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A century of decline

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Fish biomass in the world ocean: a century of decline

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Abstract

Will there be fish in the ocean in 2050? To address this question, we made a data-rich global assessment of how fish biomass has changed over the last hundred years. We built on more than 200 ecosystem models representing marine ecosystems throughout the world covering the period from 1880 to 2007, and all constructed based on the same approach. We used spatial modeling to distribute biomasses based on habitat preferences, ecology, and feeding conditions. We extracted over 68,000 estimates of fish biomass (for predatory and prey fishes, separately) distributed over time and space, and used multiple regression to predict biomass distributions. The regressions were highly significant and predict that the biomass of predatory fish in the world oceans has declined by two-thirds over the last hundred years. This decline is accelerating, with 54% having taken place in the last 40 years. We also found that the biomass of prey fish has more than doubled over the last hundred years, likely as a consequence of predation release. Jointly, these findings allow us to predict that there will be fish in the ocean in 2050, but they will be mainly of small prey fish. Our study also addresses the controversy whether ‘fishing down the food web’ is a phenomenon actually occurring in nature or a sampling artifact due to catches not representing relative abundances in ecosystems. Our study strongly indicates that the impact of fisheries has caused fishing down the food web of ecosystem resources at the global level.

Introduction

Will there be fish in the ocean in 2050? Opinions differ and many fear that we are losing ground in this last frontier on the globe; that our impact is so devastating that all fish supporting fisheries will be gone by 2050 (1). Such statements create headlines, but how founded are they in reality? Alternative interpretations of data conclude that conditions are improving and we see improvements in fish populations (2). Music in managers' ears, but is it the Titanic's orchestra? Such conflicting findings have, while creating headlines, spread confusion, and in this study we attempt to evaluate how the abundance of fish has changed in the world ocean over the last hundred years. Our study is the first to evaluate trends in global fish biomass based on stratification of the world oceans.

For the study we used an established methodology that we previously have applied to the North Atlantic, South East Asia, and West Africa (3-5). We used two hundred detailed descriptions of ecosystems in form of ecosystem models to provide snapshots of how much life there was in the ocean at given points in time and space. We then evaluated how the conditions at each point relate to environmental parameters, based on which we develop a regression model to predict biomass trend over time. Finally, we used global environmental databases to predict the spatial distribution of fish biomass.

This allowed us to predict the biomass trends for higher-trophic level predatory fish, i.e. the larger predatory 'table fish', as well as for the lower-trophic level prey fish, such as small pelagics (sardines, anchovies, capelins, etc.), which are used mainly for fishmeal and oil.

Given the recent controversy over whether 'fishing down the food web' is a phenomenon actually occurring in nature (6) or a sampling artifact (7) with no or little relation to the underlying ecosystem structure, we add to the discussion by evaluating how the biomass of high-trophic level species has changed relative to the biomass of low-trophic level species.

Results

We evaluated the biomass of fish separately for higher-trophic level predatory fish ('table fish') and for the lower-trophic level prey fish.

All our evaluations indicate that the biomass of predatory fish has declined strongly (and significantly) over the last hundred years. For the 200 models covering the entire time period from 1880-2010, we obtain the regression in Table 1. The multiple regression coefficient (r^2) is 0.70, indicating that the regression can explain 70% of the variation in the data set, which is highly significant. The predictor variables are all highly significant apart from the factorial variable for FAO areas 18 and 31 (representing the Amerasian Arctic and the Caribbean).

We note that the signs of the predictor variable coefficients all are as expected, negative for biomass, distance, and temperature, and positive for primary production and the upwelling index. Notably, the regression indicated that we annually have lost 1.5% of the biomass of higher trophic level fish, and that biomass declines with 5-6% for every degree of water temperature increase.

If we examine the relationship between observed and predicted values based on the regression in Table 1, we obtain the results in Figure 1. The regression overestimates the abundance at low biomasses and underestimates the abundance as high biomasses. This indicates that the regression is conservative, i.e., it does not overestimate changes in biomass. It also means that the residuals (predicted less observed values) are negative at low biomasses and positive at high biomasses. Such a structure in the residuals suggests that there are 'hidden' predictive variables, i.e., which have not been included in the multiple regression. This should not come as a surprise, given that we seek to predict the biomass based only on year, distance from coast, primary production, temperature, upwelling, and FAO area. While these parameters do lead to a skewed residuals overall, only the upwelling index shows indication of a divergence from linearity (Figure 2); this suggests, overall, that our predictor variables are suitable for use in the regressions.

The predictive variables we use are not the only factors of importance for the fish biomass, even if we can explain 70% of the variation based on them only. There are other important variables, for instance 'rugosity' (i.e., depth variability within spatial cells), substrate types, and fishing effort, but we did not have access to global data layers covering such variables, and had to ignore them for the time being. The implication is not that the present study is likely to be misleading, but rather that we would have obtained better predictions if we had could have added suitable predictor variables.

