	19.75	0.50	0.50	9	2.20	3.00
<i>Chelidoperca hirundinacea</i>	Princess porgy	Perciformes	Serranidae	20.10	1.50				
<i>Chelon parsia</i>	Goldspot Mullet	Mugiliformes	Mugilidae	18.70	2.10	1.43			
<i>Chirolophis japonicus</i>	Fringed blenny	Perciformes	Stichaeidae	17.20	0.60				
<i>Chitala chitala</i>	Clown Knifefish	Osteoglossiformes	Notopteridae	17.80	1.60	0.61	30		
<i>Choerodon azurio</i>	Azurio tuskfish	Perciformes	Labridae	20.30	0.70				
<i>Chromis notata</i>	Pearl-spot chromis	Perciformes	Pomacentridae	19.50	0.70				
<i>Cirrhinus cirrhosus</i>	Mrigal Carp	Cypriniformes	Cyprinidae	18.60	1.80	0.29	11		
<i>Clarias anguillaris</i>	Mudfish	Siluriformes	Clariidae	25.80	1.40	0.80	16	2.60	1.30
<i>Clarias batrachus</i>	Philippine Catfish	Siluriformes	Clariidae	10.93	0.80	0.53	15		
<i>Cleisthenes pinetorum</i>	Pointhead flounder	Pleuronectiformes	Pleuronectidae	18.10	4.00				
<i>Clidoderma asperrimum</i>	Roughscale sole	Pleuronectiformes	Pleuronectidae	17.40	0.60				
<i>Clupea harengus</i>	Atlantic Herring	Clupeiformes	Clupeidae	17.96	1.10	0.99			9.50
<i>Clupea pallasii</i>	Pacific herring	Clupeiformes	Clupeidae	16.85	0.90	1.10	18	17.40	22.00
<i>Cobitis sinensis</i>	Siberian spiny loach	Salmoniformes	Salmonidae	17.50	2.70				

Species	Common name	Order	Family	Protein	Iron	Zinc	Vit A	Vit B12	Vit D
<i>Coilia dussumieri</i>	Goldspotted Gredier Anchovy	Clupeiformes	Engraulidae	13.20	4.50	1.25			
<i>Coilia nasus</i>	Japanese gredier anchovy	Clupeiformes	Engraulidae	15.90	1.10				
<i>Collichthys niveatus</i>	Collichthys niveatus	Perciformes	Sciaenidae	17.00	1.30				
<i>Cololabis saira</i>	Pacific saury	Beloniformes	Scomberesocidae	20.15	1.50	0.80	16	15.40	14.90
<i>Conger myriaster</i>	Conger eel	Anguilliformes	Congridae	17.35	0.65	0.70	500	2.30	0.40
<i>Conger orbignianus</i>	Argentine Conger	Anguilliformes	Congridae	17.20					
<i>Coregonus autumnalis</i>	Arctic Cisco	Salmoniformes	Coregonidae	16.70	0.82	0.63			
<i>Coregonus clupeaformis</i>	Lake Whitefish	Salmoniformes	Coregonidae	16.88	0.31	0.51	11		4.40
<i>Coreoperca kawamebari</i>	Spotear brook perch	Perciformes	Percichthyidae	19.50	1.10				
<i>Coryphaena hippurus</i>	Dolphinfish	Perciformes	Coryphaenidae	17.30	0.70	0.50	8	2.60	5.00
<i>Cottus poecilopterus</i>	Alpine bullhead	Scorpaeniformes	Cottidae	15.00	2.80				
<i>Cottus pollux</i>	Japanese Sculpin/Japanese Fluvial Sculpin	Scorpaeniformes	Cottidae	15.00	2.80	1.70	180	28.20	3.00
<i>Crossocheilus latius</i>	Stone Roller	Cypriniformes	Cyprinidae	15.30	2.20	1.09			
<i>Ctenopharyngodon idella</i>	Grass carp	Cypriniformes	Cyprinidae	17.10	1.70				
<i>Cynoglossus joyneri</i>	Red tonguesole	Pleuronectiformes	Cynoglossidae	18.60	1.00				
<i>Cynoglossus semilaevis</i>	Tongue sole	Pleuronectiformes	Cynoglossidae	19.20	0.30				
<i>Cynoscion striatus</i>	Striped Weakfish	Perciformes	Sciaenidae	17.80	2.20				
<i>Cyprinus carpio</i>	Common carp	Cypriniformes	Cyprinidae	17.97	0.93	0.97	3	10.00	10.30
<i>Cyprinus carpio nudus</i>	Israeli carp	Cypriniformes	Cyprinidae	16.80	1.20				
<i>Dactyloptena peterseni</i>	Starry flying gurd	Scorpaeniformes	Dactylopteridae	19.20	1.20				
<i>Decapterus maruadsi</i>	White-tipped mackerel scad	Perciformes	Cheilodactylidae	18.45	1.45	1.30	11	9.90	18.70
<i>Decapterus muroadsi</i>	Brownstriped Mackerel Scad	Perciformes	Carangidae	23.60	1.60	1.00	4	12.80	6.00
<i>Dentex tumifrons</i>	Yellow Sea Bream	Lophiiformes	Lophiidae	19.40	0.35	0.40	50	3.20	4.00
<i>Dexistes rikuzenius</i>	Rikazen flounder	Pleuronectiformes	Pleuronectidae	19.40	0.60				
<i>Diagramma pictum</i>	Painted Sweetlips	Perciformes	Haemulidae	19.80	0.40	0.60	29	2.11	
<i>Dictyosoma burgeri</i>	Ribbed gunnel	Perciformes	Stichaeidae	22.00	1.20				
<i>Dissostichus eleginoides</i>	Patagonian Toothfish	Perciformes	Nototheniidae	13.30	0.10	0.30	1800	0.60	17.00
<i>Ditrema temminckii temminckii</i>	Surffish	Perciformes	Embiotocidae	18.90	1.00				
<i>Doederleinia berycoides</i>	Blackthroat seaperch	Perciformes	Acropomatidae	22.30	0.30				
<i>Eleginus gracilis</i>	Saffron cod	Gadiformes	Gadidae	12.60	4.00				
<i>Engraulis anchoita hubbs larini</i>	Argentine Anchovy	Clupeiformes	Engraulidae	19.20					
<i>Engraulis encrasicolus</i>	European Anchovy	Clupeiformes	Engraulidae	22.80	0.90	1.90	1	2.10	3.50
<i>Engraulis japonicus</i>	Anchovy	Clupeiformes	Engraulidae	17.95	2.25	1.00	11	13.90	4.00
<i>Engraulis ringens</i>	Anchoveta	Clupeiformes	Engraulidae	21.00	1.40				
<i>Epinephelus aeneus</i>	White Grouper	Perciformes	Serranidae	33.80	1.40	0.65	30	6.60	7.50
<i>Epinephelus akaara</i>	Red-spotted grouper	Perciformes	Serranidae	21.00	1.30				
<i>Epinephelus awoara</i>	Yellow grouper	Perciformes	Serranidae	19.40	0.90				

