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The global ocean is an ecosystem: simulating marine life and fisheries

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ABSTRACT

Aim There has been considerable effort allocated to understanding the impact of climate change on our physical environment, but comparatively little to how life on Earth and ecosystem services will be affected. Therefore, we have developed a spatial–temporal food web model of the global ocean, spanning from primary producers through to top predators and fisheries. Through this, we aim to evaluate how alternative management actions may impact the supply of seafood for future generations.

Location Global ocean.

Methods We developed a modelling complex to initially predict the combined impact of environmental parameters and fisheries on global seafood production, and initially evaluated the model's performance through hindcasting. The modelling complex has a food web model as core, obtains environmental productivity from a biogeochemical model and assigns global fishing effort spatially. We tuned model parameters based on Markov chain random walk stock reduction analysis, fitting the model to historic catches. We evaluated the goodness-of-fit of the model to data for major functional groups, by spatial management units and globally.

Results This model is the most detailed ever constructed of global fisheries, and it was able to replicate broad patterns of historic fisheries catches with best agreement for the total catches and good agreement for species groups, with more variation at the regional level.

Main conclusions We have developed a modelling complex that can be used for evaluating the combined impact of fisheries and climate change on upper-trophic level organisms in the global ocean, including invertebrates, fish and other large vertebrates. The model provides an important step that will allow global-scale evaluation of how alternative fisheries management measures can be used for mitigation of climate change.

Keywords

Ecosystem model, end-to-end model, fish biomass trends, fish catches, food security, model tuning, seafood production, world ocean.

INTRODUCTION

A golden rule of modelling is to use a scale and form that is appropriate for the questions it is to address. When dealing with the impact that fisheries policies and climate change may have on future seafood supply, that scale is global since seafood is the most traded food commodity (Smith *et al.*, 2010) and climate

change already causes distributions of marine organisms to shift beyond regional borders (Poloczanska *et al.*, 2013).

With regard to form, we note that there are several model types that may be of interest, including size-based models (Jennings *et al.*, 2008; Smith *et al.*, 2010), individual-based models (Shin & Cury, 2004; Poloczanska *et al.*, 2013) and trophic food web models (e.g. Christensen & Pauly, 1992). We

apply a food web model because of the opportunities this creates for addressing biodiversity-related questions (a topic we expect to use the present model for in future studies) and because it is by far the most used methodology for marine ecosystems, (e.g. Coll *et al.*, 2008a). However, we emphasize that there is a need to develop alternative model forms for comparative purposes.

It is also relevant to consider as an argument for global modelling that while general circulation models generally converge well at the global level, the results for individual regions show a wide range of variation (Cai *et al.*, 2009). The implications of this support the notion that models must be constructed to suit the scale of the questions they are to address. Downscaling is as much a problem as scaling up.

With this in mind, and to add to our understanding of the Earth as a system (Falkowski *et al.*, 2000), we present a spatial–temporal food web model of life in the global ocean, spanning from primary producers through to top predators and fisheries. ‘The global ocean is an ecosystem’ is the thesis behind this effort, and we intend to focus on the impact human actions will have on the food supply for future generations. Here we describe some of the steps used to build a global ocean modelling complex, and evaluate model performance with regard to fit to historic seafood landings.

Previously, we developed a global ecosystem modelling complex, EcoOcean (Alder *et al.*, 2007), that was used for global assessments (e.g. Brink, 2010). EcoOcean relied on 18 regional models that jointly covered the world ocean, and while this provided a versatile attempt at global ocean ecosystem modelling, it was a cumbersome approach to work with given the need to populate and analyse 18 food web models in sequence.

As a follow-up, we developed a new approach for database-driven ecosystem model generation in order to construct and evaluate models for each of the world’s large marine ecosystems (LMEs; Christensen *et al.*, 2009). A major advantage of this database- and rule-driven approach was automation of much of the model construction and evaluation, and it allowed for inclusion of extensive global data layers, notably as developed by the Sea Around Us project (Pauly, 2007, <http://www.seaaroundus.org>).

Here, we build on the database-driven modelling (i.e. LMEs; Christensen *et al.*, 2009) in order to develop a data and modelling framework as an updated version of the EcoOcean complex. The new model is global and temporal with a variable spatial grid resolution of 0.5° latitude by 0.5° longitude; a notable addition is that is driven by temporal–spatial data. For the initial model tuning and testing we aggregated the model processes to 1° latitude by 1° longitude to speed up the development. The model as implemented here covered the period from 1950–2050 with monthly time steps, but in this study we focus on tuning the model so as to obtain capability for hindcasting for the period 1950–2006.

Tuning the model to past data by comparing time dynamic model runs with spatial–time dynamic runs is one of the contributions of the present study. Model tuning for spatial models is always a challenge that involves a combination of spatial and non-spatial parameters and which must recognize that full

tuning based on multiple spatial runs as a rule exceeds current computational capacities.

METHODOLOGY

Biogeochemistry and primary production model

Marine populations such as invertebrates, fish and marine mammals are sensitive to primary production patterns, making it necessary to consider environmental productivity patterns as well as fisheries and trophic impacts in order to successfully replicate historic trends in marine ecosystems (Mackinson *et al.*, 2009; Christensen & Walters, 2011).

