## Functional diversity in aquatic ecosystems yields enhanced nutritional benefits

## Abstract

While food provisioning is one of the most widely acknowledged ecosystem services provided by aquatic ecosystems, the role of seafood as a source of valuable micronutrients scarce in the human diet is often overlooked. The ecological mechanisms responsible for a nutritionally diverse set of seafood species are not well understood, despite heavy research emphasis on the ecological mechanisms responsible for fisheries productivity. A primary challenge in linking ecological processes to human well-being is identifying comparable metrics for ecological properties and human benefits. For nutritional value, one metric that facilitates comparisons is the nutrient content in an edible portion relative to daily reference intake values (DRI). We used dietary food composition data to analyze the relationship between ecological structure and the nutritional value of aquatic species in terms of DRI. We find that there is a high degree of variability in nutrient profiles across taxa, and that increasing functional diversity contributes to increased nutritional diversity. For example, filter-feeding molluscs represent a nutritionally distinct and valuable source of minerals (ie. calcium, iron and zinc), which are not present at equivalent levels in other functional groups. Finally, we test whether functional traits explain species’ nutritional value to human consumers for 430 species of fish from all major oceanic and freshwater eco-regions. We find that an ecological trait-based approach is effective at simplifying the complexity of aquatic food webs into a few key axes that strongly control the composition of micronutrients in fish assemblages. For some, but not all, nutrients we analyzed (e.g. Ca, Hg, EPA, DHA), the nutrient content of edible portions varied predictably among species with latitude and body size, consistent with the physiological functional roles of micronutrients in fish. Our results suggest that the availability of micronutrients in fish assemblages may depend on geography and functional composition of the catch. Our approach integrates ecological variation and patterns in the human consumption of species to explicitly link ecological structure with one metric of human well-being to suggest that a diverse fish assemblage can support a more nutritious diet to local seafood consumers.

**Introduction**

1. **Many coastal human communities rely on wild harvests from local aquatic ecosystems to meet requirements for a wide range of macro- and micronutrients, such as vitamins and minerals (Kuhnlein and Receveur 2007, Kuhnlein et al. 2009, Kawarazuka and Bene 2011). The ecology of food security, an important ecosystem service, is not just about predicting yields, it is about understanding the ecological conditions that lead to a stable supply of nutritionally diverse foods.**
2. **A primary challenge of linking ecological processes with human well-being is finding comparable units and metrics for ecological properties and human benefits.** In the context of human nutrition, one metric that facilitates comparisons is the nutrient content in an edible portion relative to dietary reference intake values (DRI).
3. **Here, we synthesize fish nutritional content data to quantify variation in nutritional quality among aquatic taxa and test whether aspects of ecological structure (such as functional group diversity, and individual level variables such as body size and trophic position) are related to variation in nutritional profile from the perspective of a human diet.** First, we review the importance of nutrition as an ecosystem function or service. Then, we present a newly synthesized database of fish nutritional content and traits from X species of fish from all ocean regions. We analyzed this database to characterize the range of variability in fish tissue nutrient content among fish species consumed around the globe, and test whether nutrient profiles of commonly consumed fish species are related to species’ traits, including body size, trophic position and habitat associations, which are broadly related to the function and form of species in aquatic systems (Woodward et al. 2005, other ref?). Given that fish is known to be a high quality source of essential micronutrients, but fish consumption may be limited to a small number of portions per week (reference?), we sought to identify which species are the most nutrient dense and contribute at least 25% of DRI in a single portion.

4. While the nutritional value of seafood has been widely recognized, the ecological mechanisms responsible for a nutritionally diverse set of seafood species are not well understood. **This study is an important advance because it explicitly integrates well-established metrics of nutritional value (i.e. DRI) and ecological variation (i.e. functional group diversity, body size) to characterize the relationship between ecological structure and human well-being.**

**Nutrition as an ecosystem function and service**

Despite its clear links to human well being, the role of aquatic assemblages in provisioning of essential micronutrients has been under-represented in marine ecosystem service concepts. For both human and non-human consumers, the nutritional quality of prey species plays a fundamental role in ecosystem function. Food webs characterized by nutritionally valuable prey support higher consumer and predator biomass and have higher trophic transfer efficiencies (Hecky 1984, Muller Navarra et al. 2000, Brett et al. 2009). Changes in forage fish communities from lipid-rich to lipid-poor fish in the Pacific Ocean have caused predatory marine birds and mammals to shift their diet to less nutritionally valuable lipid-poor fish and suffer population declines (Rosen and Trites 2006; Romano et al. 2006, Osterblom et al. 2008).