Species	Common name	Order	Family	Protein	Iron	Zinc	Vit A	Vit B12	Vit D
<i>Epinephelus epistictus</i>	Dotted grouper	Perciformes	Serranidae	19.30	1.00				
<i>Esox lucius</i>	Northern Pike	Esociformes	Esocidae	17.83	0.18	0.70			
<i>Ethmalosa fimbriata</i>	Bonga Shad	Clupeiformes	Clupeidae	19.10	1.70	1.60			
<i>Etrumeus teres</i>	Bigeye sardine	Clupeiformes	Clupeidae	19.90	1.90	1.30	130	14.20	9.00
<i>Eumicrotremus orbis</i>	Pacific spiny lumpsucker	Scorpaeniformes	Cyclopteridae	7.20	1.20				
<i>Euthynnus affinis</i>	Kawakawa	Perciformes	Scombridae	25.00	1.30	0.27	31		3.12
<i>Eutropiichthys vacha</i>	Batchwa Vacha	Siluriformes	Schilbeidae	16.10	0.70				
<i>Evistias acutirostris</i>	Striped boarfish	Perciformes	Pentacerotidae	18.60	1.20				
<i>Gadus macrocephalus</i>	Pacific cod	Gadiformes	Gadidae	18.55	0.30	0.50	10	1.30	1.00
<i>Gadus morhua</i>	Atlantic cod	Gadiformes	Gadidae	17.76	0.25	0.40	12	0.91	2.76
<i>Genypterus blacodes</i>	Pink Cusk-Eel	Ophidiiformes	Ophidiidae	15.80					
<i>Genypterus capensis</i>	Kingclip	Ophidiiformes	Ophidiidae	18.20	0.30	0.50	5	1.30	0.00
<i>Girella punctata</i>	Girella	Perciformes	Kyphosidae	19.80	0.70	0.90	55	1.80	1.00
<i>Glossanodon semifasciatus</i>	Deep-sea smelt	Salmoniformes	Argentinidae	18.70	0.40	0.40	75	3.40	0.00
<i>Glossogobius giuris</i>	Tank Goby	Perciformes	Gobiidae	14.70	1.20	0.93			
<i>Glyptocephalus stelleri</i>	Blackfin flounder	Pleuronectiformes	Pleuronectidae	18.20	0.60				
<i>Gnathopogon caeruleus</i>	Willow Shiner	Cypriniformes	Cyprinidae	17.50	1.30	3.40	250	9.00	5.00
<i>Gudusia chapra</i>	Indian River Shad	Clupeiformes	Clupeidae	15.40	4.80	1.97	6		
<i>Gymnoanthus herzensteini</i>	Black edged sculpin	Scorpaeniformes	Cottidae	19.50	2.50				
<i>Halichoeres tenuispinis</i>	Motley stripe rainbowfish	Perciformes	Labridae	19.20	1.10				
<i>Halieutaea stellata</i>	Minipizza bat fish	Lophiiformes	Ogcocephalidae	15.80	1.00				
<i>Haplogeny mucronatus</i>	Broadbanded velvetfin	Perciformes	Haemulidae	18.50	1.10				
<i>Haplogeny nigripinnis</i>	Short barbeled velvetfin	Perciformes	Haemulidae	19.00	1.30				
<i>Helicolenus dactylopterus</i>	Blackbelly Rosefish	Scorpaeniformes	Scorpaenidae	17.10					
<i>Helicolenus hilgendorffii</i>	Hilgendorf saucord; Rosefish	Scorpaeniformes	Scorpaenidae	16.70	0.70				
<i>Hemibarbus labeo</i>	Barbel steed	Cypriniformes	Cyprinidae	17.30	1.00				
<i>Hemibarbus longirostris</i>	Long-nose barbel	Cypriniformes	Cyprinidae	17.70	1.40				
<i>Hemitripterus villosus</i>	Shaggy sea raven	Scorpaeniformes	Hemitriptidae	18.60	0.50				
<i>Henicorhynchus siamensis</i>	Siamese Mud Carp	Cypriniformes	Cyprinidae	6.25				1.60	
<i>Heteropneustes fossilis</i>	Stinging Catfish	Siluriformes	Heteropneustidae	17.20	2.10	0.55	16		
<i>Heteropriacanthus cruentatus</i>	Glasseye	Perciformes	Priacanthidae	18.00	1.10				
<i>Hexagrammos agrammus</i>	Spotty belly greenling	Scorpaeniformes	Hexagrammidae	17.50	2.90				
<i>Hexagrammos octogrammus</i>	Masked greenling	Scorpaeniformes	Hexagrammidae	17.50	1.80				
<i>Hexagrammos otakii</i>	Fat greenling	Scorpaeniformes	Hexagrammidae	20.05	0.35	0.50	6	2.20	9.00
<i>Hime japonica</i>	Hime japonica	Aulopiformes	Aulopidae	20.90	1.00				
<i>Hippoglossus stenolepis</i>	Pacific Halibut	Pleuronectiformes	Pleuronectidae	19.90	0.10	0.50	13	2.10	3.00
<i>Histiogaster typus</i>	Sailfin armourhead	Perciformes	Pentacerotidae	19.30	1.20				
<i>Hoplias malabaricus</i>	Trahira	Characiformes	Erythrinidae	18.10					