With this in mind, we linked a trophic food web model to a newly developed atmosphere–ocean circulation model called the carbon, ocean biogeochemistry and lower trophic level model (COBALT; Stock *et al.*, 2014). The COBALT model captures large-scale patterns in carbon flow through the planktonic food web, and was implemented in the GFDL modular ocean model version 4p1 (Griffies, 2012) with sea-ice dynamics as described by Winton (2000). The model was run on a global domain with a spatial resolution of 1° apart from at the equator where resolution was 1/3°. We resampled the model output to 1° latitude by 1° longitude throughout. Atmospheric forcing was from the Common Ocean-Ice Reference Experiment (CORE-II) data set (Large & Yeager, 2009) and covered the period from 1948 to 2006 after a 60-year spin-up. COBALT uses 50 vertical layers, but we aggregated over those, as the spatial food web model is two-dimensional – the depth dimension is considered implicitly through food web interactions and habitat preference patterns.

From COBALT, we obtained spatial–temporal output of production rates for three functional producer groups in the model, i.e. for large phytoplankton (nlgp in COBALT), small phytoplankton (nsm) and diazotrophs (ndi). For the simulations reported here, we used monthly output from COBALT (1950–2006) to drive the food web model, and there was no feedback to COBALT.

Food web model

We constructed a trophic submodel using a customized version of the Ecopath with Ecosim (EwE) approach and software (Christensen & Pauly, 1992; Walters *et al.*, 1999, 2000; Christensen & Walters, 2004).

As the first step we built a mass-balance (Ecopath) model as a baseline for parameterization of the time and spatial dynamic simulations. This model followed the definitions and methodology of Christensen *et al.* (2009) and separated fishes into ‘small’ (asymptotic length, $L_{\infty} < 30$ cm), ‘medium’ ($L_{\infty} = 30$ –89 cm), and ‘large’ ($L_{\infty} \geq 90$ cm) species. For fish, we distinguished pelagics, demersals, bathypelagics, bathydemersals, benthopelagics, reef fishes, sharks, rays and flatfishes. The large pelagic fishes were modelled with an age-structured model incorporating two life-stages as groupings for monthly cohorts (Walters *et al.*, 2010). Invertebrates were separated into

cephalopods, other exploitable molluscs (called ‘exploitable molluscs’), other non-exploited molluscs (called ‘other molluscs’), krill, shrimps, other crustaceans, lobsters and crabs, jellyfish, zooplankton, megabenthos (> 10 mm), macrobenthos (1–10 mm), meiobenthos (0.1–1 mm), corals and a ‘soft corals, sponges, etc.’ group. Marine mammal groupings were baleen whales, toothed whales, dolphin and porpoises, and pinnipeds (seals and sea lions), and we combined all seabirds in one group. Primary producers were included as small and large phytoplankton, diazotrophs and benthic plants. We further considered bacteria and a single detritus group. There were 51 functional groups in the food web model.

The Ecopath baseline model has the following key input variables: biomass (B), production/biomass ratio (P/B), consumption/biomass ratio (Q/B) and diet composition. Further, the model calls for input of fisheries catches for the baseline year (1950). We parameterized the baseline Ecopath model following Christensen *et al.* (2009), but let B and P/B vary based on stochastic stock reduction analysis (SRA) as described below. Further, we obtained diet composition for marine birds from Karpouzi (2005) that complemented information available from previous modelling efforts (Christensen *et al.*, 2009). Diets for marine mammals follow Christensen *et al.* (2009). Basic input tables are presented in Appendix S1 in the Supporting Information and diets in Appendix S2.

Foraging arena model

Predator–prey dynamics in the food web model was based on foraging arena theory (Walters & Juanes, 1993; Ahrens *et al.*, 2012) as implemented in the Ecosim model of EwE (Walters *et al.*, 1997, 2000). The Ecosim model describes the dynamics of predator–prey interactions based on the relationship:

$$dB_j/dt = eavB_jB_i/(2v + aB_j) - ZB_j \quad (1)$$

where B_j is predator biomass, B_i is prey biomass, Z is the total instantaneous mortality rate for the predator (combining fishing and predation mortalities), e is the growth efficiency (production/consumption; can vary during ontogeny), v is prey vulnerability exchange rate, which includes behavioural and density dependence effects, and a is the predator effective search rate. The vulnerable prey density V is represented by the foraging arena equation:

$$V = vB_i/(2v + aB_j) \quad (2)$$

with the terms as defined above. The foraging arena model is flexible for the implementation of functional responses, and has made it possible to replicate ecosystem-level historic trends in exploited marine ecosystems as well as to make plausible predictions (Christensen & Walters, 2011).

Habitat capacity model

We used a new methodology (Christensen *et al.*, 2014) to estimate relative habitat capacity by functional group as a function

of cell-specific habitat attributes, which for instance can be water depth, temperature, pH and bottom type. We linked the time-varying habitat capacity, C , to the foraging arena trophic interactions based on the assumption that the habitat capacity affects the size of the cell-specific foraging arena available to the given functional group. Using the same notations as for the foraging arena above, we have:

$$V = vB_i/(2v + aB_j/C) \quad (3)$$

Using habitat capacity as a modifier of the foraging arena consumption rate resulted in the equilibrium spatial distribution patterns for a functional group being proportional to its habitat capacity (unless there were changes in prey abundance and predation mortality).