For human consumers, fish are a good source of high quality protein, a range of micronutrients and essential fatty acids (Tacon and Metian 2013). In 2009, aquatic species accounted for 16.6% of the global total supply of animal protein, providing more than three billion people with almost 20% of their average per capita intake of animal protein (FAO ref). However, the role of fish as a source of essential micronutrients may be even more important than as a source of protein (Allison et al. 2007). Fish is important in the diets of many poor populations suffering from vitamin and mineral deficiencies (Roos et al. 2007, Tacon and Metian 2013). In many vulnerable communities around the world, fish consumption plays an important role in combating micronutrient deficiencies (Kawarazuka and Bene 2011). For example, in rural Bangladesh, some of the poorest communities are heavily dependent on small fish from capture fisheries to meet their micronutrient needs. Consumption of small indigenous fishes contributes 40% and 31% of the total recommended intakes of vitamin A and calcium, respectively, at household level in the peak fish production season (Roos et al. 2007). Locally caught seafood contributes significantly to micronutrient intakes in Arctic Canadian Indigenous populations (Kuhnlein and Receveur 2007, Johnson-Down and Egeland 2010).

**Dietary Reference Intakes as a metric of nutritional value**

A primary challenge in linking ecological processes with human well-being is finding comparable units and metrics for ecological properties and human benefits. The value of a fish species in terms of human nutrition benefits can be quantified as the nutrient content in an edible portion relative to Dietary Reference Intake (DRI) values. The DRI is the daily intake level of a nutrient that is considered to be sufficient to meet the requirements of 97–98% of healthy individuals in every demographic (National Academies of Sciences 2011). Fish species vary widely in their concentration of essential nutrients (USDA 2011). For example, assuming a serving size of 85g of fish, sardines (1.9 g DHA per 100 g tissue) and Pacific herring (0.83 g DHA/100g) provide the recommended level of 1.0g/day EPA and DHA in a single serving, while pink salmon, canary rockfish and surf smelt would require 1.2-1.5 servings, while pacific hake (0.15g/100g DHA) and pollock (0.24 g DHA/100g) would require 4-5 servings to meet the recommended daily requirements (Hyuhn and Kitts 2009). Thus, not all species are equally nutritionally valuable. This variability in essential fatty acid (EFA) content per serving size is related to the total fat content of the fish: the characteristically lean fish like pollock and hake have relatively low contents of EFAs, while the more lipid-rich fish have higher EFA contents.

*Overview of micronutrients in seafood and how humans consume them*

Micronutrients serve functional roles in the physiology of fishes:

How humans consume diverse seafood species: finfish we tend to consume only the muscle tissue (except some small fishes), molluscs and crustaceans, it depends. For some crustaceans, we eat the whole body (i.e. shrimps), for others, we consume certain parts (i.e. lobster and crab, leg meat and hepatopancreas).

Taken together, these patterns suggest that the edible portions of species from different taxonomic and functional groups may have vastly different nutrient profiles.

**Main questions and hypotheses:**

**1. What is the range of variability in the nutritional profile of edible portions across aquatic taxa?**

**2. Are ecological traits such as body size, trophic position or functional group correlated to nutritional profile?**

**3. What is the contribution of functional group diversity or species diversity to human nutritional benefits?**

## Methods

We aimed to document the range of variation in nutrient content across commonly consumed aquatic taxa. To understand how nutrient content varies among species, we tested whether ecological traits known to be both biologically important and exhibit predictable scaling relationships could explain this variation. [We synthesized SPATIALLY AND SIZE EXPLICIT DATA, TO IDENTIFY THRESHOLDS IN GEOGRAPHY AND OR BODY SIZE THAT INDICATE THAT A SPECIES ACHIEVES 25% RDI IN A SINGLE PORTION.]

### Literature search and data collection

To test how nutrient profile varies with ecological traits, we assembled a dataset of nutrient content in the edible portions of 400 aquatic species. We defined the nutritional profile of a species as the quantity of a given nutrient in 100 g of edible tissue - a metric that is commonly used in the human food composition literature (Nowak et al. 2014). We aimed to include as many species as possible, from marine and freshwater systems, covering a wide geographic range. We searched the literature for analytical compositional values for each of these species. We searched the peer-reviewed literature as well as food composition databases or tables, such as the Food and Agriculture Organization’s INFOODS database (FAO/INFOODS 2014) and the United States Department of Agriculture’s Nutrient Files (USDA 2012). We restricted our analysis to include only the edible portions of wild, raw fish (thus excluding prepared or farmed seafood items). Our dataset includes quantities for the following microelements: calcium; iron; zinc; mercury and two fatty acids: eicosapentaenoic acid (EPA); and docosahexaenoic acid (DHA). To address inconsistencies in fatty acid data reporting, we standardized fatty acid measurements using the fatty acid conversion factors proposed by Nowak et al. (2014).