Species	Common name	Order	Family	Protein	Iron	Zinc	Vit A	Vit B12	Vit D
<i>Hoplobrotula armata</i>	Armored weasel-fish	Ophidiiformes	Ophidiidae	18.20	1.00				
<i>Hypomesus japonicus</i>	Japanese Surf Smelt	Osmeriformes	Osmeridae	19.50	0.30	1.30	4	5.40	1.00
<i>Hypomesus nipponensis</i>	Japanese Smelt/Pond Smelt	Osmeriformes	Osmeridae	14.40	0.90	2.00	99	7.90	2.00
<i>Hypomesus olidus</i>	Pond smelt	Salmoniformes	Osmeridae	18.40	0.90				
<i>Hypophthalmichthys molitrix</i>	Silver big-head carp	Cypriniformes	Cyprinidae	18.25	1.35	0.28			
<i>Hypophthalmichthys nobilis</i>	Big-head carp	Cypriniformes	Cyprinidae	17.50	1.20				
<i>Hypoptychus dybowskii</i>	Korean sandlance	Gasterosteiformes	Hypoptychidae	21.50	1.70				
<i>Hyporhamphus sajori</i>	Half beak	Beloniformes	Hemiramphidae	18.70	1.90	1.90		5.50	3.00
<i>Hyporthodus septemfasciatus</i>	Convict grouper	Perciformes	Serranidae	18.80	1.00				
<i>Ilisha elongata</i>	Elongate ilisha	Clupeiformes	Pristigasteridae	20.10	0.80				
<i>Inimicus japonicus</i>	Devil stingfish	Scorpaeniformes	Synceiidae	19.05	0.50	0.70	2	0.60	1.00
<i>Johnius grypotus</i>	Corvi	Perciformes	Sciaenidae	15.20	2.60				
<i>Kajikia audax</i>	Barred marlin	Perciformes	Istiophoridae	23.10	0.60	0.60	8	4.30	12.00
<i>Kareius bicoloratus</i>	Stone flounder	Pleuronectiformes	Pleuronectidae	20.00	0.20				
<i>Katsuwonus pelamis</i>	Skipjack tuna	Perciformes	Scombridae	25.45	1.85	0.90	20	8.60	9.00
<i>Konosirus punctatus</i>	Gizzard shad	Clupeiformes	Clupeidae	19.10	1.25	0.70		10.20	9.00
<i>Labeo bata</i>	Bata	Cypriniformes	Cyprinidae	15.90	1.20	0.94			
<i>Labeo calbasu</i>	Orangefin Labeo	Cypriniformes	Cyprinidae	17.00	1.10	0.36			
<i>Labeo gonius</i>	Kuria Labeo	Cypriniformes	Cyprinidae	17.60	0.30	0.06			
<i>Labeo rohita</i>	Roho Labeo	Cypriniformes	Cyprinidae	20.60	0.40	1.13	4		
<i>Labracoglossa argenteiventris</i>	Yellowstriped butterflyfish	Perciformes	Kyphosidae	18.70	0.60	1.30	16	2.00	4.00
<i>Lagocephalus lunaris</i>	Lurtail puffer	Tetraodontiformes	Tetraodontidae	17.30	1.00				
<i>Larimichthys crocea</i>	Large yellow croaker	Perciformes	Sciaenidae	17.20	1.20				
<i>Larimichthys polyactis</i>	Yellow croaker	Perciformes	Sciaenidae	15.80	0.50				
<i>Lateolabrax japonicus</i>	Common sea bass	Perciformes	Percichthyidae	18.83	0.80	0.50	180	2.00	10.00
<i>Lates calcarifer</i>	Barramundi	Perciformes	Centropomidae	18.60	1.00	0.16	8		1.50
<i>Lepidopsetta mochigarei</i>	Dusky sole	Pleuronectiformes	Pleuronectidae	16.80	1.20				
<i>Lepidotrigla alata</i>	Fork-snout searobin	Scorpaeniformes	Triglidae	16.90	1.00				
<i>Lepidotrigla microptera</i>	Red-wing searobin	Scorpaeniformes	Triglidae	19.70	0.40				
<i>Lepomis macrochirus</i>	Bluegill	Perciformes	Centrarchidae	17.80	1.40				
<i>Leptomelanosoma indicum</i>	Indian Threadfin	Perciformes	Polynemidae	20.30	0.50	1.35			
<i>Lethrinus haematopterus</i>	Chinese emperor	Perciformes	Lethrinidae	20.40	1.00				
<i>Lethrinus nebulosus</i>	Spangled Emperor	Perciformes	Lethrinidae	20.50	0.30	0.50	8	3.70	11.00
<i>Limanda aspera</i>	Yellowfin sole	Pleuronectiformes	Pleuronectidae	16.80	1.20				
<i>Liparis tanakai</i>	Taka's silfish	Scorpaeniformes	Liparidae	16.40	0.50				
<i>Liparis tessellatus</i>	Cubed silfish	Scorpaeniformes	Liparidae	16.40	1.00				
<i>Lobotes surinamensis</i>	Tripletail	Perciformes	Lobotidae	21.00	1.10				
<i>Lophiomus setigerus</i>	Angler	Lophiiformes	Lophiidae	14.10	2.50				

Species	Common name	Order	Family	Protein	Iron	Zinc	Vit A	Vit B12	Vit D
<i>Lophius litulon</i>	Yellow goosefish	Perciformes	Sciaenidae	14.65	0.25	0.60	13	1.20	1.00
<i>Lota lota</i>	Burbot	Gadiformes	Lotidae	17.83	0.35	0.65	3		
<i>Luciopimelodus pati</i>	Pati	Siluriformes	Pimelodidae	18.20	1.90				
<i>Lumpenus sagitta</i>	Skæ prickleback	Perciformes	Stichaeidae	19.30	0.90				
<i>Macruronus novaezelandiae</i>	Hoki	Gadiformes	Merlucciidae	17.00	0.30	0.40	43	0.70	1.00
<i>Makaira mazara</i>	Pacific Blue Marlin/Blue Marlin/Black Marlin	Perciformes	Istiophoridae	22.90	0.50	0.70	2	1.50	38.00
<i>Malakichthys wakiyae</i>	Silver-belly sea perch	Perciformes	Acropomatidae	18.70	0.70				
<i>Mallotus villosus</i>	Capelin	Salmoniformes	Osmeridae						
<i>Mastocembellus armatus</i>	Zig-Zag Eel	Synbranchiformes	Mastacembelidae	16.10	0.80	1.30	829	2.40	
<i>Merluccius merluccius</i>	European Hake	Gadiformes	Merlucciidae	17.10	1.90				
<i>Microcanthus strigatus</i>	Stripey	Perciformes	Kyphosidae	19.50	0.90				
<i>Micromesistius australis</i>	Southern Blue Whiting	Gadiformes	Gadidae	16.40	0.30	0.30	6	1.60	7.00
<i>Micromesistius poutassou</i>	Blue Whiting	Gadiformes	Gadidae	17.50	1.00				
<i>Micropogonias undulatus</i>	Atlantic Croaker	Perciformes	Sciaenidae	19.50					
<i>Micropterus salmoides</i>	Largemouth black bass	Perciformes	Centrarchidae	18.20	4.50				
<i>Müichthys miiuy</i>	Mi-iuy croaker	Perciformes	Sciaenidae	18.00	0.30				
<i>Misgurnus anguillicaudatus</i>	Loach	Cypriniformes	Cobitidae	16.15	6.80	2.90	15	8.50	4.00
<i>Monopterus albus</i>	Asian swamp eel	Synbranchiformes	Synbranchidae	17.90	1.40				
<i>Mugil cephalus</i>	Common mullet	Mugiliformes	Mugilidae	20.45	0.85	0.50	8	4.70	10.00
<i>Muraenesox cinereus</i>	Silver conger eel	Anguilliformes	Muraenesocidae	20.10	1.15	0.60	59	1.90	5.00
<i>Mystus cavasius</i>	Gangetic My stus	Siluriformes	Bagridae	15.40	1.30	0.88			
<i>Mystus gulio</i>	Long Whiskers Catfish	Siluriformes	Bagridae	17.00	0.90	0.23			
<i>Mystus wolffii</i>	Mystus wolffii	Siluriformes	Bagridae	6.25					
<i>Nandus nandus</i>	Gangetic Leaffish	Perciformes	ndidae	15.80	1.90	1.42			
<i>Nemadactylus bergi</i>	Castaneda	Perciformes	Cheilodactylidae	18.40					
<i>Nemipterus japonicus</i>	Japanese Threadfin Bream	Perciformes	Nemipteridae	18.40	0.80	0.30	0	2.00	
<i>Nemipterus virgatus</i>	Golden threadfin bream	Perciformes	Nemipteridae	19.80	0.70				
<i>Neoditrema ransonnetii</i>	Surfperch	Perciformes	Embiotocidae	21.80	1.80				
<i>Niphon spinosus</i>	Ara	Perciformes	Serranidae	19.30	1.40				
<i>Notopterus notopterus</i>	Bronze Featherback	Osteoglossiformes	Notopteridae	17.80	1.00	0.74	30		
<i>Odontesthes incisa</i>	Silverside	Atheriniformes	Atherinidae	16.00	2.00				
<i>Odontesthes bonariensis</i>	Argentinian Silverside	Atheriniformes	Atherinopsidae	18.30	1.90				
<i>Odontesthes regia</i>	Chilean Silverside	Atheriniformes	Atherinopsidae	18.60					
<i>Odontobutis platycephala</i>	Fresh-water goby	Gobioidei	Odontobutidae	16.90	1.00				
<i>Ompok pabda</i>	Pabdah Catfish	Siluriformes	Siluridae	17.30	1.20	1.25			
<i>Oncorhynchus gorbuscha</i>	Pink Salmon	Salmoniformes	Salmonidae	21.70	0.40	0.60	13	4.60	22.00
<i>Oncorhynchus keta</i>	Chum salmon	Salmoniformes	Salmonidae	21.45	0.80	0.50	11	5.90	32.00
<i>Oncorhynchus kisutch</i>	Coho salmon	Salmoniformes	Salm onidae	20.65	1.40	0.60	36	5.20	15.00

