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Quantifying the primary biotic resource use by fisheries: a global assessment.

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ABSTRACT

In this paper, the specific primary production required (SPPR expressed as kg-NPP/kg-fish in wet weight) of more than 1700 marine species were calculated directly from 96 published food web models using the newly developed SPPR calculation framework. The relationship between SPPR and other ecological factors were then statistically analyzed. Among- and within-species variability of SPPR were found to be both explained by trophic level (TL), suggesting similar mechanisms underpinning both sources of variability. Among species, we found that harvesting species at higher mean trophic levels (MTL) increases the mean SPPR by a factor of 19 per 1 unit increase in MTL. Based on our empirical relationship, the mean SPPR of more than 9000 marine species were predicted and subsequently used to assess the primary production required (PPR) to support fisheries in five major fishing countries in Europe. The results indicated that conventional approach to estimating PPR, which neglects food web ecology, can underestimate PPR by up to a factor of 5. Within species, we found that harvesting populations occupying a higher TL leads to a higher SPPR. For example, the SPPR of Atlantic cod in the Celtic Sea (TL=4.75) was 5 times higher than in the Gilbert Bay (TL = 3.3). Our results, which are based on large amounts of field data, highlight the importance of properly accounting for ecological factors during the impact assessment of fisheries.

Keyword: food web modeling, primary production required, linear regression model, trophic level, fishery's impact

1. INTRODUCTION

The annual average fish consumption per capita has doubled to 19.7 kg since the 1960s, accounting for 17% of the global population's animal protein intake in 2013 (FAO, 2016b). Beside the beneficial amounts of protein, fish also provides humans with many lipids as well as many essential micronutrients (e.g., omega 3 long chain polyunsaturated fatty acids, vitamins D₃, B₁₂ and minerals calcium (Khalili Tilami and Sampels, 2018)). Globally, capture fisheries contribute about 56% to total fish production, of which marine fisheries account for approximately 88% (FAO, 2016b). Considerable amount of landed fishes, including: Peruvian anchovy, Atlantic herring, Blue whiting, Gulf menhaden, Antarctic krill, are reduced to fishmeal and fish oil which are important for livestock production as well as aquaculture systems (FAO, 2016b; Parker and Tyedmers, 2012b). Because of impacts of capture fishery on marine ecosystems (e.g., on the diversity, structure and functioning of benthic communities) various stakeholders (e.g., authorities, consumers) have raised concern about the sustainability of seafood production through capture fisheries (Henriksson et al., 2012; Jennings and Kaiser, 1998; Pelletier et al., 2007). A main concern is the extraction of marine biotic resources through fishing. Indeed, fishing does not only extract the harvested biomass itself, but also indirectly extracts the amount of net primary production (NPP) synthesized by algae or seaweeds that is needed to sustain the harvested biomass. Many ecological footprint and life cycle assessment studies rely on the estimates of primary production required (PPR) to assess the ecological impacts of fishing (e.g., Borucke et al., 2013; Kautsky et al., 1997; Larsson et al., 1994; Papatryphon et al., 2004; Pauly and Christensen, 1995a; Pelletier and Tyedmers, 2007; Pelletier et al., 2009; Swartz et al., 2010) making its correct estimation essential. PPR has been used either directly as a single indicator (e.g., Papatryphon et al. (2004) and Pauly and Christensen (1995b)), or in more complex integrative indices (e.g., Parker and Tyedmers (2012b) and Langlois et al. (2015)).

The PPR of the harvested biomass of a species can be calculated as the product of the *specific primary production required* (SPPR, expressed as kg-NPP/kg-harvested biomass in wet weight) and the total amount of harvested biomass. SPPR of a species is therefore the PPR of one unit of its harvested biomass. Using SPPR thus allows direct comparison of impact from the same amount of harvested biomass among species, and the calculation of total PPR from landing data. SPPR is currently calculated from a conventional approach assuming that (1) simple food chains with a constant efficiency of biomass transfer between trophic levels are an appropriate approximation of natural food webs, and (2) trophic level data listed in available databases are representative of the harvested fish (Borucke et al., 2013; Papatryphon et al., 2004; Pauly and Christensen, 1995a; Pelletier and Tyedmers, 2007). Evidence indicates that both assumptions are invalid in many cases. This is because, in reality, fish species are embedded in complex food webs of which the structure can vary considerably in space and time thus potentially leading to different and more variable SPPR estimates than previously represented (Baird et al., 1998; De Laender et al., 2010). Luong et al. (2015) recently developed a new calculation framework that relies on food web flow matrices to estimate SPPR, as such allowing examination of the variability of SPPR with changes in spatial or temporal food web structure. This new calculation framework addresses a number of limitations of the previously developed food-web approach to SPPR calculation by (1) taking into account only the fraction of detritus originating from primary producers, thus reducing the overestimation of SPPR estimates, and (2) accounting for cycles in food webs when estimating SPPR. They have shown that SPPR estimates of some species from the new calculation framework were more than 100% higher than from the previously developed technique, and that the differences were largely dependent on degree of recycling.

Parker and Tyedmers (2012b) point out that the magnitude of uncertainty in species-specific marine footprint assessments should be decreased by using species-specific and ecosystem-specific data. Obtaining site- and time-specific ecological data is time consuming and labor intensive. Therefore, a

better understanding of which factors are most important in determining SPPR will provide a simple alternative way for getting more reliable SPPR values. The objective of this paper is therefore to identify, for the first time, the ecological factors driving among- and within-species variability of SPPR at a global scale. Using our recently developed calculation framework, we first estimated SPPRs for species embedded in 96 food webs representing 75 local marine ecosystems spread across 5 continents. We then statistically tested which ecological factors best explain among- and within-species variability of SPPR. Next, we use available data on these ecological factors to extrapolate our results to food webs for which no detailed information is available and predict SPPRs of species whose ecological factors can be obtained from available databases. Finally, we compared PPR of 5 major European fishing countries (with most details of landing data) calculated using FAO catch data with SPPR estimated the results from our approach and the conventional one as an illustrative example.