For the habitat capacity model, we obtained minimum and maximum depth distributions for 1418 fish and invertebrate species from FishBase (<http://www.fishbase.org>) and SeaLifeBase (<http://www.sealifebase.org>), and used these to obtain a depth distribution based on triangular distributions with maximum occurrence at a third of the depth range. Each of the species was allocated to a functional group of the trophic model, and the depth distribution for each functional group was then averaged across species applying the total catch by species as weighting. For species without catches we used the smallest catch for a species by functional group as the weighting factor. The resulting depth distributions are in Figure S2 of Appendix S3. For each spatial cell in the model, the habitat suitability was then calculated based on the relative productivity for each species at the average cell depth. The habitat capacity model was made spatially and temporally explicit using new GIS linkage capabilities (Steenbeek *et al.*, 2013). The large pelagics (both adult and juvenile groups) were further distributed with a sea surface temperature preference based on a meta-analysis for tuna (Boyce, 2004), assuming that tuna constitutes the bulk of the biomass for these functional groups.

Fisheries

Fleet effort distribution

We derived effort from a global spatial effort database (Anticamara *et al.*, 2011; Watson *et al.*, 2013) which covered the period from 1950 to 2006 with country- and fishing gear-specific fleets for a total of 1365 fleets. The effort was standardized across gear types and years in kWh. The database operated with 14 gear types (see Table 2), and we used these as ‘fleets’ in the global food web model. The ‘effort creep’, i.e. increase in effort that is related to technological development (e.g. echosounders and GPS systems) was set to 2% year⁻¹, which is at the low end of global estimates (Pauly & Palomares, 2010) but higher than what was estimated for Greek fisheries (Damalas *et al.*, 2014).

The global effort database is still under development, and by checking the effort by country and by fleet we found a number of issues that needed consideration. In some cases, this resulted in changes to the database, with notable issues being:

- Effort for the purse seine, non-tuna boat (fleet 10) in Peru was vastly underestimated, not allowing for the vast expansion that has taken place in anchoveta fisheries since the 1960s.
- Where there were missing effort values for certain years by country and by fleet, the missing values were interpolated linearly.
- For tuna fleets (fleets 12–14) there were very low efforts in the 1950s; the effort was therefore scaled with 1960 as the base year for these fleets.

The relative effort by fleet is shown in Figure S1 of Appendix S3. In order to consider regional differences in effort for the non-tuna fleets (fleets 1–11 in Table 2), the relative fleet efforts were distributed spatially by large marine ecosystems (LMEs; Sherman *et al.*, 2005) for which the relative efforts were set based on historic effort. For each LME, the effort was scaled as a proportion of the total effort (measured in kilowatt days) across all fished cells. Where a country's EEZ spanned several LMEs, the country effort was as a rule distributed equally between the LMEs.

Fishing effort was distributed using a gravity model where the effort allocated to each spatial cell is based on the profitability of fishing estimated as the difference between expected income (biomass \times catchability \times fish price) and the cost of fishing by cell (Caddy, 1975; Hilborn & Walters, 1987). We estimated the spatial cost of fishing as proportional to the distance (in km) from the nearest coast (apart from in polar regions, where we assumed that there were no ports in the polar LMEs). An additional cost of fishing in areas with ice cover, I_i , was added to the spatial cost of fishing (to limit fishing there), and estimated based on a logistic function:

$$I_i = I_{\max} / (1 + e^{-20(\delta_i - 0.3)}) \quad (4)$$

where I_i was estimated from the proportion of each cell, δ_i , that is covered by ice each year. I_{\max} , the maximum cost of fishing, was set to the cut-off point for spatial allocation of fishing effort. We have no empirical background for estimating I_i , but the logistic function we applied provides what we consider to be reasonable behaviour by limiting fishing in areas with substantial ice.

Tuna fleets (fleets 12–14) were assumed to work throughout the world ocean, so that the only restrictions were on the depth range in which they could operate (Table 2), and where it would be profitable to operate based on the gravity model.

We obtained prices per functional group from a global price database (Sumaila *et al.*, 2007), expressed as real prices for 2000 by functional group (see Table S2 in Appendix S1).

Catches

The Sea Around Us project uses a geographic information system to map global fisheries catches from 1950 to the present, with explicit consideration of coral reefs, seamounts, estuaries and other critical habitats of fish, marine invertebrates, marine mammals and other components of marine biodiversity (Watson *et al.*, 2004; <http://www.seaaroundus.org>). In the present study, we linked directly to the underlying spatial catch dataset and we used these catches as 'observed catches' to evalu-

ate model runs. The catches for the base year, 1950, were also used to parameterize the landings by fleets in the initial underlying Ecopath initial model.

Time dynamic model tuning

Evaluation of model time dynamics (without any spatial resolution) before using a model for spatial and time dynamic simulations makes it possible to evaluate and tune many model drivers and save time in the model tuning process. Here, we used the time dynamic Ecosim model (Walters *et al.*, 1997, 2000) to evaluate settings for a number of parameters (notably the baseline biomasses and P/B rates for exploited groups) based on the model's ability to replicate catch time series (e.g. Shannon *et al.*, 2004; Coll *et al.*, 2008c; Walters *et al.*, 2008).