Using a resampling methodology we randomly drew 30% of the 68,939 estimates of biomass over space and time and performed a multiple regression with each subsample. Based on this we obtained a distribution for each predictor variable (Figure 3).

We then used each of the resampled regressions and the database of environmental parameters to predict global biomasses. From this we estimate the biomass of predatory fishes to have declined by around 75% during the hundred years from 1910-2010.

Dividing the models into three time periods to obtain higher temporal resolution, and with the splits made in 1970 and 1990, we obtain multiple linear regressions similar to reported above for the entire time period (Table 2). Again the predictor variables are highly significant ($P<10^{-16}$) and the regressions explain 66-91% of the variability in the biomass data.

Evaluating the time trends based on resampling the three regressions 1000 times based on randomly selecting 30% of the biomass estimates for each case leads to Figure 4. From this, we estimate that the biomass of predatory fishes has declined by two-thirds (66.4% with 95% confidence intervals ranging from 60.2-71.2%) over the last hundred years. The decline is estimated to have been slow (10.8% or 0.2% year^{-1}) up to 1970, for then to be severe during 1970-1990 (41.6% or 4.0% year^{-1}), and more slow since 1990 (14.0% or 2.9% year^{-1}).

Repeating the multiple linear regression for the entire time period and focusing on predicting the biomass of lower trophic level fish ($2.0 \leq TL < 3.0$) led to the regression coefficients in Table 3.

The regression coefficient for year (0.0085) indicates that the biomass of prey fish has been increasing over time by 0.85% year^{-1}. Over a one hundred year time period this increase corresponds to 130%, i.e., indicating that there are now more than twice as much prey fish in the global ocean as there were a century ago.

Discussion

Through this study, we have further developed a methodology we originally introduced to describe how the biomass of predatory fish have changed in the North Atlantic, West Africa, and Southeast Asia (3-5). The aim has been to provide a first global estimate for how fish biomass has changed over the last century, drawing on a vast amount of information made available through data-rich ecosystem models.

We found major declines in the biomass of predatory fish, i.e., of the larger fish that humans tend to eat, amounting to a decline of two-thirds over the last century, with 55% of the decline occurring in the last 40 years. Indications are that the decline was sharpest during 1970-1990, and has since leveled somewhat off. This does not mean, however, that conditions have started to improve globally; we found no indications of increase in biomass of predatory fish. There may be regional improvements as reported by Worm et al. (2); however, we do not see this at the global level.

Our finding that the biomass of the larger, predatory fish have decreased by two-thirds over the last century, could by a casual reader be interpreted that we now are fishing at the maximum sustainable yield (MSY) level. Productivity for higher-trophic level fish populations (e.g., tuna) may indeed be maximized when populations are reduced to between one-third and half of their original biomass, but our study shows that this reduction is an overall average. The implication of this is that some species among the higher-trophic level ones, notably the larger will be reduced much more, while smaller will have declined less, still the overall average indicate a large reduction. This is incidentally in accordance with one of the most thorough studies of top predator abundance (8). For the Pacific Ocean it was thus estimated that the largest pelagics (>175 cm fork length) had decreased to 17% of the unexploited biomass, while the decline was much lower for the smaller species. We also note that it indeed is impossible to fish all species at the MSY level; doing so may have severe impact on the trophic structure of the ecosystem (9).

The decline in predatory fish biomass is closely linked to increased fishing effort. Anticamara et al. (10) found that global fishing capacity (measured in kilowatt days) increased 54% from 1950 to 2010 with no indication of a decrease in recent years. Noting that this study did not include any ‘technology creep’ factor, (which averages 2 – 3% annually; 11), conclude that our results are consistent with the study of Anticamara et al. (8). We see the decline in biomass that can be expected, given a steadily increasing global fishing capacity.

Our study contributes to the recent discussion of whether ‘fishing down the food web’ is a sampling artifact or something that occurs in reality. We estimated that the predatory fish have declined with two-thirds, while the prey fish have more than doubled. Such doubling is likely to be linked to predation release, i.e., the mechanism where reduction in predator populations leads to increase in prey abundance, e.g., as documented in Myers et al. (12). Combined, the decrease of large-trophic level fish and increase of low-trophic level fish serves as a clear indication that fishing down the food web occurs at the global scale, and it should be noted that our methodology is less dependent of fisheries catch estimates than previous studies – an issue that has been central to this debate.

Materials and methods

Ecosystem models

We built our study on a database with 230 ecosystem models assembled for the purpose, all of which were based on the Ecopath with Ecosim (EwE) approach and software (13, 14). Each of these models was constructed by ecosystem modelers, (i.e. fisheries scientists, ecologists or marine biologists), usually with the aim of providing a snapshot of an ecosystem in a given year, and jointly the cover a large proportion of the world ocean (Figure 5). The models represented years between 1880 and 2007 with the number by time period indicated in Table 4. The models with key characteristics are listed at www.ecopath.org/biomasspnas, from where many of the models also are available.