2. MATERIAL AND METHODS

2.1. Food-web collection

We found a list of more than 450 published food web models of which 184 models are freely downloadable in the Ecobase database (Colléter et al., 2015). These food webs were already constructed and solved by using the Ecopath with Ecosim (EwE) software which is the most widely used tool in marine food web modeling (Christensen and Pauly, 1992). Each compartment in a food web model can consist of a single species or many different species which share ecological characteristics (e.g., feeding behavior). From these 184 food web models, only 96 models in which the species composition (with scientific name) of all or some model compartments could be identified were retained for further analysis. These models also included at least one fishing fleet to represent the fished biomass flows. The locations of the marine ecosystems represented by these models are shown in the Supporting Information A (Figure S1).

These 96 food web models were downloaded and imported into the EwE software version 6.5. Matrices of consumption (material flows among model's compartments), respiration, landing and discard (the amount of landing and discard from different fleets included in the model), and other production (immigration/emigration and changes in stock size) were extracted. These data were used to check the mass balance and then used to calculate the SPPR of the species in these food webs. We also obtained several ecological factors associated with these species (trophic level (TL - dimensionless), gross growth efficiency (PQ – dimensionless), specific ingestion rate (QB – year⁻¹), specific production rate (PB – year⁻¹)), which could be used as potential explanatory variables for the prediction of SPPR.

2.2. Specific primary production required (SPPR) calculation

For each of the 96 retrieved food webs, we calculated the SPPR of every (group of) species, using the calculation framework proposed by Luong et al. (2015). More specifically, for each food web model, we obtained the biotic transaction matrix ($\mathbf{Z}=(z_{ij})_{n \times n}$), the production-normalized transaction matrix ($\mathbf{A}=(a_{ij})_{n \times n}$) from the consumption, landing, discard, and other production matrices. Each element z_{ij} and a_{ij} represents the biomass flow from the i^{th} to the j^{th} (group of) species and the amount of the i^{th} (group of) species directly required to produce one unit of the j^{th} (group of) species' biomass, respectively. The production-normalized transaction matrix was formed by normalizing the elements of each column of \mathbf{Z} by the production of the corresponding (group of) species to that column. The total requirement of biomass (directly and indirectly) from the i^{th} (group of) species to produce one unit of the j^{th} group of species' biomass is represented by l_{ij} element of the production requirement matrix ($\mathbf{L}=(l_{ij})_{n \times n}$), which is the inverse matrix of $(\mathbf{I}-\mathbf{A})$ where \mathbf{I} is the identity matrix (matrix with 1s in the diagonal and 0s elsewhere). SPPRs for different (groups of) species in each food web models were then obtained from those rows of matrix \mathbf{L} that correspond to primary producers. More details about how these matrices are derived are described in Luong et al. (2015).

2.3. Analyzing among and within species variability of SPPR

From the set of SPPR values obtained from 96 food web models, we selected those species that occurred at least 10 times (107 species). This selection was based on the compromise between the number of the analyzed species (which should be enlarged as much as possible) and the sample size of each species for subsequent statistical analysis. The distribution of SPPR was very skewed so we applied a base-10 logarithmic transformation before proceeding further analysis. We made the correlation analysis for both average and original data. The results revealed that the relationships between $\log_{10}(\pi_{\text{SPPR}})$ and means of the ecological factors and $\log_{10}(\text{SPPR})$ and the ecological factors are likely to be linear. Therefore, we applied linear regression analysis to test which ecological factors (TL, QB, PB, PQ), explained among- and within-species variability of SPPRs as calculated from the food web models. This is an established approach and has been applied before by Chassot et al. (2010) to test for the effects of different ecological factors on the total PPR of large marine ecosystems. The amount of data (1726 data points for each of SPPR and ecological factors from 107 species) on which our analysis is based allows us to reliably use this linear regression to predict the SPPR of species not included in this analysis, but for which the relevant ecological factors are known.

We developed two models: (1) one to analyze among-species variability of mean SPPRs (model 1), and (2) one to analyze within-species variability of SPPRs (model 2). In model 1, we analyzed the linear relationship of the spatio-temporal mean of the $\log_{10}(\text{SPPR})$ of 107 species (i.e. $\log_{10}(\pi_{\text{SPPR}})$, where π_{SPPR} is the geometric mean of SPPRs of a species) with the corresponding means of all ecological factors. In model 2, the linear relationship of $\log_{10}(\text{SPPR})$ and the ecological factors was analyzed using all data points of 107 selected species with species as a categorical explanatory variable. For both models, we used a stratified random selection (based on values of the response in model 1 and the names of the species in model 2) of 70% of the data for model fitting (training dataset) and used the remaining 30% for model validation.

Model selection and validation

The most important ecological factors were selected using the Boruta and the cforest functions in the R packages Boruta and party, respectively (Hothorn et al., 2005; Kursa and Rudnicki, 2010; Strobl et al., 2007; Strobl et al., 2008). We fitted the full model (containing all selected ecological factors from the previous step) to the training data and left out insignificant ecological factors (p-value > 0.05). We repeated this process until all ecological factors had statistically significant effects. We also checked for multi-collinearity (caused by correlations among the ecological factors) and eliminated the ecological factors with maximum variance inflation factors (VIF) until all VIFs were below 4 (Kabacoff, 2015). The selected ecological factors in this step were subsequently used to fit model 1 and 2.

