Database-driven models of the world's Large Marine Ecosystems

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ABSTRACT

We present a new methodology for database-driven ecosystem model generation and apply the methodology to the world's 66 currently defined Large Marine Ecosystems. The method relies on a large number of spatial and temporal databases, including FishBase, SeaLifeBase, as well as several other databases developed notably as part of the *Sea Around Us* project. The models are formulated using the freely available Ecopath with Ecosim (EwE) modeling approach and software. We tune the models by fitting to available time series data, but recognize that the models represent only a first-generation of database-driven ecosystem models. We use the models to obtain a first estimate of fish biomass in the world's LMEs. The biggest hurdles at present to further model development and validation are insufficient time series trend information, and data on spatial fishing effort.

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1. Introduction

There is a global trend toward ecosystem-based management of marine resources. This is in line with international agreements, most recently as expressed through the Johannesburg and Reykjavik Declarations, and supported by the UN Food and Agricultural Organization through the Code of Conduct for Responsible Fisheries (FAO, 2003). Ecosystem modeling has an important role to play in implementation of ecosystem-based fisheries management through its capabilities to examine ecological, economical and social tradeoff in an integrated manner. Though there has been progress, we are still far from seeing ecosystem models used for management in more than a few of the world's Large Marine Ecosystems (LMEs). LMEs refer to 66 marine ecosystems with unique sets of ecological, oceanographic and biogeochemical characteristics

identified by Sherman over the last two decades (Sherman et al., 2005). We attribute the limited application of ecosystem modeling in the LME context to a combination of factors, of which lack of experience may be more important than lack of data. Ecosystem modeling indeed calls for integration and analysis of data from the entire ecosystem, and this can be a daunting task for anyone. Ecosystem models are data hungry, and few models have been fed sufficiently. This is not, generally, because "data are not available", as many believe. Rather, it is a question of realizing what is needed, what is available, and how to best use the data for analysis. Particularly, there are increasing numbers of global databases that greatly help researchers obtain the basic biological and physical parameters to develop ecosystem models. The many training courses that we have conducted around the world have served to build capacity for ecosystem modeling. We have realized, however, that training alone does not suffice; there is considerable work involved in the steps described above, and we here report on a procedure for 'database-driven ecosystem model generation', expected to further enhance the level of ecosystem modeling, as well as to make it more accessible. In this paper, we describe how we link into a large

number of spatial and temporal databases describing the world's oceans, their resources, and how the resources are exploited. We extract data from these databases, and use these data to modify a generic ecosystem model in order to obtain ecosystem models for each of the 66 LMEs in the World's oceans. Here we use these models to estimate fish biomass in the world's LMEs, and anticipate that the models will see much further use and enhancement.

2. Model methodology

2.1. The Ecopath with Ecosim (EwE) modeling approach

EwE is an ecosystem modeling approach and software that is being used for ecosystem-based fisheries management throughout the world (see Christensen and Walters, 2005). The approach started out in the early 1980s when Jeff Polovina of the NOAA Pacific Islands Fisheries Science Center in Honolulu was tasked with developing an ecosystem model to integrate information from a major, multi-disciplinary study of productivity in the French Frigate Shoals ecosystem in the Northwestern Hawaiian Islands (Polovina, 1984; Polovina, 1993). Polovina examined the ecosystem models then in use for fisheries research (notably Andersen and Ursin, 1977; Laevastu and Favorite, 1980), and developed a simple mass-balance model, with the main purpose of evaluating consistency in estimates of production (and by deduction, state variables) for ecosystem components at all trophic levels, as well as to estimate how much demand there was for production (and, again, by deducing state variables) for groups where no estimates of biomass were available. Polovina called his model 'Ecopath', and this quantified food web model has since been further developed to become the most-widely applied approach for ecosystem modeling, with hundred of published models (Morissette, 2007). We have described the modeling approach in many publications over the years, and refer to such for computational details (e.g., Christensen and Pauly, 1992; Walters et al., 1997, 1999, 2000; Christensen and Walters, 2004; Christensen et al., 2005).

Of special importance here is that we recently have re-developed the approach in an object-oriented programming environment (Christensen and Lai, 2007), a prerequisite for the automated model setup. We rely on being able to call the various components of the EwE modules, read, add, and change parameters, run the various models, make new scenarios etc, all from code, in order to be successful with an undertaking of this scale.