We evaluated each of the ecosystem models, and eliminated thirty of the models we had access to. As criteria for evaluation we used that the models should include biomass information for different fish groups, and that the food webs be detailed. For example, we eliminated models that only specified fish groups as “fishes”.

For each of the 200 models remaining, we evaluated which of its functional groups belonged to the wider category of ‘exploitable fish species’. We excluded mesopelagic species, which mainly occur disperse in the deep open ocean and which cannot be exploited economically with existing technology (15). We also excluded juvenile fish, which cannot form the basis of sustainable fisheries.

We performed the analysis separately for fish with a trophic level of 3.5 or higher, and for fish with a trophic level between 2.0 and 3.0. The higher-trophic level group are predatory fish and represents the larger ‘table fish’ that tends to be used directly for human consumption. While catch levels are high for the lower trophic level groups, they tend to be ‘forage fish’, a major prey for the table fish. Humans tend to use forage fish mainly for fishmeal and oil (16).

There were approximately 3,000 types (unique names) of functional groups in the models. Each functional group represents individual species, life stages of species, or a collection of similar species, for instance “small pelagic fishes”. We assigned each of the functional groups to depth categories, based on information from FishBase (www.fishbase.org), SeaLifeBase (www.sealifebase.org), Wikipedia, online searches, and general knowledge of the species involved. The depth stratification we used was <10 m, 10-49 m, 50-99 m, 100-199 m, 200-499 m, 500-999 m, 1000-1999 m, and >2000 m. Each functional group could be assigned to any number of the depth strata, with most pelagic species, for example, being assigned to all habitats.

We used the spatial-dynamic Ecospace module of EwE (17) to spatially assign the populations in each ecosystem based on standardized habitat distributions as described above. The spatial resolution of the ecosystem models was ½° latitude by ½° longitude. In addition to the depth stratification, the models used primary production as input, derived from SeaWiFS satellite data.

The ecosystem models were distributed spatially based on information in the model descriptions (Figure 1); their wide coverage of the global ocean will be noted. It is also important to note that, for many locations several models are available from different periods, which is important for obtaining estimates of how fish abundance has changed over time. From the spatial models, we extracted 68,039 predictions of fish biomass by location and year, which subsequently was used as a basis for multiple regression analyses.

Regression analyses

The regression analyses were done using the open source R-package, where we considered the following predictor variables: (1) year, (2) latitude, (3) bottom depth, (4) distance from coast, (5) density of seamounts, (6) primary production, (7) average of surface and bottom temperature, (8) zooplankton biomass, (9) macrobenthos biomass, (10) mesopelagic fish biomass, (11) upwelling index, (12) FAO statistical area.

We used additive and variance stabilizing transformations as implemented in the AVAS module of the *Acepack* R-library to check for linearity between the predictive variables and the independent variable, i.e., the biomass of potentially exploitable fish with trophic level of 3.5 or higher. Based on this and model exploratory model selection using the *lm* module of R (library *gamair*), we excluded (2) latitude because of its covariance with temperature and FAO area, (3) depth because of its covariance with distance from coast, (5) density of seamounts because our sample of the ecosystem model collection did not have a good coverage of seamount models, (8) zooplankton biomass because of its covariance with primary production, (9) macrobenthos biomass because of its covariance with depth, and (10) mesopelagic fish biomass because it did not significantly correlate with the independent variable.

We included the 19 marine FAO statistical areas as potential factorial variables, but ignored four of these areas, for which we had less than 5 models. We thus did not use FAO areas 51, 58, 81, and 88 as factorial variables in the regressions; however, models from these areas were used for the predictions, i.e. they were treated as if the FAO areas in which they occur were not specified.

The AVAS transformations (Figure 6) indicate that the independent variable, (biomass) should be log-transformed, along with two of the predictor variables, (primary production and distance from the coast). The temperature transformation has a peculiar shape indicating divergence from linearity, which likely is due to only very limited observations being available for waters where the average of bottom and surface temperature exceeds 20˚C.

We used the 200 models to evaluate the time trend in fish biomass over the last hundred years. Given this large number, we were also able to estimate how fish biomass has changed during three time periods, 1910-1970, 1970-1990, and 1990-2010 (Table

4). We chose these split as the North Atlantic fish catches peaked around 1970, and this was the period when fisheries expansion gained momentum throughout the world (18). By 1990 this expansion had reached a new level and fisheries resource depletion had become a global phenomenon.