Using a time dynamic version of a global ocean model in essence assumes that the world ocean is an ecosystem and that some of the model drivers can be used without explicit spatial considerations. This allows an evaluation of consistency between key model drivers, rates and state variables without the confounding effects of spatial ecological and fishing dynamics. On the other hand, the time dynamic model will let all fleets operate everywhere, thus assuming that spatial fishing effort is completely additive. Here, we developed a series of model tuning and evaluation steps that involved the aspects described below for an initial tuning of key model parameters.

Stock reduction analysis

We extracted catches by functional group and by year from the catch database described above. Based on this, we constructed a time series in Ecosim with 'forced catches', i.e. a SRA (Kimura *et al.*, 1984), implemented as a stochastic SRA (Walters *et al.*, 2006) with two, additive, search criteria. The first was that catches could be replicated in Ecosim, which notably requires that the populations are maintained through the simulation. SRAs are very sensitive to the initial biomass, B_0 ; if the initial biomass is too low the population will crash. The second criterion was to avoid B_0 that are too high as this results in biomasses being unrealistically steady. For this, we assumed as a target that the terminal fishing mortality for fish in the world ocean should be close to the natural mortality for the species groups. We ran a minimization routine 10,000 times in order to minimize the summed squared residuals (SS):

$$SS = \sum_{i,y} [(Y'_{i,y} - Y_{i,y})^2 + (F'_{i,y} - M_i)^2] \quad (5)$$

where $Y'_{i,y}$ is the estimated catch of group i in the last year (y) of simulation, $Y_{i,y}$ is the 'observed' catch in year y , $F'_{i,y}$ is the estimated fishing mortality in year y , and M_i is the total natural mortality (predation and other mortality) for group i in the base year (1950).

We allowed biomasses for large pelagic fish and small bathypelagic fish (the only exploited groups with input biomasses; see Table 1) to vary with a coefficient of variation

Table 1 Characteristics of the functional groups in the trophic submodel. The number of species that were used for each group for deriving depth distributions is indicated. The estimated parameters are either *B* (biomass) or *EE* (ecotrophic efficiency). See Appendix S1 for basic input parameters.

No.	Group name	No. of species	Estimated parameter	Examples of species/groups
1	Pelagics, small	67	<i>B</i>	Anchovy, menhaden, sprat
2	Pelagics, medium	102	<i>B</i>	Jacks, mackerel, herring
3	Pelagics, large	53	<i>EE</i>	Tuna, Spanish mackerel
4	Demersals, small	54	<i>B</i>	Sculpins, gobies, sand lance
5	Demersals, medium	176	<i>B</i>	Rockcod, mullet, snapper
6	Demersals, large	67	<i>B</i>	Ling, grouper, haddock
7	Bathypelagics, small	7	<i>EE</i>	Lanternfish
8	Bathypelagics, medium	16	<i>B</i>	Orange roughy, grenadiers
9	Bathypelagics, large	4	<i>B</i>	Escolar, opah
10	Bathydemersals, small	9	<i>B</i>	Dragonfish, cardinalfish
11	Bathydemersals, medium	25	<i>B</i>	Dories, gurnards, hake
12	Bathydemersals, large	18	<i>B</i>	Monkfish, sablefish, Patagonian toothfish
13	Benthopelagics, small	15	<i>B</i>	Codling, croaker, seabream
14	Benthopelagics, medium	81	<i>B</i>	Seabass, pompano, icefish
15	Benthopelagics, large	54	<i>B</i>	Cod, salmon, hake, grenadiers
16	Reef fish, small	33	<i>B</i>	Wrasse, bream, damselfish, rabbitfish
17	Reef fish, medium	124	<i>B</i>	Moray, snapper, grunts, groupers
18	Reef fish, large	49	<i>B</i>	Groupers, snappers, trevally, barracuda
19	Sharks, small medium	11	<i>B</i>	Dogfishes, catsharks, smooth-hound
20	Sharks, large	59	<i>B</i>	Thresher, hammerhead, tiger, mako
21	Rays, small medium	19	<i>B</i>	Skate and rays
22	Rays, large	35	<i>B</i>	Eagle and manta rays
23	Flatfish, small medium	54	<i>B</i>	Sole, flounder, plaice
24	Flatfish, large	7	<i>B</i>	Turbot, halibut, European plaice
25	Cephalopods	27	<i>B</i>	Squids, cuttlefishes, octopus
26	Shrimps	71	<i>B</i>	Pandalus, tiger prawns, brown shrimp
27	Lobsters, crabs	79	<i>B</i>	Snow crab, king crab, spiny lobster
28	Jellyfish		<i>EE</i>	
29	Molluscs, exploitable	134	<i>B</i>	Clams, scallops, sea urchins and other non-cephalopods
30	Krill	3	<i>B</i>	Euphausia, Antarctic krill, Norwegian krill
31	Baleen whales		<i>B</i>	
32	Toothed whales		<i>B</i>	
33	Pinnipeds		<i>B</i>	
34	Birds		<i>B</i>	
35	Megabenthos		<i>EE</i>	
36	Macrobenthos		<i>B</i>	
37	Corals		<i>B</i>	
38	Soft corals, sponges, etc.		<i>B</i>	
39	Zooplankton other		<i>EE</i>	
40	Phytoplankton, large		<i>B</i>	
41	Benthic plants		<i>EE</i>	
42	Pelagics, large young	53	<i>EE</i>	
43	Meiobenthos		<i>EE</i>	
44	Dolphins, porpoises		<i>EE</i>	
45	Microzooplankton		<i>B</i>	
46	Other crustaceans		<i>B</i>	
47	Other molluscs		<i>B</i>	Non-exploited molluscs
48	Phytoplankton, small		<i>B</i>	
49	Diazotrophs		<i>B</i>	
50	Bacteria		<i>B</i>	
51	Detritus		<i>EE</i>	