The final regression equation of model 1 can be written with the following form:

$$\log_{10}(\pi_{SPPR_j}) = \alpha + \sum_{i=1}^n \beta_i \times \overline{p_{ij}} \quad (\text{Equation 1})$$

Where α is the model intercept, β_i is linear regression coefficients which represent the effect of the mean of ecological factor i ($\overline{p_{ij}}$) on $\log_{10}(\pi_{SPPR_j})$ of the species j , and n is the number of the selected ecological factors.

As opposed to model 1 where average data of species were used, model 2 utilized all individual observations of all 107 selected species. Because effects of the ecological factors (numerical explanatory variables) on $\log_{10}(\text{SPPR})$ can be dependent on species, we fitted model 2 using species as a categorical explanatory variable. One way to introduce the categorical explanatory variable to the model is by using dummy variables. To present a k -level categorical explanatory variable, we need $k-1$ dummy variables (each variable has two possible values of 0 or 1). Each new dummy variable was created that has a value of one for each observations of a given species and zero for all others. The species which is not

represented explicitly by a dummy variable (having zero values in all dummy variables) is called the reference species. The estimated coefficients of the other species in the model are compared to this reference species – in this case was Acadian redfish (*Sebastes fasciatus*). We made two versions of model 2. One version considered interactions of species and the other ecological factors (i.e., effect of ecological factors on SPPR is dependent on species) with the final regression equation written in the following form:

$$\log_{10}(SPPR_j) = (\alpha_0 + \alpha_j) + \sum_{i=1}^n (\beta_{0i} + \beta_j) \times p_{ij} \quad (\text{Equation 2})$$

Another version of model 2 assumes that the effects of ecological factors on $\log_{10}(SPPR)$ is independent of species, meaning that there is no interaction of species and the ecological factors on $\log_{10}(SPPR_j)$:

$$\log_{10}(SPPR_j) = (\alpha_0 + \alpha_j) + \sum_{i=1}^n \beta_{0i} \times p_{ij} \quad (\text{Equation 3})$$

where α_0 and β_{0i} represent the model intercept and the effect of the ecological p_i on $\log_{10}(SPPR)$ of the reference species; α_j and β_j represent the differences in the intercept and the effect of the ecological factor p_i on $\log_{10}(SPPR)$ of species j compared to those of Acadian redfish; n is the number of the ecological factors in the model.

We evaluated the goodness of fit of the models with different ecological factors combinations based on the following criteria: R-squared, adjusted R-squared, Akaike information criterion (AIC), and Bayesian information model (BIC) (James et al., 2013). We also assessed the models' predictive capacities using the root mean squared error (RMSE) which represents the average distance between the observed values and the model predictions (Kuhn and Johnson, 2013). Detailed explanations of these criteria and how to interpret them are listed in the Supporting Information A (Section 2.1). We selected the models that scored best on these criteria. In addition, if two models had similar goodness of fit and predictive

performance, we preferred the more parsimonious one (with the smaller number of ecological factors) (James et al., 2013). The residuals of the final models were diagnosed to see if all the underlying assumptions (homogeneity and normality of residuals) were satisfied. Data manipulation and model construction were done using R version 3.3.1 (R Development Core Team, 2016).

2.4. Assessing the ecological impact of European fisheries

The ecological factors of 9575 marine species were obtained from Fishbase (Froese and Pauly, 2000) and Sealifebase (Palomares and Pauly, 2017) database using the R package rfishbase (Boettiger et al., 2012). The SPPRs of these species were then calculated using model 1, and the conventional approach that represents food webs by food chains. This conventional approach proposed by Pauly and Christensen (1995b) calculates the PPR (kgC-NPP) for harvesting m kg biomass of a species:

$$PPR = \frac{m}{9} TE^{1-TL} \quad (\text{Equation 4})$$

where $1/9$ is the wet weight to carbon conversion ratio.

The SPPR (kg-NPP/kg-fish in wet weight) is derived from above equation as follows:

$$SPPR = TE^{1-TL} \quad (\text{Equation 5})$$

where TE is transfer efficiency and TL is trophic level.

The conventional approach uses a 10% of TE, as obtained through averaging transfer efficiency across 48 aquatic food web models (Pauly and Christensen, 1995a). However, here we decided to revise this estimate based on 146 available marine food web models in which transfer efficiencies can be calculated. TLs used in the conventional approach are also obtained from the Fishbase and Sealifebase databases which use stomach content analysis (SCA) to derive TL of a species. TLs can be alternatively estimated from the stable isotope analysis (SIA). SIA is sometimes considered as the most rigorous

method of estimating TL (Carscallen et al., 2012). However, this approach also has limitations (i.e. non-representative isotopic baseline and trophic discrimination factor), which are often not acknowledged, leading to biased TL estimations (Layman et al., 2012). Fishbase and Seabase are still the most reliable global databases providing the trophic level of marine species at comparable accuracy with those from SIA (Mancinelli et al., 2013). More information about TL estimating approaches can be found in the Supporting Information A (Section 3).

Finally, we calculated and compared PPR to sustain fisheries in 5 major fishing countries in Europe (i.e. Norway, Spain, Denmark, UK, and Iceland), using FAO catch data (FAO, 2016a) and SPPR estimates from our current analysis and the conventional approach.