Species	Common name	Order	Family	Protein	Iron	Zinc	Vit A	Vit B12	Vit D
<i>Oncorhynchus masou</i>	Cherry salmon	Salmoniformes	Salmonidae	20.60	1.20	0.50	63	7.60	10.00
<i>Oncorhynchus masou ishikawae</i>	Masu Salmon	Salmoniformes	Salmonidae	18.30	0.40	0.80	7	5.50	9.00
<i>Oncorhynchus mykiss</i>	Rainbow trout	Salmoniformes	Salmonidae	21.10	1.80				
<i>Oncorhynchus nerka</i>	Sockeye salmon	Salmoniformes	Salmonidae	22.50	0.40	0.50	27	9.40	33.00
<i>Oncorhynchus tshawytscha</i>	Chinook Salmon	Salmoniformes	Salmonidae	18.80	0.25	0.35	111	2.35	16.00
<i>Oplegnathus fasciatus</i>	Rock bream	Perciformes	Oplegthidae	18.65	0.45	0.60	39	1.30	3.00
<i>Oplegnathus punctatus</i>	Spotted knifejaw	Perciformes	Oplegthidae	18.90	0.70				
<i>Oreochromis mossambicus</i>	Mozambique tilapia	Perciformes	Cichlidae	20.05	0.80	1.40	2		5.50
<i>Oreochromis niloticus</i>	Nile Tilapia	Perciformes	Cichlidae	19.80	0.50	0.40	3	2.30	11.00
<i>Osmerus mordax</i>	Pacific rainbow smelt	Salmoniformes	Osmeridae	17.40	1.40				
<i>Ostichthys japonicus</i>	Big-eye soldierfish	Beryciformes	Holocentridae	21.30	1.20				
<i>Pagrus major</i>	Genuine porgy	Perciformes	Sparidae	19.50	0.35	0.40	8	1.20	5.00
<i>Pagrus pagrus</i>	Red Porgy	Perciformes	Sparidae	20.40	1.80	3.30			
<i>Pampus argenteus</i>	Silver/white pomfret	Perciformes	Stromateidae	17.13	0.40	0.39	90	1.40	5.00
<i>Pampus chinensis</i>	Chinese Silver Pomfret	Perciformes	Stromateidae	15.90	0.40	0.59			
<i>Pangasianodon hypophthalmus</i>	Striped Catfish	Siluriformes	Pangasiidae	6.25				4.50	
<i>Pangasius pangasius</i>	Pangas Catfish	Siluriformes	Pangasiidae	15.90	0.10	1.85	5		
<i>Parabembras curtus</i>	Matron flathead	Scorpaeniformes	Bembridae	20.10	1.30				
<i>Parajulis poecilopterus</i>	Multicolor finfish	Perciformes	Labridae	19.30	2.60				
<i>Paralichthys olivaceus</i>	Bastard halibut	Pleuronectiformes	Paralichthyidae	20.75	0.38	0.40	12	1.00	3.00
<i>Parapercis multifasciata</i>	Bicolor-barred weever	Perciformes	Pinguipedidae	18.30	0.90				
<i>Parapercis sexfasciata</i>	Grub fish	Perciformes	Pinguipedidae	20.80	1.30				
<i>Parapristipoma trilineatum</i>	Grunt	Perciformes	Haemulidae	17.10	0.80	0.60	41	5.80	15.00
<i>Parascloopsis inermis</i>	Unarmed dwarf monocle bream	Perciformes	Nemipteridae	19.20	0.60				
<i>Parastromateus niger</i>	Black Pomfret	Perciformes	Carangidae	19.60	0.90	0.48			
<i>Parona signata</i>	Paro Leatherjacket	Perciformes	Carangidae	20.10					
<i>Pennahia argentata</i>	White croaker	Perciformes	Sciaenidae	18.65	0.40	0.60	5	2.50	2.90
<i>Percophis brasiliensis</i>	Brazilian Flathead	Perciformes	Percophidae	20.10					
<i>Pholis nebulosa</i>	Tidepool gunnel	Perciformes	Pholidae	20.70	1.10				
<i>Platycephalus indicus</i>	Bartailed flathead	Scorpaeniformes	Platycephalidae	20.00	0.60				
<i>Plecoglossus altivelis</i>	Sweet fish	Salmoniformes	Plecoglossidae	17.50	1.10	0.80	35	10.30	1.00
<i>Plectorhynchus cinctus</i>	Crescent sweetlips	Perciformes	Haemulidae	19.50	0.70				
<i>Pleurogrammus azonus</i>	Arabesque greenling	Scorpaeniformes	Hexagrammidae	18.45	4.15	1.10	25	10.70	3.00
<i>Pleuronectes herzensteini</i>	Brown sole	Pleuronectiformes	Pleuronectidae	19.50	0.35	0.80	5	3.10	13.00
<i>Pleuronectes yokohamae</i>	Marbled sole	Pleuronectiformes	Pleuronectidae	18.95	0.35	0.80	6	1.80	6.70
<i>Pleuronichthys cornutus</i>	Ridged-eye flounder	Pleuronectiformes	Pleuronectidae	17.60	1.10				
<i>Polynemus quadrifilis</i>	Giant African Threadfin	Perciformes	Poly nemidae	17.60	0.30	1.00			
<i>Pomatomus saltatrix</i>	Bluefish	Perciformes	Pomatomidae	21.50	1.40				