(CV; SD/mean) of 0.05, P/B for all exploited groups to vary with CV 0.05, and the ecotrophic efficiency (EE) for exploited groups (apart from large pelagics and small bathypelagics) to vary with CV 0.05. For each run, the minimization routine samples for these parameters, evaluated if the model was mass-balanced, and resampled iteratively when this was not the case, and then evaluates the minimization criteria. We used a fast and efficient Matyas (1965) search routine, which allowed the use of nonlinear search criteria for mass-balance of the ecosystem model. When an improved parameter set was found, the search routine used these parameters as basis for the subsequent sampling. This allowed for a Markov chain random walk through the parameter space.

From the SRA we obtained a modified set of parameters for the model state variables and production rates for the fished groups, and we used these as the basis for the subsequent model runs. We also obtained a set of fishing mortality rates (by group and by year) which we used for comparison with the fishing mortalities from a temporal (Ecosim) run with fleet effort as driver.

Model implementation framework

We developed a framework for constructing the modelling complex leading to the global ocean model, EcoOcean, through database extraction following Christensen *et al.* (2009). The framework extracts spatial models for different areas and with different spatial resolutions. By default the area is global (or rather 90° N to 80° S ignoring the Antarctic landmass), and the resolution is 0.5° latitude by 0.5° longitude.

The first step in the process was to develop an Ecopath model (Christensen & Pauly, 1992) to be used for the modelling framework. For this we used a database-derived model (Christensen *et al.*, 2009) updated with spatial and ecological information from global databases (as explained above). The model biomasses were updated for those groups where information was available from databases (see Christensen *et al.*, 2009). Then, catches were read from the catch database for the base year (which here was 1950).

Using a diet database from FishBase (Froese & Pauly, 2006), the diet for each functional group was averaged where there was species-specific information available. These diets were then used to replace the initial diets in the Ecopath model.

Then the framework read the fleet effort database (Anticamara *et al.*, 2011), which was by country and gear type (see Table 2), and performed the modifications and interpolations that were described in the 'Fleet effort distribution' section above. It then constructed time series with effort by year and by gear (Fig. S1 in Appendix S3), and these time series were stored in the model database.

Information about preferred depth zones by species were read by species and averaged by functional group to obtain average depth distributions for the different functional groups in the model. These were added to each of the time dynamic scenarios. Further, spatial basemaps were created with selectable resolution (0.5° or 1°), and the basemaps were populated with spatial data

Table 2 Fishing gear types. Target groups indicate only major groups or 'diverse' where there are many groups. Depth range (m) indicates depths at which each fleet was allowed to operate.

No.	Name	Target groups	Depth range (m)
1	Other	Molluscs, pelagics, demersals	0–1000
2	Lines, non-tuna	Demersals, very diverse	0–2000
3	Longline, non-tuna	Large fish	0–2000
4	Trap	Diverse	0–1000
5	Dredge	Molluscs	0–1000
6	Trawl, bottom	Diverse	0–1000
7	Trawl, shrimp	Shrimp	0–1000
8	Trawl, midwater	Pelagics	0–1000
9	Seine	Pelagics, demersals	0–1000
10	Purse seine, non-tuna	Pelagics, demersals	0–1000
11	Gillnet	Diverse	0–1000
12	Pole and line tuna	Large pelagics	All
13	Longline, tuna	Large pelagics	>10 m
14	Purse seine, tuna	Large pelagics	>10 m

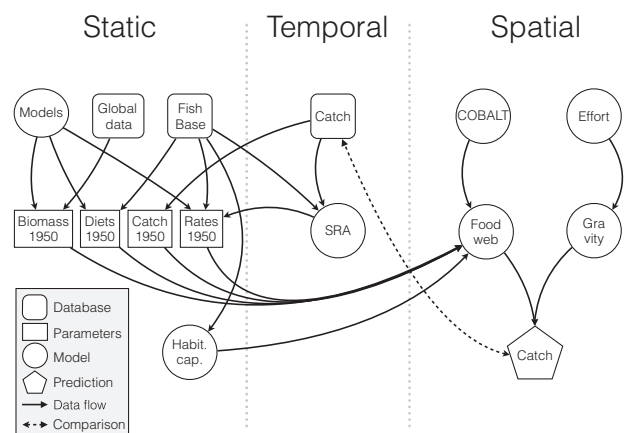


Figure 1 Overview of the modelling process involving construction of the static Ecopath model, the temporal Ecosim model with stock reduction analysis (SRA) and the spatial-temporal modelling complex. Habit. cap. refers to a habitat capacity model, and the environmental impacts are obtained from the COBALT model. Effort is distributed based on a gravity model. Arrows indicate flow of information or comparisons as indicated.

and saved with the model database. We provide a schematic overview of the modelling process in Fig. 1.