3. RESULTS AND DISCUSSION

3.1. Worldwide estimation of specific primary production required (SPPR)

We obtained the first worldwide estimation of SPPRs of more than 1700 marine species by coupling our new calculation framework with 96 published food web models from 75 local marine ecosystems spread across 5 continents. Some species can occur in more than one marine food web and at different points in time, such that we could test which ecological factors explained among- and within-species variability of SPPR.

SPPR varied considerably among and within 107 selected species (Figure 1). The species-specific geometric mean of SPPR varies up to 3 orders of magnitude among species, while within-species SPPR variability (the ratio of max to min SPPR) ranged from 3 (Round scad – *Decapтерus punctatus*) to nearly 1000 (Swordfish – *Xiphias gladius*).

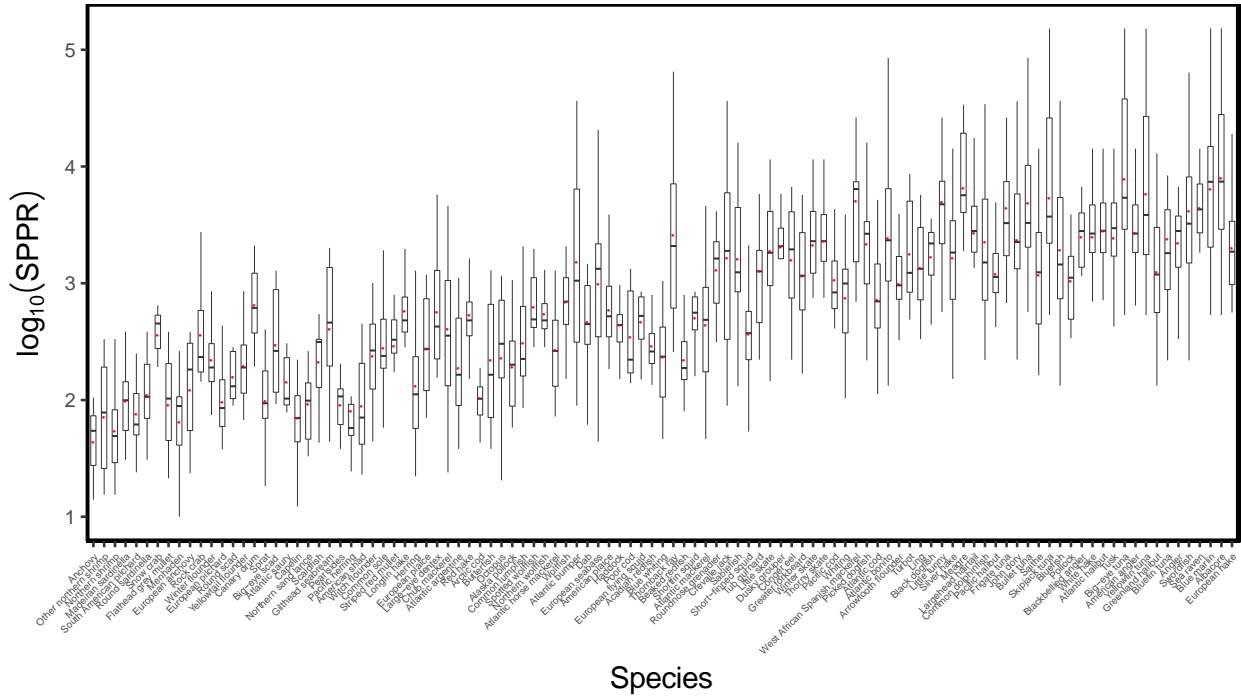


Figure 1. The \log_{10} -transformed specific primary production required (SPPR) for the 107 most occurring species. Boxplots denote extremes (minima and maxima). Bars denote first quartiles, medians, and thirds quartiles. Red dots represent the logarithm with base 10 of geometric means of the SPPRs. Species are sorted from low (left) to high mean trophic level (right).

3.2. Among-species variation of mean SPPR

We found that the among-species variability of SPPR is explained best by two ecological factors: the mean trophic level and the mean growth efficiency (details on variable screening and model selection are available in the Supporting Information A – Section 2.2). More specifically, the logarithm of the geometric mean SPPR ($\log_{10}(\pi_{\text{SPPR}})$) is positively and negatively correlated with mean trophic level and mean growth efficiency, respectively. This result makes sense from an ecological point of view, as species occupying higher trophic levels or growing less efficiently tend to require more primary production for biomass production, and thus having a higher SPPR. The model with two explanatory variables i.e., mean growth efficiency and mean trophic level, explained 79% of the total among-species

variability ($R^2=0.79$), while the model with mean trophic level alone already explained 77% of the total variability. The effects of mean trophic level on $\log_{10}(\pi_{\text{SPPR}})$ (estimated coefficient = 1.24) was not impacted by excluding the mean growth efficiency (estimated coefficient = 1.28). The residual standard errors of two models are 0.27 and 0.28, respectively. In addition, these two models only differed marginally in model fit and predictive performance (Supporting Information A, Table S2). We therefore retained the simplest model (the mean trophic level as the sole predictor) (Figure 2). Model assumptions (normality and equal variance of residuals) were verified and the details can be found in the Supporting Information A (Figure S3). Overall, these results imply that a difference of 1 unit in mean trophic level between any two given species leads to an ecological impact that is 19 times higher when harvesting the species at the higher trophic level.