The multiple linear regression that we obtained had the following form,

$\log_e(\text{biomass}) = a + b_1 \bullet \text{year} + b_2 \bullet \log_e(\text{distance}) + b_3 \bullet \log_e(\text{primary production}) + b_4 \bullet \text{temperature} + b_5 \bullet \text{upwelling index} + b_i \bullet \text{factor(FAO)}$,

where a is the regression intercept, b_1 to b_5 are the regression coefficients, and b_i a coefficient for each of the categorical FAO variables.

In the regressions we weighted each of the 68,039 estimates of fish biomass by time and space with $1/\log_e$(number of spatial units), i.e., with the inverse of the log of the number of half degree cells covered by each of the ecosystem models. This was done to limit the influence of models covering very large spatial areas.

The regressions naturally depend on what models are included as data material. We evaluated the robustness of the regression by jackknifing (leaving out one model at the time) and found that this had no noteworthy effects on the results.

We further evaluated uncertainty by resampling. For this we 1000 times randomly selected 30% of the 68,039 estimates of fish biomass and evaluated predicted biomass trends from the subsampling.

Finally, we used the regression (based on the total data set and on resampled sets), jointly with a global database with the predictor parameters (with half-degree resolution) to estimate global, spatial biomass distributions.

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Tables

Table 1. Parameter coefficients and associated test statistics for multiple linear regressions to predict the global marine biomass of predatory fishes. The multiple r^2 is 0.70. The t-value is the ratio between an estimate and its standard error, and Pr(>|t|) indicates the probability of obtaining a larger t-value. The smaller this probability is, the more significant (*'s) the parameter.

	Estimate	t-value	Pr(>|t|)	Significance
Intercept	24.2500	54.8	2.00E-16	***
Year	-0.0151	-69.7	2.00E-16	***
log(distance)	-0.1008	-28.0	2.00E-16	***
log(prim. prod.)	1.1040	142.8	2.00E-16	***
Temperature	-0.0608	-69.6	2.00E-16	***
Upwelling index	0.0002	42.4	2.00E-16	***
FAO 18	0.0978	2.0	0.0407	*
FAO 21	0.6361	19.9	2.00E-16	***
FAO 27	0.7966	28.4	2.00E-16	***
FAO 31	0.0605	1.7	0.0907	.
FAO 34	-0.1952	-6.0	2.33E-09	***
FAO 37	-0.4279	-8.4	2.00E-16	***
FAO 41	1.0460	31.0	2.00E-16	***
FAO 47	0.6778	18.2	2.00E-16	***
FAO 48	1.1660	32.8	2.00E-16	***
FAO 57	1.1920	26.1	2.00E-16	***
FAO 61	1.1250	35.6	2.00E-16	***
FAO 67	1.5880	51.4	2.00E-16	***
FAO 71	1.2270	36.1	2.00E-16	***
FAO 77	0.4832	14.9	2.00E-16	***
FAO 87	0.3341	9.7	2.00E-16	***

Table 2. Regression coefficients for predictor variables for the three time periods considered, used to estimate the log(biomass) of predatory fishes. Regressions explain 66-91% of the variability (r^2). Coefficients for FAO areas are not listed for clarity.

	1880-1970	1970-1990	1990-2010
Intercept	0.5489	76.5400	51.5800
Year	-0.0021	-0.0411	-0.0293
log(distance)	-0.1054	-0.1183	-0.0700
log(prim. prod.)	1.1000	1.0530	1.1950
Temperature	-0.1917	-0.1008	-0.0335
Upwelling index	0.0001	0.0001	0.0004
r^2	0.9117	0.6721	0.6562

Table 3. Regression coefficients for predictor variables for a prey fish regression ($2.0 \leq TL < 3.0$) covering the entire time period. Coefficients for FAO areas are not listed for clarity.

	Estimate	t-value
Intercept	-14.5200	54.8
Year	0.0085	-69.7
log(distance)	-0.5958	-28.0
log(prim. prod.)	0.7790	142.8
Temperature	-0.1269	-69.6
Upwelling index	0.0001	42.4
r^2	0.5572	

Table 4. Number of ecosystem models by time period that were included in the analyses. 1970 and 1990 are included twice.