Programming environments

The modelling framework was implemented as a VB.NET module that was coupled with the EwE model. Through its integration with EwE the model had full access to the EwE graphic user interface, which facilitated both model development and evaluation.

The model runtime for a 56-year run (with a 10-year spin-up period) with 1° resolution is 90 min on a 24-core PC, and more than 12 h for the version with 0.5° resolution. While this is fast for a global spatial model it must be noted that evaluating uncertainty calls for a very large number of model runs, and this can be prohibitively time-consuming. With this in mind, the model was ported to a LINUX cluster computing environment (at Compute Canada's WestGrid). Given the amount of .NET legacy code involved, which is tied to the Windows environment, a version of the spatial model without the user interface was prepared so that it could be run under Mono 3.0, a cross-platform runtime environment that enables execution of .NET code on other operating systems such as LINUX.

RESULTS AND DISCUSSION

We obtained a reasonable fit to fishing mortality for many of the exploited groups (Fig. 2). Therefore, the main conclusion is that the SRA and temporal model approach produced fishing mortalities that were of similar magnitude for the majority of the

groups. Further, there were temporal differences in the series that may well be caused by not considering that prices vary differentially over time (Sumaila *et al.*, 2007), and this will affect how fishers allocate effort between different target fish species (Salas *et al.*, 2004).

Our main fitting criterion for the spatial model was to produce a reasonable fit to observed catches. We did not apply a formal fitting approach based on an objectivity function as is the norm for temporal dynamic ecosystem modelling (Christensen & Walters, 2011), as that exceeds what is feasible at present for global spatial models. As a consequence we note that in this study not applying a formal fitting procedure minimizes the chance that we will be overfitting the model, which tends to result in poor predictive capability.

We compared observed catch data by functional groups aggregated spatially with the catch data predicted by the global spatial model. Even though the model used the average catch by fishing fleet in 1950 as its baseline – and this does come from the observed catch data – the predicted catches over time are based on the fleet effort database, which is independent of the catch

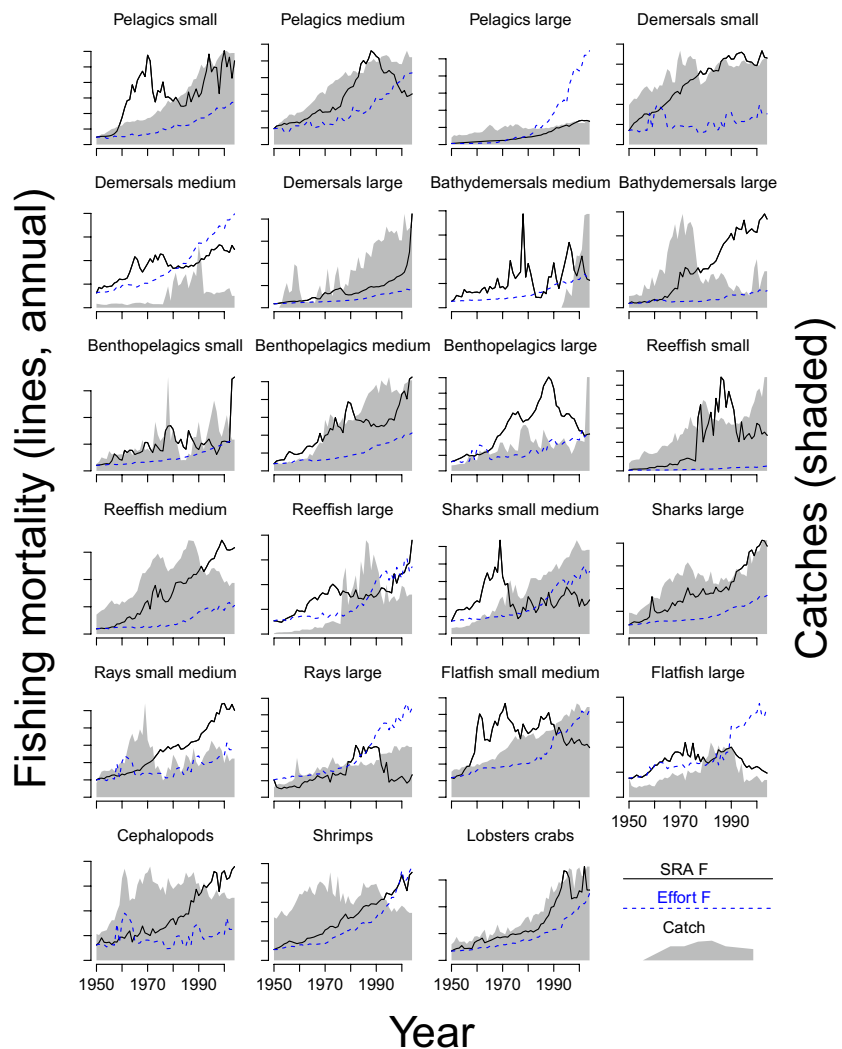


Figure 2 Fishing mortality for functional groups at the global level as obtained from stochastic stock reduction analysis (SRA; solid line) and from fleet effort based on the time dynamic global ocean model (Effort; stippled line). The catch trends from the Sea Around Us database are indicated by shading.