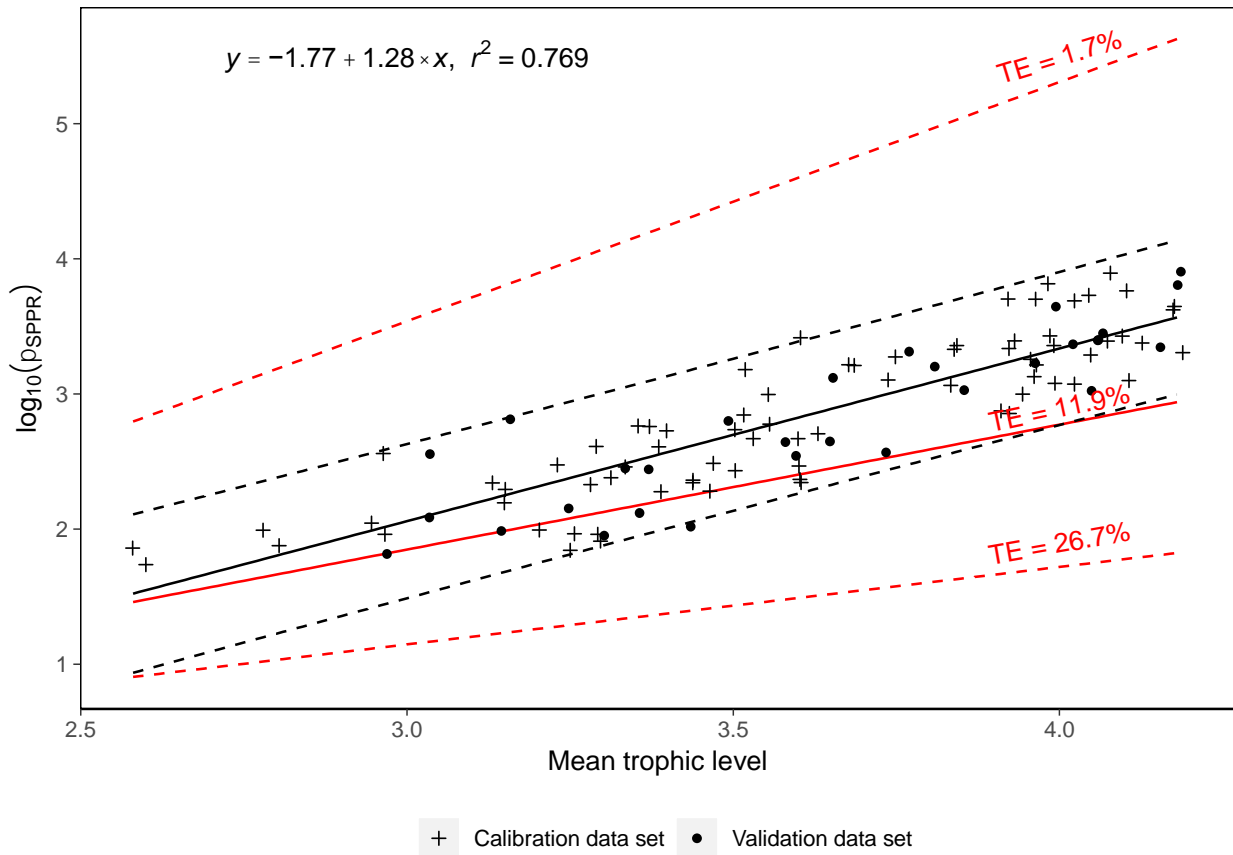


Figure 2. Comparison of mean SPPRs estimation using newly derived linear regression equation ($\log_{10}(\pi_{\text{SPPR}}) = -1.77 + 1.28 \times \text{mean trophic level}$; solid black line) and the conventional approach (assuming a mean TE of 11.9%; red line). The black dashed lines represent the 95% prediction interval of the prediction using the newly derived linear regression equation; the red dashed line represent the most likely range of SPPR calculated from conventional approach (95% of realized transfer efficiency in 146 marine food web models are in between 1.7 and 26.7%).

3.3. Within-species variation of SPPR

SPPR varied substantially within species (Figure 1) along with the ecological factors (Supporting Information A, Figure S4-S7). As such, finding which ecological factors explain this variability of SPPR is needed to predict the SPPR of a species in a given food web at a certain time. We found that this variability is best explained by the trophic level (positive effect) and the growth efficiency (negative effect). Including more ecological factors did not improve the fit and predictive capacity of the model (Supporting Information A, Table S3). Details on variable screening and model selection can be found in the Supporting Information A (Section 2.3). The effects of trophic level and growth efficiency were not species-specific, i.e. the two ecological factors affected SPPR equally for all species (Supporting Information A, Table S4). Furthermore, the linear regression model with two ecological factors (trophic level and growth efficiency) only marginally improved model fit and predictive capacity compared to the model with trophic level as the sole predictor. As a result, the simpler model was retained (Supporting Information A, Figure S9). All details on validation of model assumptions are also provided in the Supporting Information A (Figure S11). Some deviation from normality were observed to the right hand side of the QQ plot; however, this is not a serious problem when the sample size is large (Zuur et al., 2009).

Our results show that, when the trophic level of a species is increased by 1 unit, the SPPR will increase more than 3 times. Our regression model for within-species SPPR variability probably allows predicting SPPR of 107 most occurring species in a given ecosystem at a specific time using their trophic level. For example, Atlantic cod (*Gadus morhua*) has trophic level of 4.75 in the Celtic Sea, whereas it occupies the trophic level of 3.3 in the Gilbert Bay (Chassot et al., 2008; Wroblewski, 2006). This leads to a difference of a factor of 5 in the SPPR of these two Atlantic cod populations (1883 and 335 tonnes-NPP/tonnes-fish, respectively). However, one limitation of the current analysis so far is that the 96 food web models are mainly located in Africa, Europe and America (Supporting Information A, Figure S1); extrapolation to food webs in other continents with less available data should therefore be done with care.