Species	Common name	Order	Family	Protein	Iron	Zinc	Vit A	Vit B12	Vit D
<i>Priacanthus macracanthus</i>	Red bigeye	Perciformes	Priacanthidae	18.90	1.20				
<i>Prionotus punctatus</i>	Bluewing Searobin	Scorpaeniformes	Triglidae	18.90					
<i>Protonibea diacanthus</i>	Blacksotted Croaker	Perciformes	Sciaenidae	18.60	0.40	0.65	17		0.60
<i>Psenopsis anomala</i>	Butterfish	Perciformes	Centrolophidae	16.35	0.55	0.80	95	2.70	2.00
<i>Pseudaesopia japonica</i>	Wavy -banded sole	Pleuronectiformes	Soleidae	18.40	1.10				
<i>Pseudambassis ranga</i>	Indian Glassy Catfish	Perciformes	Ambassidae	15.50	2.00	2.45	106		
<i>Pseudoblennius cottoides</i>	Sunrise sculpin	Scorpaeniformes	Cottidae	22.40	1.70				
<i>Pseudocaranx dentex</i>	Striped Jack/White Trevally	Perciformes	Carangidae	21.90	0.70	1.10	10	3.20	18.00
<i>Pseudogobio esocinus</i>	Pike gudgeon	Cypriniformes	Cyprinidae	15.70	1.20				
<i>Pseudolabrus japonicus</i>	Bambooleaf wrasse	Perciformes	Labridae	18.90	1.10				
<i>Pseudoplatystoma corruscans</i>	Spotted Sorubim	Siluriformes	Pimelodidae	18.20	1.90				
<i>Pseudorasbora parva</i>	Stone moroko	Cypriniformes	Cyprinidae	16.40	2.50				
<i>Pterocaesio digramma</i>	Double-Lined Fusilier	Perciformes	Caesionidae	20.20	0.50	0.70	7	4.40	2.00
<i>Puntius sophore</i>	Pool Barb	Cypriniformes	Cyprinidae	17.60	2.00	3.00			
<i>Rastrelliger brachysoma</i>	Short Mackerel	Perciformes	Scombridae	6.25					
<i>Rastrelliger kanagurta</i>	Indian mackerel	Perciformes	Scombridae	20.51					
<i>Rexea prometheoides</i>	Royal escolar	Perciformes	Gempyidae	20.00	0.80				
<i>Salangichthys microdon</i>	Icefish	Salmoniformes	Salangidae	13.45	0.55	1.20	50	3.30	1.00
<i>Salminus maxillosus</i>	Dorado	Characiformes	Bryconidae	18.80					
<i>Salmo salar</i>	Atlantic Salmon	Salmoniformes	Salmonidae	20.10	0.30	0.40	17	8.90	10.00
<i>Salmophasia bacaila</i>	Large Razorbelly Minnow	Cypriniformes	Cyprinidae	18.10	5.40	3.10			
<i>Salmophasia phulo</i>	Razorbelly Minnow	Cypriniformes	Cyprinidae	15.30	1.90	3.10			
<i>Salvelinus alpinus</i>	Arctic Char	Salmoniformes	Salmonidae	18.75	0.34	0.42	32		25.80
<i>Salvelinus leucomaenis</i>	White-Spotted Char/Char/Japanese Char	Salmoniformes	Salmonidae	19.00	0.30	0.80	5	4.20	5.00
<i>Salvelinus namaycush</i>	Lake Trout	Salmoniformes	Salmonidae	15.78	0.23	0.62	40		19.70
<i>Sarda orientalis</i>	Striped bonito	Perciformes	Scombridae	24.60	2.10				
<i>Sarda sarda</i>	Atlantic Bonito	Perciformes	Scombridae	22.00					
<i>Sardina pilchardus</i>	European pilchard	Clupeiformes	Clupeidae	17.33					21.20
<i>Sardinella zunasi</i>	Japanese sardinella	Clupeiformes	Clupeidae	16.30	1.90				
<i>Sardinops sagax</i>	South American Pilchard	Clupeiformes	Clupeidae	18.77	2.00	1.60	8	15.70	32.00
<i>Satyrichthys rieffeli</i>	Spotted armored-gurrd	Scorpaeniformes	Peristediidae	19.30	2.10				
<i>Saurida undosquamis</i>	Lizard fish	Aulopiformes	Synodontidae	20.80	0.40				
<i>Scomber australasicus</i>	Blue Mackerel	Perciformes	Scombridae	23.00	1.60	1.10	8	12.60	4.30
<i>Scomber colias</i>	Black Drum	Perciformes	Sciaenidae	18.80					
<i>Scomber japonicus</i>	Mackerel	Perciformes	Scombridae	19.00	1.60	1.10	37	12.90	5.10
<i>Scomber scombrus</i>	Atlantic Mackerel	Perciformes	Scombridae	17.20	0.90	0.90	44	8.10	10.00
<i>Scomberomorus cavalla</i>	King Mackerel	Perciformes	Scombridae	20.90	0.50	0.60	17	0.55	

Species	Common name	Order	Family	Protein	Iron	Zinc	Vit A	Vit B12	Vit D
<i>Scomberomorus commerson</i>	row-Barred Spanish Mackerel	Perciformes	Scombridae	19.80	2.00	0.40	30		
<i>Scomberomorus guttatus</i>	Indo-Pacific King Mackerel	Perciformes	Scombridae	20.90	0.80	0.78			
<i>Scomberomorus koreanus</i>	Korean seerfish	Perciformes	Scombridae	17.90	0.70				
<i>Scomberomorus niphonius</i>	Spanish mackerel	Perciformes	Scombridae	19.73	0.70	0.80	12	4.00	7.00
<i>Scombrops boops</i>	Japanese blue fish	Perciformes	Scombrotidae	18.75	0.65	0.40	8	1.90	4.00
<i>Scorpaena neglecta</i>	Izu scorpionfish sting fish	Scorpaeniformes	Scorpaenidae	15.50	0.90				
<i>Scorpaenopsis cirrhosa</i>	Weedy stingfish	Scorpaeniformes	Scorpaenidae	19.00	1.10				
<i>Sebastes alutus</i>	Pacific Ocean perch, Longjaw rockfish	Scorpaeniformes	Scorpaenidae	16.45	0.25	0.40	20	1.60	3.00
<i>Sebastes hubbsi</i>	Amorclad rockfish	Scorpaeniformes	Scorpaenidae	18.30	0.90				
<i>Sebastes inermis</i>	Black rock fish	Scorpaeniformes	Scorpaenidae	19.30	0.60				
<i>Sebastes iracundus</i>	Angry Rockfish	Scorpaeniformes	Scorpaenidae	16.30	0.20	0.40	85	3.30	3.00
<i>Sebastes matsubarae</i>	Matsubara's Red Rockfish	Scorpaeniformes	Scorpaenidae	16.80	0.30	0.40	26	0.70	1.00
<i>Sebastes oblongus</i>	Oblong rockfish	Scorpaeniformes	Scorpaenidae	21.30	0.70				
<i>Sebastes pachycephalus</i>	Spotbelly rockfish	Salmoniformes	Salmonidae	19.10	0.80				
<i>Sebastes schlegelii</i>	Korean rockfish	Scorpaeniformes	Scorpaenidae	21.40	0.50				
<i>Sebastes taczanowskii</i>	White-edged rockfish	Perciformes	Sciaenidae	19.70	1.70				
<i>Sebastes thompsoni</i>	Gold eye rockfish	Scorpaeniformes	Scorpaenidae	18.60	1.50				
<i>Sebastes vulpes</i>	Fox jacopever	Scorpaeniformes	Scorpaenidae	22.40	1.00				
<i>Sebastiscus marmoratus</i>	Scorpion fish	Scorpaeniformes	Scorpaenidae	19.60	0.45	0.50	3	1.20	2.00
<i>Sebastolobus macrochir</i>	Kichiji Rockfish/ Broadbanded Thorny head	Scorpaeniformes	Sebastidae	13.60	0.30	0.40	65	1.00	4.00
<i>Semicossyphus reticulatus</i>	Cold porgy	Perciformes	Labridae	18.50	0.30				
<i>Seriola dumerili</i>	Greater Amberjack	Perciformes	Carangidae	21.00	0.60	0.70	4	5.30	4.00
<i>Seriola lalandi</i>	Amberjack	Perciformes	Carangidae	22.45	0.85	0.70	19	2.10	5.00
<i>Seriola quinqueradiata</i>	Yellow tail	Perciformes	Carangidae	21.20	1.00	0.70	50	3.80	8.00
<i>Seriolella punctata</i>	Silver Warehou	Perciformes	Centrolophidae	18.60	0.60	0.50	100	1.80	3.00
<i>Setipinna phasa</i>	Gangetic Hairfin Anchovy	Clupeiformes	Engraulidae	17.70	1.80	3.20	12		
<i>Setipinna taty</i>	Scaly Hairfin Anchovy	Clupeiformes	Engraulidae	19.30	2.30	1.60	8		
<i>Siganus fuscescens</i>	Mottled spinefoot	Perciformes	Siganidae	20.30	1.20				
<i>Sillago japonica</i>	Japanese Whiting	Perciformes	Sillaginidae	18.50	0.10	0.40	1	2.20	0.70
<i>Sillago sihama</i>	Silver sillago	Perciformes	Sillaginidae	19.50	2.30				
<i>Silurus asotus</i>	Amur catfish	Siluriformes	Siluridae	15.10	0.80				
<i>Siniperca scherzeri</i>	Leopard mandarin fish	Perciformes	Percichthyidae	17.20	2.10				
<i>Sperata seenghala</i>	Giant River-Catfish	Siluriformes	Bagridae	15.90	0.70	0.23			
<i>Sphyaena japonica</i>	Japanese barracuda	Perciformes	Sphyaenidae	18.90	0.30				
<i>Sphyaena pinguis</i>	Red barracuda	Perciformes	Sphyaenidae	19.70	0.60	0.50	12	2.30	11.00
<i>Spratelloides gracilis</i>	Blue Sprat	Clupeiformes	Clupeidae	18.80	1.10	1.90		8.30	10.00
<i>Sprattus fuegensis</i>	Falkland Sprat	Clupeiformes	Clupeidae	14.00					