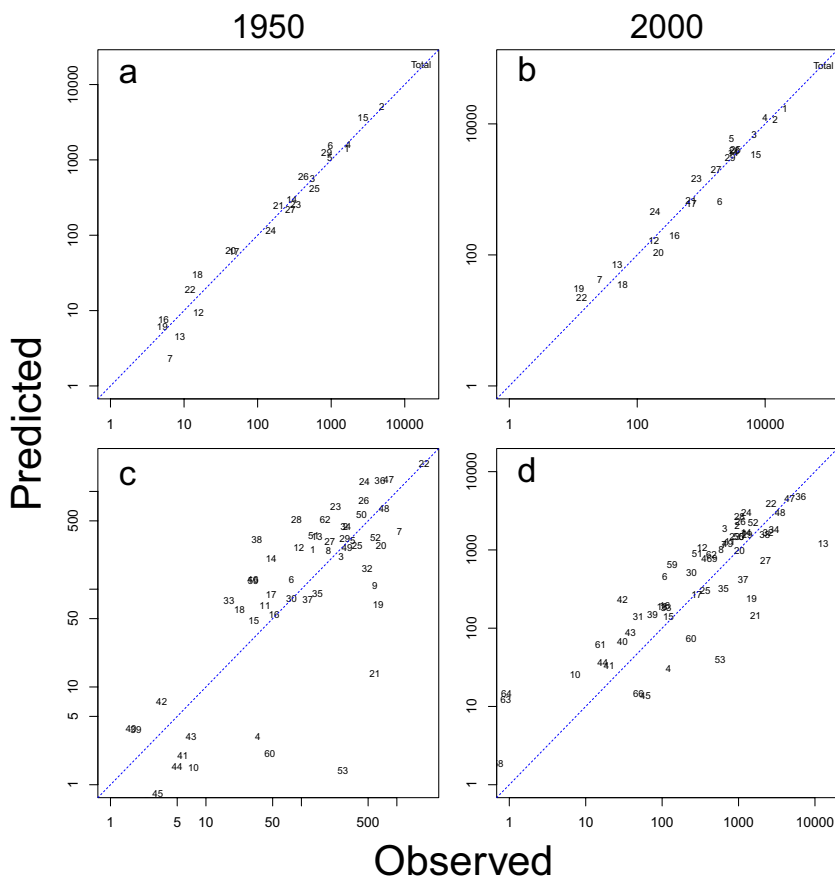


Figure 3 Predicted versus observed catches (log scale, in 1000 tonnes) for the global ocean model with years indicated above the plots. The dotted lines indicate observed = predicted. In (a) and (b) numbers indicate functional group numbers (see Table 1) and in (c) and (d), numbers indicate numbers for large marine ecosystems (listed in Appendix S4). In Appendix S5, there are additional figures with spatial comparisons of observed and predicted catches for 1950 and 2000.

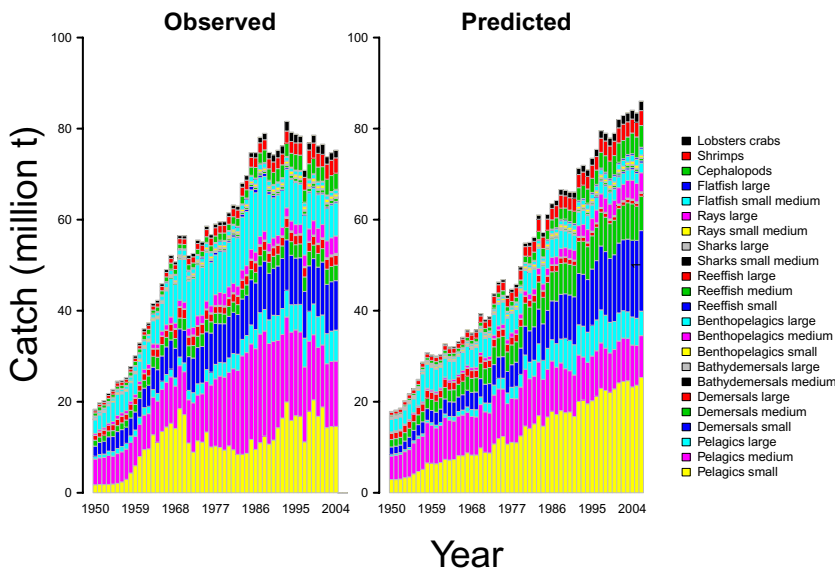


Figure 4 Observed (from the Sea Around Us catch database) and predicted (from the spatial EcoOcean model) global catches by functional groups from 1950 to 2006.

database and is spatially explicit. We therefore concluded that the observed and predicted catches over time can be considered independent. Figure 1 serves to illustrate this conclusion.