2.2. Data sources

We base the database-driven model-generation approach for the world's LMEs on a number of spatial, global databases, the majority of which were and are being developed by the *Sea Around Us* project at the Fisheries Centre of the University of British Columbia

(www.seaaroundus.org). The project is designed to document how we exploit the ocean's living resources, the consequences of the exploitation, and what can be done to improve ocean conditions (Pauly, 2007). As part of this the *Sea Around Us* project has developed spatial databases for catches, effort, and prices, and other information related to productivity and fisheries (see below). Here, we build on these databases in combination with the EwE ecosystem modeling approach and software, which is developed as part of the project to construct ecosystem models of each of the world's 66 LMEs.

Given that most of the databases we use for the ecosystem model construction have been developed and described elsewhere, we give here only a very brief introduction to the individual data sources, and we concentrate our description on the aspects that have direct relevance for the model construction. We present an overview of the data sources in Table 1.

2.3. Functional groups and basic parameters

Ecopath, and also the time-dynamic Ecosim model (Walters et al., 1997, 2000) and the time- and spatial–dynamic Ecospace model (Walters et al., 1999), all rely on describing quantified food webs of life in the ocean. For practical reasons (not only due to uncertainty about diets for individual species but also to make the model parameterization more manageable) we aggregate species in 'functional groups,' which may consist of ecologically similar species, of individual species, or of life-stages of individual species or groups of species.

To develop the database-driven models we have cooperated with FishBase (Froese and Pauly, 2009) to define a functional taxonomy for fishes based on their asymptotic length, their feeding habits, and their vertical distribution characteristics. While the information is available from FishBase for splitting the fishes into piscivores, benthivores, and herbivores, we simplify the model parameterization by omitting this classification in the definition of the functional groups. We do, however, consider the feeding habits implicitly when deriving diet compositions for the individual LMEs.

We separate between 'small' species with asymptotic length <30 cm, 'medium' with length 30–89 cm, and 'large' with asymptotic length of 90 cm or more. We further separate between pelagics, demersals, bathypelagics, bathydemersals, benthopelagics, reef fishes, sharks, rays, and flatfishes. We separate invertebrates into cephalopods, other molluscs, krill, shrimps, lobsters and crabs, jellyfishes, zooplankton, megabenthos (>10 mm), macrobenthos (1–10 mm), meio-benthos (0.1–1 mm), and corals, soft corals, sponges, etc. Marine mammals are split into baleen whales, toothed whales, dolphins and porpoises, and pinnipeds (seals and sea lions), and aggregate all seabirds in one functional group. Primary producers are included as phytoplankton and benthic plants.

An overview of the functional groups is presented in Table 2, which also shows the basic (default) input parameters for all groups,

Table 1

Data sources and databases used for the database-driven ecosystem model construction. All data sets are digitized and allocated to spatial cells of with either 1/2° latitude by 1/2° longitude, or 1° latitude by 1° longitude resolution. Datasets currently available online are indicated.

Topic	Data source, reference
Fish species, growth parameters, diets	FishBase; www.fishbase.org
Non-fish species, growth parameters, diets	SeaLifeBase; www.sealifebase.org
Marine mammal diet	Pauly et al. (1998b), Kaschner (2004)
Marine mammal abundance	Christensen (2006)
Marine bird, abundance, diet and consumption	Karpouzi (2005), Karpouzi et al. (2007)
Primary productivity	Carr (2002), Marra et al. (2003), Behrenfeld and Falkowski (1997), Dunne et al. (in preparation)
Zooplankton biomass	FAO (1972, 1981)
Meio- and macro-benthos biomass	Peters-Mason et al. (unpublished data)
Mesopelagics	Gjøsaeter and Kawaguchi (1980); digitized by Sea Around Us project
Abundance trends for marine populations	Sea Around Us project (unpublished data)
Fisheries catches	Sea Around Us project; www.seaaroundus.org
Off-vessel prices	Sea Around Us project; www.seaaroundus.org

Table 2
Functional groupings and basic input parameters for the LME models. B is biomass (t km^{-2}), P/B the production/biomass ratio (year^{-1}), EE is the (dimensionless) ecotrophic efficiency, P/Q the (dimensionless) production/consumption ratio. The 'e' indicates that the parameter is estimated as part of the mass-balance calculations of Ecopath, '–' indicates a trivial parameter that does not need input (e.g., if P/B and Q/B are given, then P/Q is known), '*' indicates that the parameter in question is obtained from databases as part of the model construction, and 'n.a.' indicates that the parameter is not defined.