Species	Common name	Order	Family	Protein	Iron	Zinc	Vit A	Vit B12	Vit D
<i>Sprattus sprattus</i>	Sprat	Clupeiformes	Clupeidae	22.63					
<i>Stenodus leucichthys</i>	Sheefish	Salmoniformes	Salmonidae	19.00	0.40	0.30			
<i>Stephanolepis cirrhifer</i>	Thread-sail filefish	Tetraodontiformes	Mocanthidae	18.95	0.30	0.40	2	1.30	43.00
<i>Stichaeus grigorjewi</i>	Long shanny	Perciformes	Stichaeidae	19.10	1.20				
<i>Strangomera bentincki</i>	Araucanian herring	Clupeiformes	Clupeidae	16.50					
<i>Suggrundus meerdervoorti</i>	Big-eyed flathead	Scorpaeniformes	Platycephalidae	17.50	0.20	0.60	2	3.00	11.00
<i>Synchiropus altivelis</i>	Highfin bigeye dragonet	Perciformes	Callionymidae	16.90	0.60				
<i>Synodus myops</i>	Snakefish	Aulopiformes	Synodontidae	20.00	0.60				
<i>Systemus sarana</i>	Olive Barb	Cypriniformes	Cyprinidae	17.40	0.60	0.74			
<i>Tachysurus fulvidraco</i>	Yellow catfish	Siluriformes	Bagridae	15.55	0.90				
<i>Takifugu pardalis</i>	Panther puffer	Tetraodontiformes	Tetraodontidae	18.90	2.50				
<i>Takifugu poecilonotus</i>	Fine-patterned puffer	Tetraodontiformes	Tetraodontidae	15.90	1.00				
<i>Takifugu porphyreus</i>	Purple puffer	Tetraodontiformes	Tetraodontidae	20.20	0.25	1.50	7	3.00	6.00
<i>Takifugu rubripes</i>	Tiger puffer	Tetraodontiformes	Tetraodontidae	19.05	0.25	0.90	3	1.90	4.00
<i>Takifugu stictonotus</i>	Spotty-back puffer	Tetraodontiformes	Tetraodontidae	19.30	3.10				
<i>Takifugu vermicularis</i>	Purple puffer	Tetraodontiformes	Tetraodontidae	20.25	1.20				
<i>Takifugu xanthopterus</i>	Yellowfin puffer	Tetraodontiformes	Tetraodontidae	19.30	4.40				
<i>Tanakius kitaharae</i>	Willow flounder	Perciformes	Carangidae	18.30	1.90				
<i>Tenualosa ilisha</i>	Hilsha Shad	Clupeiformes	Clupeidae	18.00	1.30	0.54			
<i>Thamnaconus modestus</i>	Black scraper	Tetraodontiformes	Mocanthidae	18.05	0.45	0.50		1.40	8.00
<i>Theragra chalcogramma</i>	Alaska pollack	Gadiformes	Gadidae	17.45	0.85	0.50	10	2.90	0.50
<i>Thunnus alalunga</i>	Albacore	Perciformes	Scombridae	26.00	0.90	0.50	4	2.80	7.00
<i>Thunnus albacares</i>	Yellowfin tuna	Perciformes	Scombridae	24.10	1.80	0.50	2	5.80	6.00
<i>Thunnus maccoyii</i>	Southern Bluefin Tuna	Perciformes	Scombridae	23.30	1.60	0.50	39	0.70	
<i>Thunnus obesus</i>	Big-Eye Tuna	Perciformes	Scombridae	22.80	1.40	0.40	3	4.50	2.00
<i>Thunnus thynnus</i>	Bluefin tuna	Perciformes	Scombridae	26.20	2.05	0.50	61	6.90	12.00
<i>Thymallus arcticus</i>	Arctic Grayling	Salmoniformes	Salmonidae	20.00	1.00	0.70			
<i>Thyrsites atun</i>	Barracouta	Perciformes	Gempylidae	21.70	0.60	0.50	55	6.50	2.00
<i>Trachipterus ishikawae</i>	Slender ribbonfish	Lampriformes	Trachipteridae	18.10	0.30				
<i>Trachurus japonicus</i>	Horse mackerel	Perciformes	Carangidae	20.20	0.75	1.10	7	7.10	8.90
<i>Trachurus picturatus</i>	Bluejack Mackerel	Perciformes	Carangidae	19.00					
<i>Trachurus trachurus</i>	Atlantic Horse Mackerel	Perciformes	Carangidae	19.60	1.00	0.90	16	8.10	8.00
<i>Tribolodon hakonensis</i>	Far eastern dace	Cypriniformes	Cyprinidae	19.20	1.10	3.40	41	8.50	19.00
<i>Trichiurus lepturus</i>	Hair tail	Perciformes	Trichiuridae	17.50	0.60	0.50	52	0.90	14.00
<i>Trichogaster fasciata</i>	Banded Gourami	Perciformes	Belontiidae	15.80	0.90	1.35	39		
<i>Umbrina canosai</i>	Argentine Croaker	Perciformes	Sciaenidae	19.10					
<i>Upeneus japonicus</i>	Bensasi goatfish	Perciformes	Mullidae	7.10	1.40				
<i>Uranoscopus japonicus</i>	Stargazer	Perciformes	Uranoscopidae	18.20	0.70				
<i>Urophycis brasiliensis</i>	Brazilian Codling	Gadiformes	Phycidae	17.60	2.10				