Period	Number
1880-1970	35
1970-1990	97
1990-2010	108

Figures

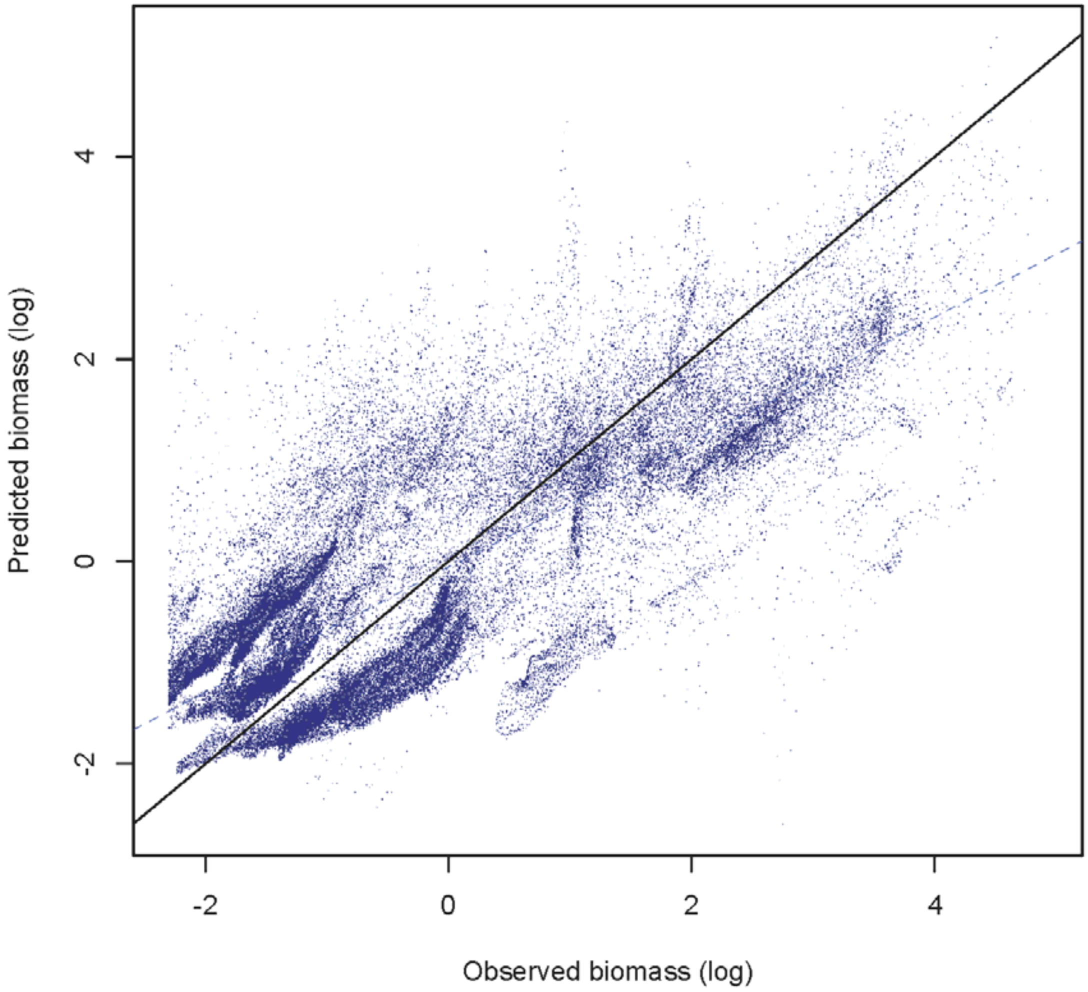

Figure 1. Predicted versus observed biomass (log-scales, t km^{-2}) for higher trophic level fish in the world ocean. The solid line indicates the 1:1 line, and the dotted line the average trend. The predicted variables underestimate the observed variability.