3.4. Assessing the ecological impact of European fisheries

Using the obtained linear regression equation in model 1 (Figure 2) with mean trophic level data from two well-known databases, i.e., Fishbase and Sealifebase, we calculated the mean SPPR for a total of more than 7000 species (with mean trophic levels ranging from 2.6 to 4.2). Next, we used the conventional approach proposed by Pauly and Christensen (1995a) to estimate mean SPPRs of these species but using the mean transfer efficiency of 11.9% calculated from 146 marine food web models (95% of values lies in the range of 1.7 to 26.7%) (Supporting information A, Figure S15). We found that the conventional approach systematically predicts lower mean SPPRs compared to our new analysis. Differences between both methods were more pronounced with increasing mean trophic level and attained a factor of 4.4 at a mean trophic level of 4.2. However, the estimates from the conventional approach (with mean TE of 11.9%) lie within the 95% prediction interval of the estimations from our linear regression model. SPPR estimated from the conventional approach exhibits a wide range of variation due to the large variability in transfer efficiency. The SPPR resulting from our novel analysis, however, are less variable (Figure 2). Extrapolations for species with mean trophic levels outside the range mentioned above (more than 2500 species) can be found in the Supporting information B.

Based on the landing data retrieved from FAO statistics (FAO, 2016a) and the mean SPPRs of different species derived from model 1, we estimated the PPR to support fisheries of five major fishing countries in Europe (Figure 3B). We found remarkable differences between countries despite comparable catches. Specifically, during the period of 2005-2014, the total catch of Denmark and Spain were not much different (Figure 3A) but the fisheries of Spain required 7-15 times more primary production than those of Denmark. Towards the end of the considered period, Spanish fisheries even required 1.2 times more primary production than those of Norway, despite the latter being the country with the highest catches in that same period. These results reflect the fact that Spain harvested species at the top of the food web (more than 60% of total catches were at trophic levels higher than 4.0), whereas Denmark harvested species at lower trophic levels (more than 50% of catches were below 3.1). Thus, one ton of harvested fish of Spain, on average, required more than 9.5 times primary production than the same amount of caught of Denmark. Using SPPRs estimated from the conventional approach does not change the differences between countries' dependence on primary production but does estimate this dependence to be lower than when taking the food web structure into account (Figure 3C). The discrepancy in PPR requirements estimated by the two approaches is a function of the trophic levels of catch because the difference in estimated mean SPPRs increased with mean trophic levels as mentioned above.

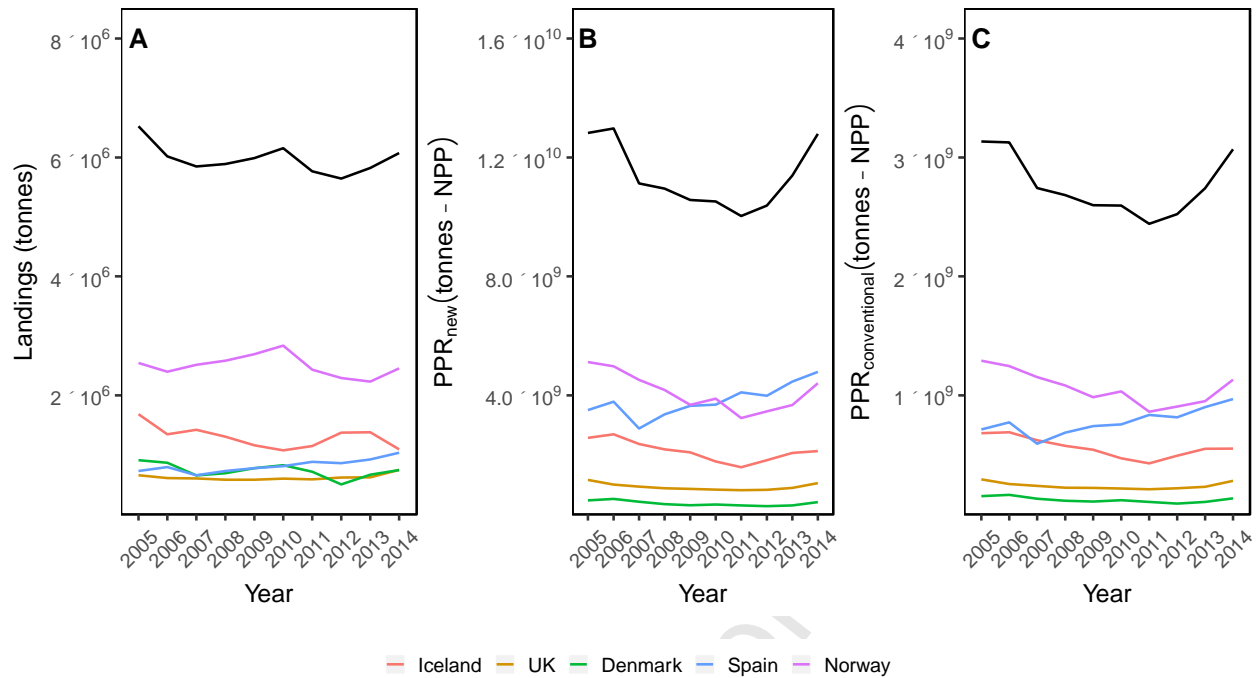


Figure 3. Landings in 5 major fishing countries in Europe from 2005 to 2014 (panel A). The total primary production required (PPR) to support landings of these 5 countries, which were calculated by our newly derived linear regression equation (PPR_{new} , panel B), and by conventional approaches ($PPR_{conventional}$, panel C). The black line represents the total values for all 5 countries.