Species	Common name	Order	Family	Protein	Iron	Zinc	Vit A	Vit B12	Vit D
<i>Verasper variegatus</i>	Spotted halibut	Pleuronectiformes	Pleuronectidae	18.20	0.20				
<i>Wallago attu</i>	Wallago	Siluriformes	Siluridae	15.40	0.80	0.27	1		
<i>Xenentodon cancila</i>	Freshwater Garfish	Beloniformes	Belonidae	16.60	0.80	0.94	65		
<i>Xenocephalus elongatus</i>	Blue-spotted stargazer	Perciformes	Uranoscopidae	17.40	0.40				
<i>Xiphias gladius</i>	Swordfish	Perciformes	Xiphiidae	18.10	3.35	0.70	61	1.90	8.80
<i>Zacco platypus</i>	Common minnow	Cypriniformes	Cyprinidae	18.85	1.25	2.50	10	11.30	10.00
<i>Zalanthias kelloggi</i>	Eastern flower porgy	Perciformes	Serranidae	19.00	1.00				
<i>Zebrias zebra</i>	Zebra sole	Pleuronectiformes	Soleidae	18.90	1.20				
<i>Zenopsis nebulosa</i>	Mirror dory	Zeiformes	Zeidae	20.30	0.80				
<i>Zeus faber</i>	John dory	Zeiformes	Zeidae	19.10	0.60				
<i>Zoarces gillii</i>	Blotched eelpout	Perciformes	Zoarcidae	18.50	0.40				

Supplementary Table 2. Nutrient content of fish species in dataset.^{2,3,4,5,6,7,8,9,10,11,12,13,14,15}

Category	Nutrient	# Valid Species	Min	Max	Median	Mean	SD
Protein, fats (g/100g)	Protein	371	6.3	33.8	18.6	18.5	2.9
	Total fat	367	0.1	26.8	2.3	3.6	4.1
	Omega-3 fatty acids	238	0.01	7.68	0.69	0.97	1.12
	Omega-6 fatty acids	238	0.00	4.41	0.11	0.20	0.41
Minerals (mg/100g)	Iron	344	0.10	9.10	1.00	1.19	1.04
	Zinc	177	0.06	3.90	0.65	0.91	0.73
Vitamins (µg/100g)	Vitamin A (retinol activity equivalents)	146	0.0	2680.0	15.0	96.6	356.5
	Vitamin B12	124	0.0	28.2	2.9	4.6	4.4
	Vitamin D	122	0.0	43.0	5.0	8.1	8.2

Supplementary Table 3. Summary statistics for life history traits.

Continuous Variables	# Valid Species	Min	Max	Median	Mean	SD
Minimum depth (m)	259	0	320	3.0	28.15	59.4
Maximum depth (m)	249	2	3850	200.0	247.5	484.8
Maximum length (cm)	370	8.0	505.1	48.0	71.7	70.4
<i>a</i> (L/W scalar)	333	.0004	.0263	0.0089	0.0097	0.0055
<i>b</i> (L/W exponent)	332	2.79	3.39	3.05	3.05	0.08
Trophic level	373	2.0	4.7	3.6	3.6	0.5

Categorical Variables	Categories	# Species	Percent
Habitat	Bathydemersal	15	4.0
	Benthopelagic	90	23.9
	Demersal	149	39.6
	Pelagic	25	6.6
	Pelagic-neritic	51	13.6
	Reef-associated	44	11.7
Latitudinal range	Tropical	126	33.5
	Subtropical	104	27.7
	Temperate	126	33.5
	Boreal/austral	5	1.3
	Polar	8	2.1

Supplementary Table 4. Evolutionary correlation matrix, with omega-3 and omega-6 fatty acids included. Correlations with $p < 0.1$ are in **bold**.

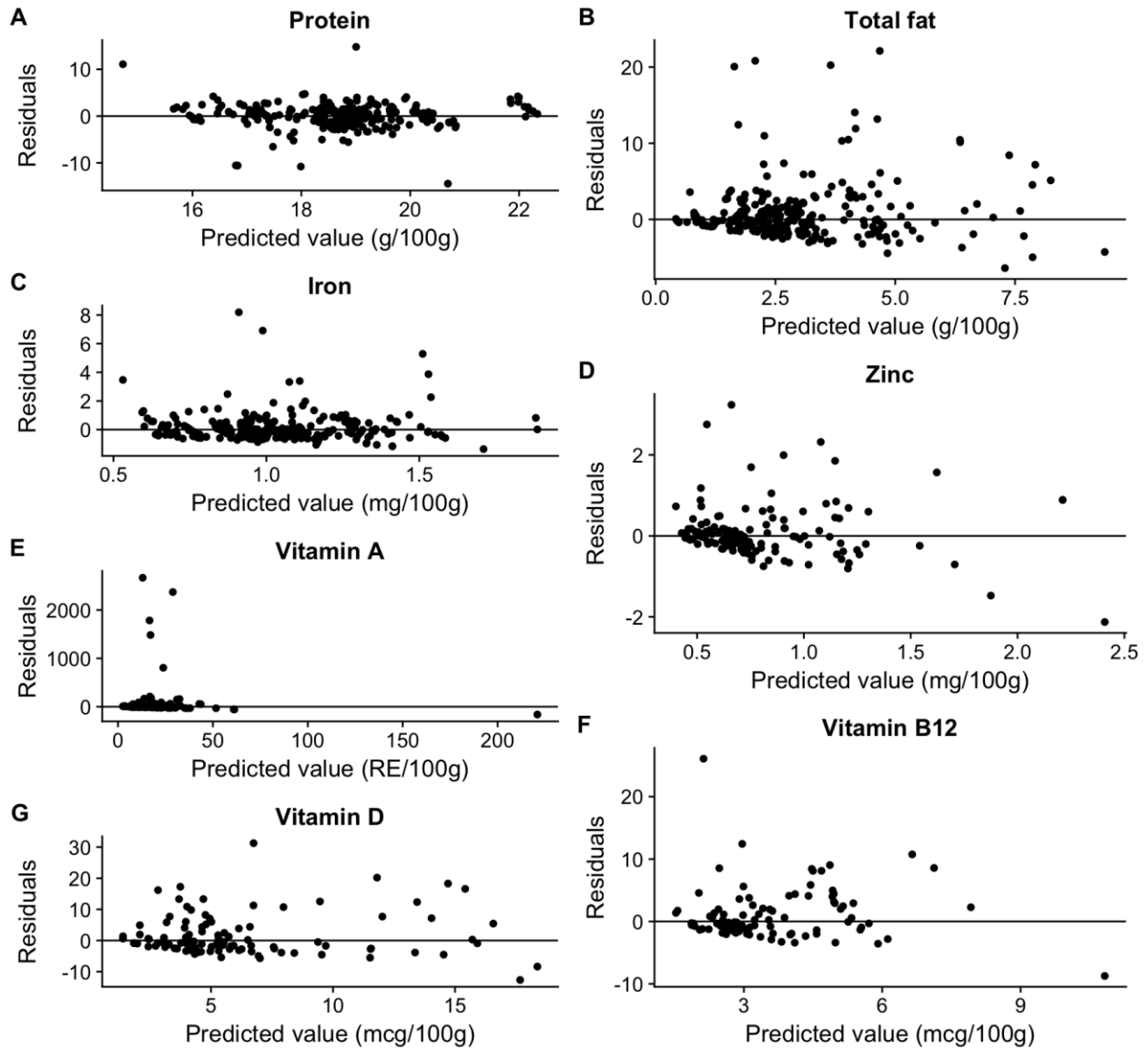
	depmin	depmax	maxlen	a_lw	b_lw	troph	protein	fat	iron	zinc	vitA	vitb12	vitd
depmin	1.00	0.22	0.07	-0.06	0.05	0.09	-0.02	0.06	-0.04	-0.08	0.17	0.00	-0.11
depmax	0.22	1.00	0.46	-0.32	0.15	0.43	-0.23	0.37	-0.07	-0.25	0.46	-0.09	0.04
maxlen	0.07	0.46	1.00	-0.13	-0.10	0.44	0.11	0.12	-0.06	-0.45	0.31	-0.21	0.13
a_lw	-0.06	-0.32	-0.13	1.00	-0.60	-0.22	0.13	-0.18	-0.13	-0.11	-0.13	-0.15	0.09
b_lw	0.05	0.15	-0.10	-0.60	1.00	0.00	-0.15	0.10	0.20	0.23	0.15	0.06	0.04
troph	0.09	0.43	0.44	-0.22	0.00	1.00	0.17	0.01	-0.13	-0.24	0.06	-0.16	-0.06
protein	-0.02	-0.23	0.11	0.13	-0.15	0.17	1.00	-0.39	0.08	0.07	-0.41	0.14	0.01
lipid	0.06	0.37	0.12	-0.18	0.10	0.01	-0.39	1.00	0.16	-0.04	0.69	0.31	0.42
iron	-0.04	-0.07	-0.06	-0.13	0.20	-0.13	0.08	0.16	1.00	0.55	0.21	0.56	0.26
zinc	-0.08	-0.25	-0.45	-0.11	0.23	-0.24	0.07	-0.04	0.55	1.00	-0.03	0.38	0.18
ret_eq	0.17	0.46	0.31	-0.13	0.15	0.06	-0.41	0.69	0.21	-0.03	1.00	0.05	0.27
vitb12	0.00	-0.09	-0.21	-0.15	0.06	-0.16	0.14	0.31	0.56	0.38	0.05	1.00	0.22
vitd	-0.11	0.04	0.13	0.09	0.04	-0.06	0.01	0.42	0.26	0.18	0.27	0.22	1.00