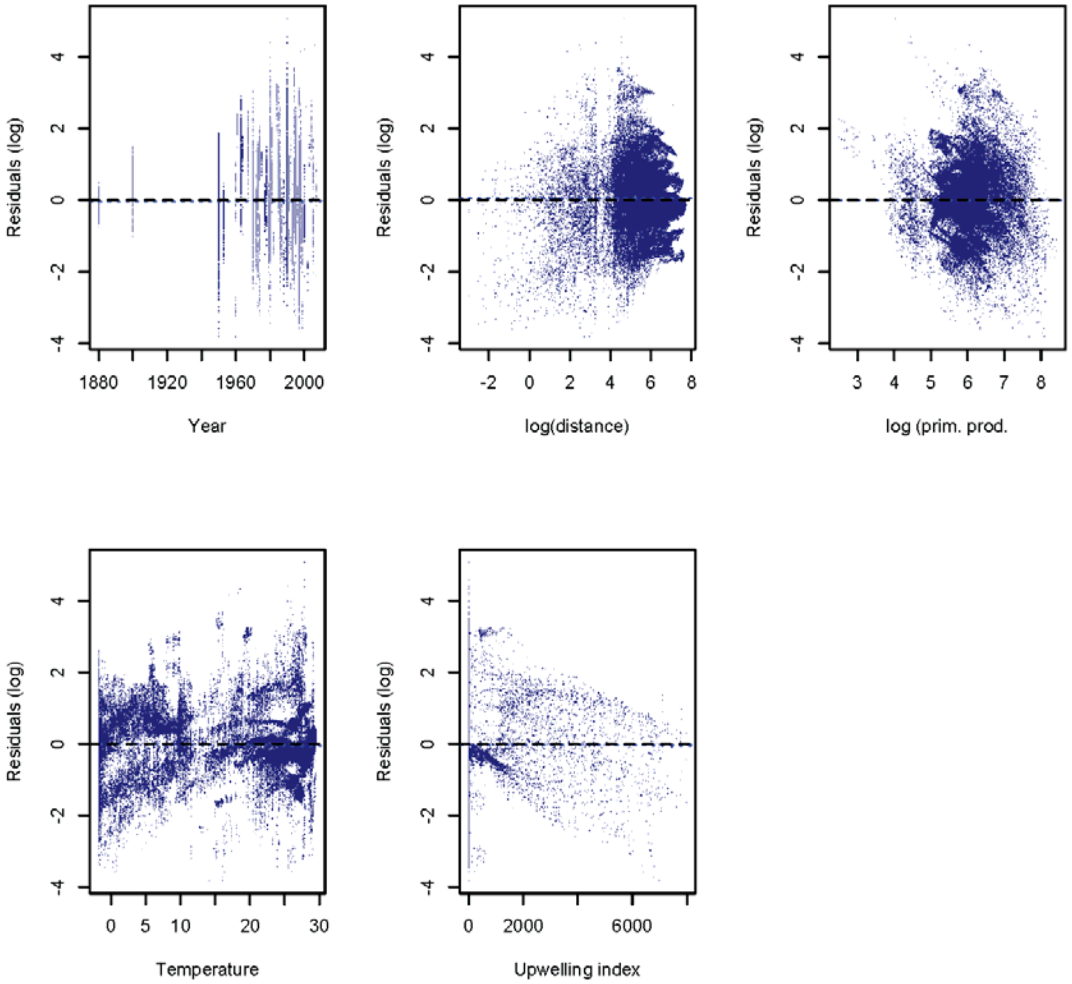

Figure 2. Residuals (predicted less observed values) for the predictor variables in the multiple linear regression analysis covering the entire time period.

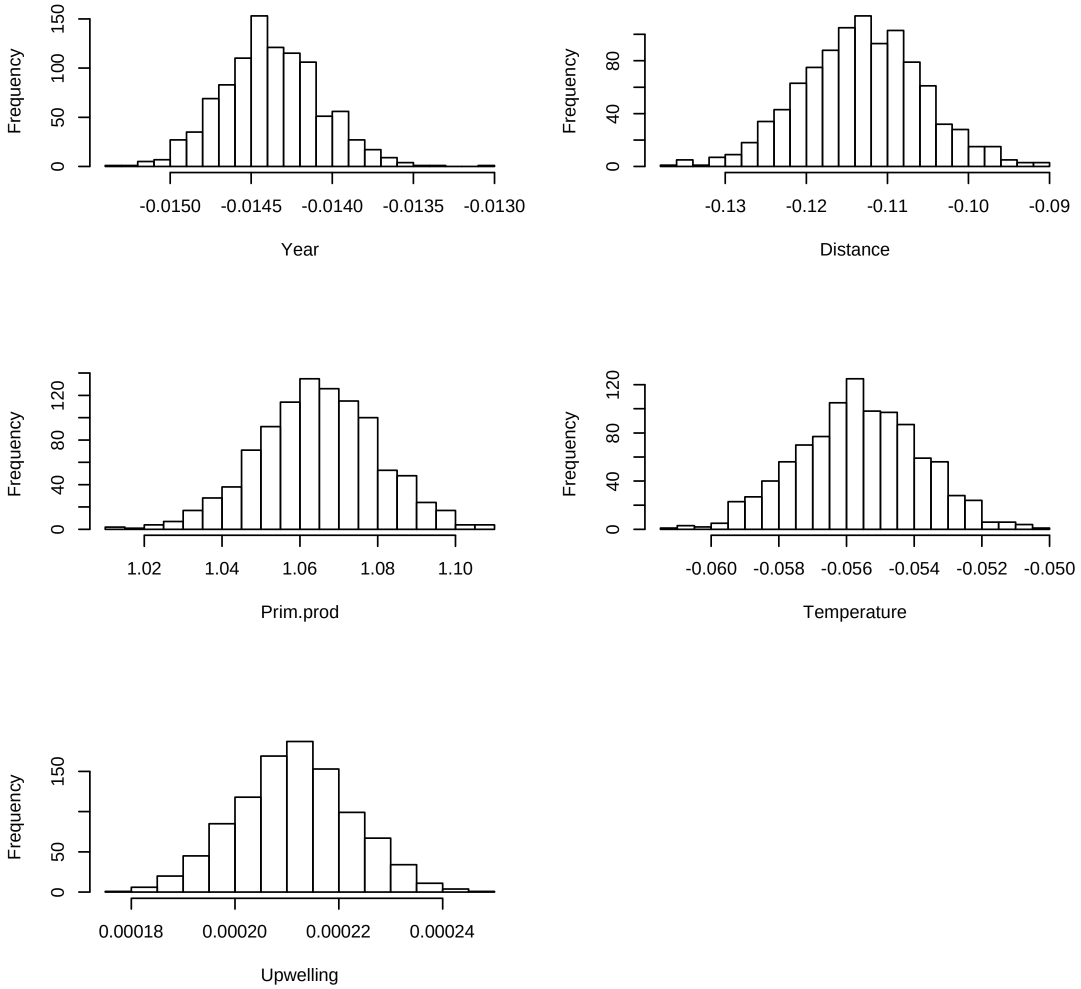

Figure 3. Frequency distributions for predictor variables in the regression covering the entire time period.