Ecological trait information was collected for each species from FishBase (Froese and Pauly 2014) and SeaLifeBase (Palomares and Pauly 2014). We included body size (maximum length), fractional trophic position, temperature preference (using latitude as a proxy) and habitat preference (Marine, Freshwater, brackish…). We converted body length data into body mass, using established length-mass relationship data (*mass*= *a\*length^b*). We used species-specific or taxon-specific *a* and *b* parameter values published in Froese et al. (2013).

### Statistical Analysis

We modeled the relationship between nutrient content and species’ traits with linear regression models using a log-transformed power function. The full model included the entire set of predictors:

ln(nutrient content) = *Β0.i* + *Β1.i*\*ln(body size)\*latitude + *Β2.i*\*ln(body size)\*(trophic position) + *Β3.i*\*ln(body size)\*(habitat) + εi

We created models from subsets of the full model that represented hypotheses based on the known physiological roles of micronutrients **and their relationships to our set of predictors**. We identified the best subset of models using the Akaike Information Criterion, adjusted for small sample sizes (AICc). We used AICc, δaic and Akaike weights (w) to compare models. We ranked models based on w, and selected the set of models that produced a cumulative w > 0.95, meaning that we are 95% confident that the chosen set includes the best model (Burnham and Anderson 2002).

We report all models with AICc differences ( δaic = AICi − AICmin) less than or equal to two ( δaic ≤ 2). In cases where we could not obtain measurements of all traits for all species, we performed model selection on reduced datasets without missing values (Appendix A). To account for model uncertainty, we performed model averaging of coefficients in all models with δaic < 2, and included zeros as coefficients when variables did not enter a particular model (Burnham and Anderson 2002). We conducted all our analyses in R version 3.1.2 (R Core Development 2014) using the MuMIn package (<http://r-forge.r-project.org/projects/mumin/>).

-somewhere here, need to address multi-collinearity of predictor variables etc.

**Results:**

**Main messages:**

1. **There is considerable variability in nutritional profile among aquatic taxa. Variability is highest for micronutrients, lower for macronutrients.**
2. **Functional groups have distinct multi-nutrient profiles (mds plot with finfish/crustaceans/molluscs color coded).**
3. **Within functional groups, some traits such body size and latitude are strongly associated with nutritional profile.**
4. **Few species contain reach DRI targets for multiple nutrients.**
5. **Functional group diversity enhances dietary nutritional diversity and nutritional benefits that human communities may derive from seafood assemblages.**
6. **ADD SOME SORT OF CASE STUDY THAT LOOKS AT NUTRITIONAL FUNCTIONAL DIVERSITY IN A GIVEN COUNTRY OR TAXON??**

**Discussion:**

We found that the substantial variation in the nutritional content of an edible portion among seafood species can be explained partly major ecological traits: functional group, latitude, body size and habitat associations.

In particular, some functional groups, such as molluscs, have ….

In the context of DRI, very few species reach 25% of DRI for more than one micronutrient in a single portion. This means that to achieve RDI targets for a broad range of micronutrients, human diets must contain a variety of seafood species.

**The two axes that most strongly control nutritional content of the edible portion are body size and latitude. In order to meet at least 25% of RDI for a range of nutrients, species must be XX size and come from XX latitude. For calcium, all species that contain 25% of RDI in one portion are 6.43kg or smaller.** In contrast to much of the existing work on stoichiometry in fishes, which address patterns of macroelement and macronutrient variability, here we studied variability in microelemental composition. We found even greater levels of variability in micronutrient stoichiometry than have been documented in the literature for macroelements. We found that Calcium content per edible portion varied by more than 500-fold (min=2.99, max=1503.00, median=45.15 mg/100 g). Fatty acids varied by X amount. Essential microelements varied by X fold, while non-essential elements such as mercury varied by X amount. It is possible that we found higher levels of variability than have been previously documented because we focused on micronutrients, which may be more variable across taxa than macronutrients due to their higher degree of functional specificity or lower level of homeostasis (Karimi et al. 2006). In addition, we sampled fishes over a much greater range of taxa, body sizes, geographic origins etc. Further, our data are for the edible portion of fish, which includes different body tissues depending on the species and its size. Sometimes the edible portion contains organs such as liver and skeleton, sometimes it is just muscle tissue. Nonetheless, in spite of the diversity of fishes included in our analysis, we found that our models had relatively high levels of explanatory power, suggesting that we have identified some traits that have a strong influence on whole body stoichiometry as well as the stoichiometry of the edible portion.

The degree of variability we documented in the edible portion is substantially higher than variability documented among whole body measurements of elemental composition of fishes documented in the ecological literature. This could be due to the fact we are sampling across much broader habitat/latitudinal/phylogenetic ranges, and/or because nutrient deposition is not uniform across body tissues, so including samples that are not uniform in their inclusion of body parts could increase the range of variability. Nonetheless, the relevant metric of nutritional value from the human perspective is the nutrient content of the edible portion, not the whole body. Thus, documented variability in whole body elemental composition may underestimate the variability in nutritional value of the edible portion.