P-VALUES

	depmin	depmax	maxlen	a_lw	b_lw	troph	protein	fat	iron	zinc	vitA	vitb12	vitd
depmin	NA	0.085	0.340	0.351	0.372	0.301	0.392	0.351	0.376	0.322	0.157	0.397	0.271
depmax	0.085	NA	0.000	0.014	0.186	0.001	0.071	0.004	0.337	0.050	0.000	0.308	0.381
maxlen	0.340	0.000	NA	0.232	0.281	0.000	0.269	0.258	0.355	0.000	0.016	0.097	0.223
a_lw	0.351	0.014	0.232	NA	0.000	0.087	0.234	0.135	0.228	0.267	0.226	0.188	0.308
b_lw	0.372	0.186	0.281	0.000	NA	0.397	0.198	0.283	0.112	0.068	0.199	0.351	0.379
troph	0.301	0.001	0.000	0.087	0.397	NA	0.150	0.396	0.240	0.064	0.354	0.175	0.359
protein	0.392	0.071	0.269	0.234	0.198	0.150	NA	0.002	0.317	0.333	0.001	0.207	0.395
lipid	0.351	0.004	0.258	0.135	0.283	0.396	0.002	NA	0.170	0.374	0.000	0.017	0.001
iron	0.376	0.337	0.355	0.228	0.112	0.240	0.317	0.170	NA	0.000	0.097	0.000	0.041
zinc	0.322	0.050	0.000	0.267	0.068	0.064	0.333	0.374	0.000	NA	0.385	0.003	0.134
ret_eq	0.157	0.000	0.016	0.226	0.199	0.354	0.001	0.000	0.097	0.385	NA	0.362	0.034
vitb12	0.397	0.308	0.097	0.188	0.351	0.175	0.207	0.017	0.000	0.003	0.362	NA	0.082
vitd	0.271	0.381	0.223	0.308	0.379	0.359	0.395	0.001	0.041	0.134	0.034	0.082	NA

Supplementary Figures

Supplementary Figure 1. Residual plots for nutrient prediction: protein (A), total fat (B), iron (C), zinc (D), vitamin A (E), vitamin B12 (F), and vitamin D (G).



Supplementary References

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Description of Additional Supplementary Files:

- **Supplementary data file 1.** *SD1_fish_database.csv*. Database of life history and nutrient content values for all included species.
- **Supplementary data file 2.** *SD2_phyloPred_lambda.totalfat.csv*. Predicted total fat content for Actinopterygii species.
- **Supplementary data file 3.** *SD3_phyloPred_lambda.omega3.csv*. Predicted omega-3 fatty acids content for Actinopterygii species.
- **Supplementary data file 4.** *SD4_phyloPred_lambda.omega6.csv*. Predicted omega-6 fatty acids content for Actinopterygii species.
- **Supplementary data file 5.** *SD5_phyloPred_lambda.iron.csv*. Predicted iron content for Actinopterygii species.
- **Supplementary data file 6.** *SD6_phyloPred_lambda.zinc.csv*. Predicted zinc content for Actinopterygii species.
- **Supplementary data file 7.** *SD7_phyloPred_lambda.vitA.csv*. Predicted vitamin A content for Actinopterygii species.
- **Supplementary data file 8.** *SD8_phyloPred_lambda.vitB12.csv*. Predicted vitamin B12 content for Actinopterygii species.
- **Supplementary data file 9.** *SD9_phyloPred_lambda.vitD.csv*. Predicted vitamin D content for Actinopterygii species.
- **Supplementary data file 10.** *SD1_phyloPred_lambda.protein.csv*. Predicted protein content for Actinopterygii species.
- **Supplementary data file 11.** *SD11_bionut.evolCorMat.R*. Script for evolutionary correlations.
- **Supplementary data file 12.** *SD12_bionut.PGLS.R*. Script for phylogenetic least squares regression.
- **Supplementary data file 13.** *SD13_phylosigByVar.R*. Script for estimating phylogenetic signal of nutrient variables.
- **Supplementary data file 14.** *SD14_predValidation.lambda-only.R*. Script for carrying out validation for predictions under the lambda model.
- **Supplementary data file 15.** *SD15_predValidation.pgls-lambda.R*. Script for carrying out validation for predictions under the lambda plus phylogenetic regression model.