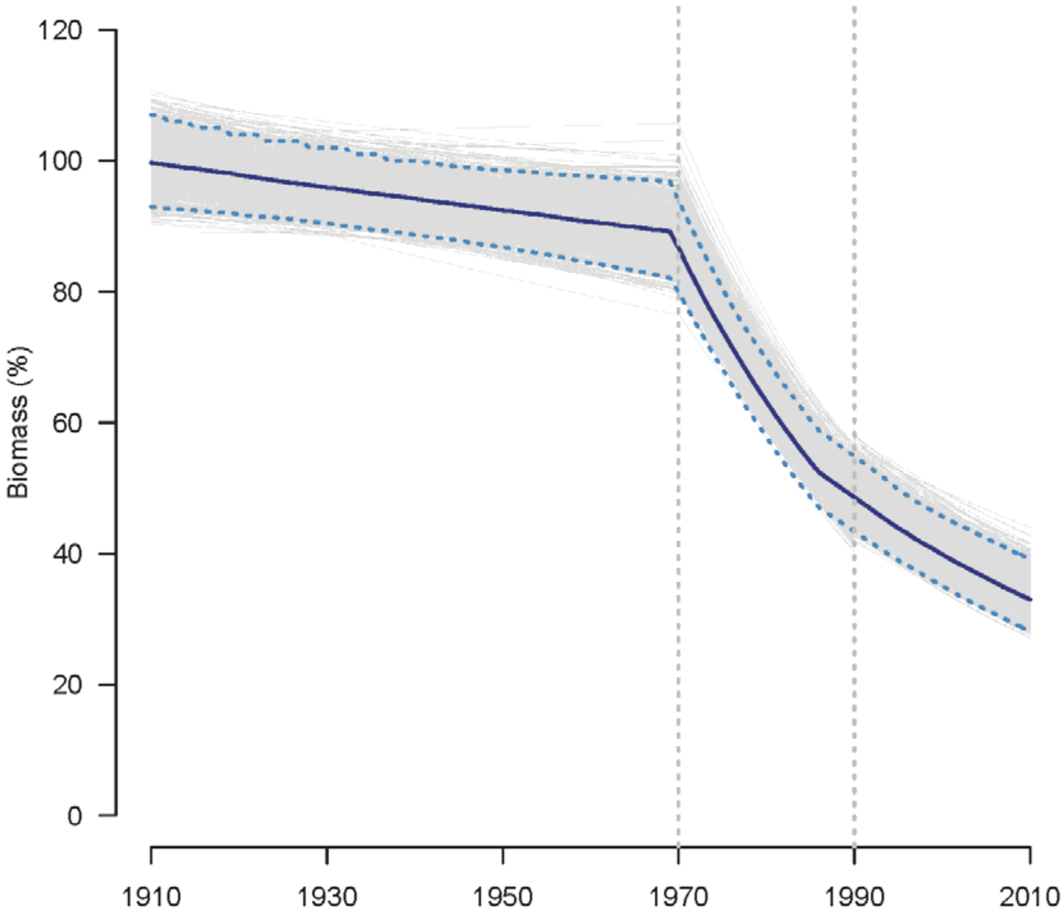

Figure 4. Global biomass trends for predatory fish during 1910-2010 as predicted based on 200 ecosystem models and 1000 times random resampling of 30% of data points. The lines indicate median values and 95% confidence intervals.