The primary production required to sustain fisheries calculated as above can subsequently be used to calculate the marine fishprint (the amount of area required to sustain fishery of a given country) by dividing PPR by total primary production (Borucke et al., 2013; de Leo et al., 2014). In previous studies (e.g., Essington et al., 2006; Pauly and Christensen, 1995a) and our assessment, the mean trophic levels of the species were obtained from databases (e.g., Fishbase and SeaLifeBase) and were assumed invariant across individual size, time, and location. Consequently, the changes in PPR of a given country over time or differences in PPR among countries only reflect the changes or differences in the number of landings and the species composition of catches. They do not account for potentially large trophic level variability associated with food web dynamics and ontogenetic changes of populations (Branch et al.,

2010; Chassot et al., 2008). This variability of trophic level can be accounted for by using spatio-temporal specific SPPR estimates of 107 species in Model 2. More specifically, SPPR of these species in a given ecosystem at a specific time can be calculated if specific value of their trophic level available rather than depending on average value from database.

3.5. Implications and future perspective

SPPR of a species cannot be directly measured in the field, and can only be estimated using food web modeling. Our current analysis is the first one using the large amount of data from published food web models with an advanced calculation framework to estimate SPPR of more than 1700 species globally and then statistically test which ecological factors are important in explaining variability of SPPR. Our results indicate that among- and within-species variability of SPPR were both explained by trophic level (TL), suggesting both are driven by similar mechanisms. Such mechanisms may be linked to the inefficient energy/material transfer in food webs.

One limitation of our current analysis is the choice of the species included in the statistical analysis following the worldwide estimation of SPPRs. The criteria of 10 times occurrence of a species in all studied food web models we made was arbitrary represented a compromise regarding the coverage of the analyzed species and the sample size for statistical analysis, but was based on the data availability. In this study, we could utilize just 96 out of 184 downloadable Ecopath food web models available in Ecobase database due to the lack of details in the species composition in the other food web models. As a result, 107 species were considered in our analysis and the prediction of the spatio-temporal specific SPPRs from trophic level (model 2) is only available for these species. However, these 107 species represent the most fished species in many countries, e.g., they accounted for more than 70% of total landings in the United Kingdoms and Iceland in the period from 2005 to 2014. The relationship between SPPR and trophic level might also be dependent on the ecosystem types from which it was harvested.

However, this dependency was not analyzed in our current study due to the lack of data and should be further investigated in the future when data are available.

Concerning uncertainty in food web modelling, we recommend that both information on species composition and data uncertainty should be reported in future Ecopath food web modeling studies. In the present study, we could not account for the uncertainty of the food web flow matrices which were used to calculate the SPPRs. Methods are available to do so, if data availability permits. Recently, Guesnet et al. (2015) provided an easy-to-use routine that allows incorporating uncertainty of Ecopath models' input data. In this way, the uncertainty in the input data (e.g., dietary, biomass, growth efficiency) can be propagated to the resulting food web flow matrices and thus SPPR estimates. Unfortunately, the uncertainty in the input data, often expressed as 'pedigree scores', was unavailable when carrying out the present study, making the assessment of uncertainty of estimated SPPRs impossible. Another approach which has been widely used in marine food web modeling is linear inverse modeling coupled with Markov chain Monte Carlo approach (LIM-MCMC) (Chaalali et al., 2015; Luong et al., 2014; Van Oevelen et al., 2010). LIM-MCMC allows for quantification of the uncertainty in both energy/material flows in the food webs and ecological indices (SPPR estimates are included) characterizing the structure and functioning of a food web (Kones et al., 2009). LIM-MCMC is a more relevant tool to represent the bacterial loop processes in ecosystem functioning (Chaalali et al., 2015). It therefore can lead to a better estimation of the SPPR. As a result, all these advancements can help to improve our SPPR estimates and regression models when more relevant data are available.

This study provides SPPR values of more than 9000 marine species which will enhance further applications of SPPR metric and its derivations in different fields such as: human appropriation of net primary production (HANPP), ecological footprint (EF), and life cycle assessment (LCA). Human appropriation of net primary production (HANPP) is an integrated indicator quantifying the effects of

human-induced changes in productivity and harvest on ecological biomass flows. Haberl et al. (2014) defined HANPP as the difference between the NPP of the natural pristine ecosystems and the remaining NPP in the ecosystem after harvest under current conditions. As such, HANPP consists of harvested NPP (abbreviated as $\text{HANPP}_{\text{harv}}$) and changes in NPP resulting from land use and land transformation (denoted as $\text{HANPP}_{\text{luc}}$). Most of existing HANPP studies only consider the $\text{HANPP}_{\text{harv}}$ from terrestrial ecosystems without considering the harvested marine biomass (Haberl, 1997; Haberl et al., 2014; Rojstaczer et al., 2001). The future HANPP studies should consider also the $\text{HANPP}_{\text{harv}}$ from the marine ecosystems by using the SPPR calculated from our work and the landing data. This $\text{HANPP}_{\text{harv}}$ is then can be used to account for ecological footprint of biomass harvested from marine ecosystems. Currently, PPR calculated from landing data and global average values of species' SPPR are still the most reliable and applicable in assessing the ecological impacts of biomass removal (e.g., Papatryphon et al., 2004; Parker and Tyedmers, 2012a; Vázquez-Rowe et al., 2012). Our new approach provides a more conservative assessment of PPR compared to the conventional one. As shown previously in the example, the conventional approach can underestimate the PPR of 5 major fishing countries in Europe by a factor of 3 to 5.