The immediate conclusion when comparing observed versus predicted catches by functional group for the years 1950 to 2000 (Fig. 3a, b) as well as for the time series (1950–2006; Fig. 4) was

that the global model is capable of replicating group-specific landings, even if far from perfectly. The spatial model used the observed catches for the 1950 baseline, and one should therefore assume that the observed and predicted catches should be the same or very similar for this year. It must be stressed, however, that the functional groups and fishing fleets have to be distributed

spatially, and that this spatialization involves concentrating most of the groups in the shallow coastal parts of the ocean – where the bulk of global fish production indeed takes place. The fisheries were likewise concentrated in these areas, and overall the 1950 results (Fig. 3a) showed good agreement in trend between observed and predicted catches, with a general distribution around the 1:1 line (and within half an order of magnitude of the observed; see Appendix S5 for the spatial results of predicted and observed catch). Spatially by LME, these results show how the catches in 1950 were concentrated in the Northern Hemisphere and Asia.

The predicted group catches for year 2000 (Fig. 3b) were distributed along the 1:1 line, and showed good agreement with the observed catches. The predicted catches for the dominant groups (i.e. those with catches exceeding 1 million tonnes) are well within half an order of magnitude from the observed catches. Catches by LME were generally overestimated for the LMEs with low catches in both 1950 and 2000 (Fig. 3c, d), but with considerably more variation than for catches by functional groups. The main implication of Fig. 3 is that catches were better predicted at the functional group level than they were regionally, which we find promising as our interest in the model primarily centres around predictions of future seafood production overall.

Closer examination of Fig. 4 shows that some key problems are overestimation of the small pelagic catches and underestimation of the medium-sized pelagics. Overall, however, this almost evens out. The figure also reflects that the model does not capture well the recent stagnation in global catches – assuming it is real; ‘observed’ catches are estimates as well. The key factor for this is the continued increase in small pelagics and small demersals, both of which will have to be examined in more detail. However, we expect that updates of the global effort database will help remedy this.

With this study we have developed a functional global spatial-temporal ocean model that can be used for evaluating how major drivers in the form of environmental productivity combined with fishing effort affect the ocean. For the first time this approach allows the future impact of alternative climate models on life in the ocean to be evaluated. Here we focused on the initial model fit to historic data and on evaluating the impact of historic environmental productivity and fisheries on fish biomasses. In future we will develop the modelling complex further.

Results from the model regarding catch suggest that our modelling complex can generally make a successful prediction of fisheries in the ocean. While we did fit some of the model production parameters to catches based on non-spatial model runs, the spatial-temporal model runs relies strongly on spatial patterns that were not considered in the non-spatial runs, and we therefore conclude that it is not a circular argument to fit the initial model to catches, and then to subsequently evaluate how the spatial model fits catches.

We found that catches are better predicted at the functional group level than they are regionally, and this highlights that further efforts need to be developed in the study of spatial-temporal allocation of fishing effort. A factor that may contribute to a better match of predicted and observed catches is that

observed catches are probably underestimated due to large illegal, unreported and unregulated (IUU) amounts being missed in official statistics (Agnew *et al.*, 2009). The spatial catch distributions over time illustrate the expansion of fisheries, mainly in the Northern Hemisphere in 1950, to southern regions and Asian countries in 2000. This spatial-temporal pattern is in line with the previously described expansion and ecological footprint of fisheries (Coll *et al.*, 2008b; Swartz *et al.*, 2010). It is a short-coming of the effort data included here that we do not have effort from outside the LMEs for non-tuna fleets. This is a topic that will need consideration in coming iterations of the model.

There are still considerable improvements needed for the modelling complex presented here before it is fully functional for all its intended uses. On the parameter front, we do not, for instance, include temperature effects directly in the food web model, only indirectly through the linked climate model. For future development we will extend the modelling complex with a focus on: (1) governance aspects to evaluate fisheries policies that promotes resilience to climate change; (2) the interplay between aquaculture and capture fisheries; and (3) global seafood trade. However, this study shows that global modelling efforts are not only needed but are indeed both possible and making progress.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

Appendix S1 Basic input parameters for the Ecopath model and prices.

Appendix S2 Diet composition for the Ecopath model.

Appendix S3 Fleet effort over time and depth distributions.

Appendix S4 List and map of large marine ecosystems.

Appendix S5 Observed and predicted fisheries catches in large marine ecosystems.

BIOSKETCH

Villy Christensen is professor at the Fisheries Centre of the University of British Columbia and leads the development of the Ecopath with Ecosim modelling approach and software. His research is focused on understanding how climate change may affect the future ocean and what role mitigation through ocean management may serve to ensure that there will be seafood and healthy oceans for future generations.

The authors jointly represent an interdisciplinary group that was required for this almost very large data analysis of the global ocean. Their webpages include: <http://www.globaloceanmodeling.org> (V.C., J.B., J.S., M.C.); <https://sites.google.com/site/mcmsea/> (M.C.); <http://coru.sites.olt.ubc.ca> (W.W.L.C.); <http://www.tfroelicher.com> (T.F.); <http://www.gfdl.noaa.gov/charles-stock-homepage> (C.A.S.); <http://ecomarres.com> and <http://www.imas.utas.edu.au/people/profiles/current-staff/w/reg-watson> (R.A.W.); and <http://www.fisheries.ubc.ca/faculty-staff/carl-walters> (C.J.W.).

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