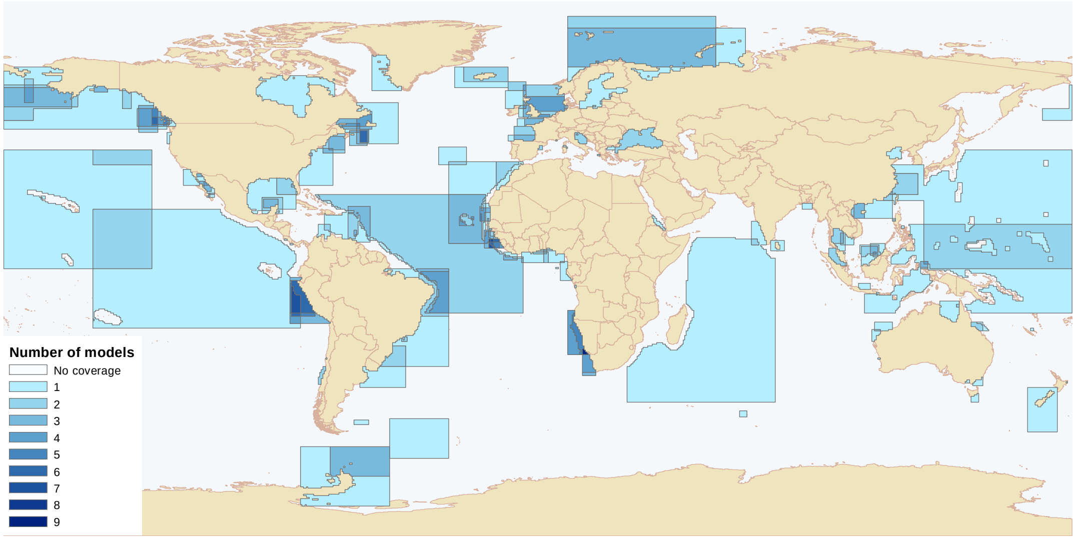

Figure 5. Spatial distribution of the ecosystem models used in this study, illustrating wide global coverage. Color density is indicative of the number of models at each location.

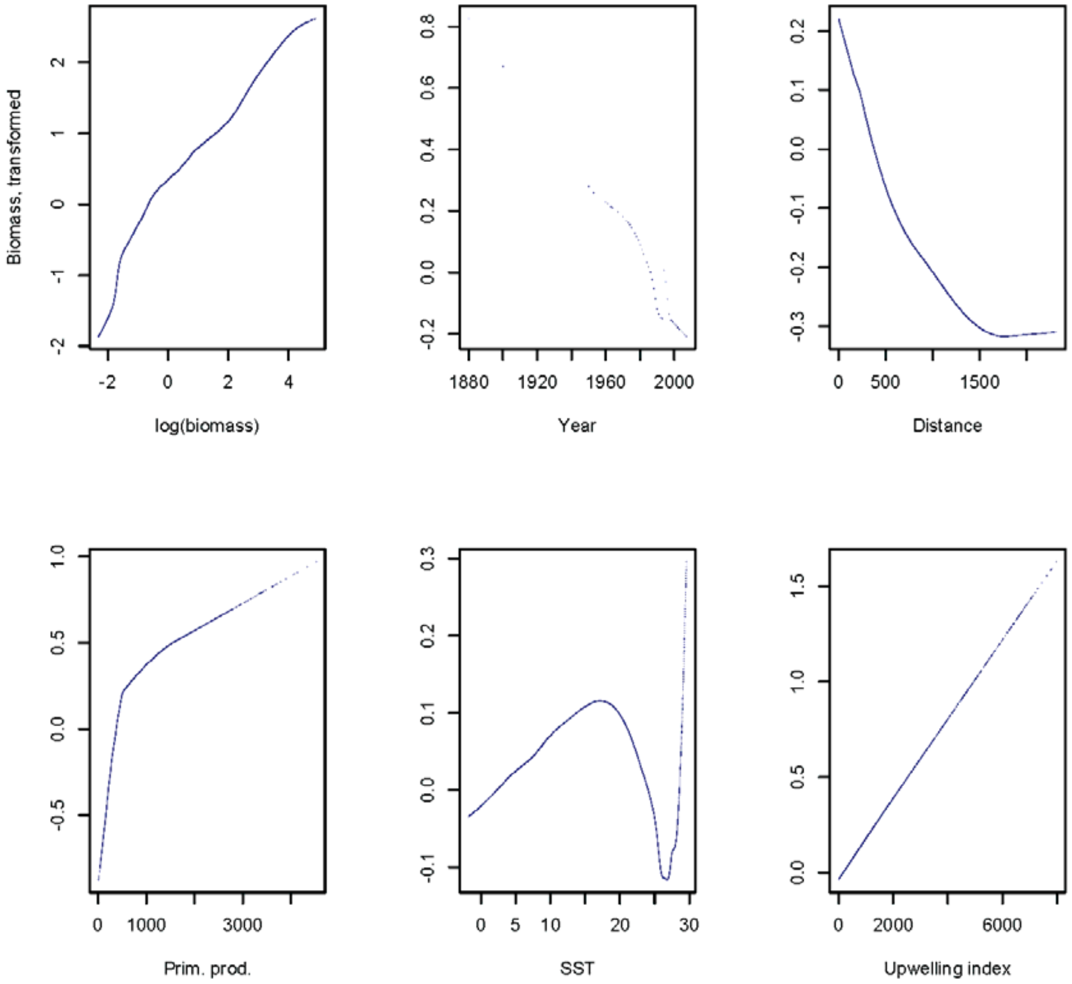

Figure 6. AVAS transformation of variables. The analysis indicates that log-transformation should be used for biomass, primary production, and distance from coast.