In the field of life cycle assessment (LCA), PPR was first used by Papatryphon et al. (2004) and subsequently has been widely used to account for the impacts of fishery and aquaculture on marine ecosystems (Cashion et al., 2016). However, it was criticized as providing only the relative impacts in seafood LCA and not an absolute measure of sustainability. Recently, Langlois et al. (2014) used SPPR to derive the new metrics in order to assess the impact of biotic resource depletion at the ecosystem level (amount of net primary production removed in relation to the total net primary production of the ecosystem). They classified all marine species into 34 groups and used the conventional approach to calculate the average SPPRs of these groups of species. Our result helps to refine their methods by providing the large amount of SPPR values of marine species with the corresponding 95% prediction

intervals, which hence allows for uncertainty to be taken into account. Model 2 in this study also brings benefit to these kinds of study by allowing for the effect of changes in TL on SPPR of a specific species to be taken into account. SPPRs calculated from this study can also be used to improve the Cumulative exergy extraction from natural environment (CEENE) method.

CEENE is a resource accounting method which has been extensively applied in LCA studies of aquaculture systems (Huysveld et al., 2013; Nhu et al., 2016). In this method, all material and energy flows are quantified in one single unit (joule of exergy), thus making the calculation of overall resource efficiency metric straightforward (Alvarenga et al., 2013; Dewulf et al., 2007; Huysveld et al., 2015; Taelman et al., 2014). The overall resource efficiency from life cycle perspective, called cumulative degree of perfection (CDP), can be defined as the ratio of exergy contained in the product to CEENE of its supply chain. The SPPR is a metric reflecting the overall efficiency of resource use (i.e., net primary production) in the natural systems. Converting the SPPR as calculated from our new empirical equation into exergy allows for coupling of the overall resource use efficiency of human-made production systems with natural ones. This integrated overall resource efficiency metric will provide a more comprehensive picture of resource use efficiency and should be investigated in the future LCA of fisheries and aquaculture.

4. CONCLUSION

In this study, SPPRs of more than 1700 species were directly calculated based on food web flow matrices obtained from 96 food web models using the advanced SPPR calculation framework. The relationship between mean SPPR and mean trophic level were then derived statistically for the first time. Mean SPPR of more than 9000 marine species were inferred using the mean trophic level retrieved from Fishbase and Seabase life databases (Froese and Pauly, 2000; Palomares and Pauly, 2017). The results from this study can be used to enhance the future application of primary production required (PPR) in ecological

footprint and life cycle assessment studies. The PPRs of fishery in five major European fishing countries were calculated and compared with the results from the conventional approach. The results indicate that the conventional approach underestimates PPRs in the five countries by up to a factor of 5. Therefore, our new approach gives a more conservative assessment of marine biotic resource use.

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Author Contributions

The manuscript was written through contributions of all authors. All authors have given approval to the final version of the manuscript.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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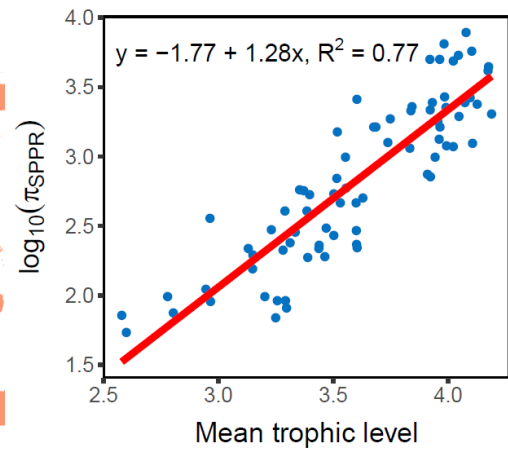
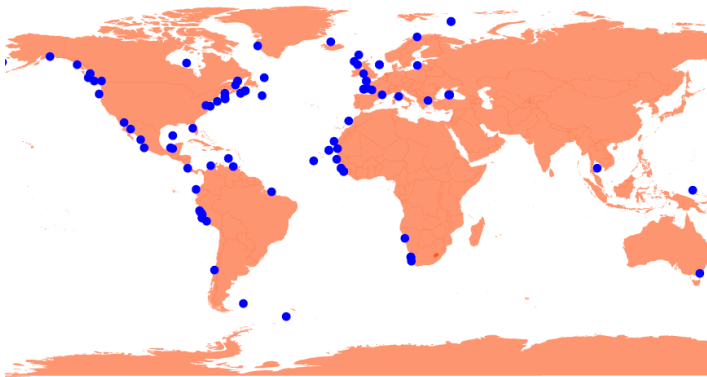
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Credit author statement

Anh D Luong: Conceptualization, Methodology, Software, Writing Original Draft. **Jo Dewulf:** Conceptualization, Writing – Review and editing; **Frederik De Laender:** Conceptualization, Writing – Review and editing, Supervision.

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Locations of the food web models



Graphical abstract

Highlights

- Specific primary production required (SPPR) were calculated for more than 1700 species
- Trophic level is the most important ecological factor determining species's SPPR.
- Mean SPPR increases 19 times when mean trophic level increases by 1 unit
- Biotic resource use for fishery of 5 major European fishing countries were calculated
- New approach gives the result up to 5 times higher than conventional one.

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