	Group name	B	P/B	EE	P/Q
1	Pelagics small	e	0.9 (*)	0.8	0.25
2	Pelagics medium	e	0.5 (*)	0.8	0.25
3	Pelagics large	e	0.3 (*)	0.8	0.2
4	Demersals small	e	1.5 (*)	0.8	0.25
5	Demersals medium	e	0.6 (*)	0.8	0.2
6	Demersals large	e	0.3 (*)	0.8	0.15
7	Bathypelagics small	*	0.5 (*)	–	0.25
8	Bathypelagics medium	e	0.3 (*)	0.8	0.2
9	Bathypelagics large	e	0.1 (*)	0.8	0.2
10	Bathydemersals small	e	0.5 (*)	0.95	0.2
11	Bathydemersals medium	e	0.3 (*)	0.7	0.2
12	Bathydemersals large	e	0.1 (*)	0.85	0.25
13	Benthopelagics small	e	0.6 (*)	0.95	0.25
14	Benthopelagics medium	e	0.4 (*)	0.9	0.25
15	Benthopelagics large	e	0.2 (*)	0.9	0.25
16	Reef fish small	e	1.0 (*)	0.8	0.25
17	Reef fish medium	e	0.6 (*)	0.8	0.2
18	Reef fish large	e	0.3 (*)	0.5	0.15
19	Sharks small medium	e	0.5 (*)	0.9	0.2
20	Sharks large	e	0.2 (*)	0.2	0.15
21	Rays small medium	e	0.4 (*)	0.6	0.2
22	Rays large	e	0.2 (*)	0.8	0.15
23	Flatfish small medium	e	0.8 (*)	0.9	0.25
24	Flatfish large	e	0.3 (*)	0.9	0.15
25	Cephalopods	e	2.0	0.7	0.2
26	Shrimps	e	2.5	0.7	0.3
27	Lobsters crabs	e	2.0	0.9	0.3
28	Jellyfish	0.5	10	e	0.25
29	Molluscs	e	2.0	0.8	0.3
30	Krill	e	5.0	0.9	0.25
31	Baleen whales	*	0.03	e	*
32	Toothed whales	*	0.05	e	*
33	Pinnipeds	*	0.15	e	*
34	Birds	*	0.1	e	*
35	Megabenthos	e	3.0	0.8	0.3
36	Macro-benthos	*	10	e	0.35
37	Corals	0.1	1.0	e	0.67
38	Soft corals, sponges, etc	2	0.2	e	0.2
39	Zooplankton other	e	30	0.9	0.25
40	Phytoplankton	*	*	e	n.a.
41	Benthic plants	2	10	e	n.a.
42	Meio-benthos	4	40	e	0.4
43	Dolphins porpoises	*	0.08	e	*
44	Detritus	100	n.a.	e	n.a.

as well as indicating the parameters that are supplied as part of the database-driven model-generation. The combined excretion and egestion rate was set to 0.2 (dimensionless) for all groups, apart from zooplankton where 0.4 was used based on experience from many other models (Christensen and Walters, 2004).

The ecotrophic efficiencies (EE), in Table 2 for the exploited species are used only for initial parameterization. Once the model-generation procedure is past the initial step, the default EE input would be used to calculate a start biomass. The calculated biomass will subsequently be changed to ensure that the functional group does not crash (i.e., is reduced by 99%) over time when observed catches are removed by subtraction from biomass at each time step, and in order to fit the biomass better using a random optimization search procedure We explain the fitting in more details in the sections "database-driven model generation" and "time series weighting for SS", below.

We used an assumed diet composition for each functional group as a starting point (Christensen et al., 2008). For each LME, however, we modify the diets through an automated procedure based on diet data extracted from global databases of marine animals, notably, for fish from FishBase and for invertebrates from SeaLifeBase (Palomares and Pauly, 2009), for marine mammals from Pauly et al. (1998b) and Kaschner (2004), and for marine birds from Karpouzi (2005). We refer to these sources for details.

2.4. Production rates for exploited groups

To obtain a weighted production/biomass ratio (which for biomass-dynamic groups corresponds to total mortality rate, Z, when there is no biomass accumulation) for each of the exploited functional groups, we develop a simple population dynamics model with monthly time steps for each species (i) represented in the catches. For this, we estimate bodyweight, W_t at age (t, months) based on the von Bertalanffy growth equation,

$$W_t = W_\infty \cdot (1 - e^{-K \cdot t})^3$$

where K is the von Bertalanffy metabolic parameter (year^{-1}), and W_∞ is the asymptotic weight (g). The natural mortality rate at age (M_t, year^{-1}) is then estimated from the weight at age, based on Lorenzen (1996) as,

$$M_t = M_u \cdot W_t^{W_b}$$

where M_u is 3.08 at latitudes <30°, 3.13 at latitudes between 30° and 60°, and 1.69 at higher latitudes. The values for W_b are −0.21, −0.309 and −0.292 for the same latitudes, respectively. For each LME we estimate the mean latitude of all cells of a 1/2° latitude by 1/2° longitude grid, and use this for the calculations.

We next assume that the fishing mortality at age (F_t, year^{-1}) in 1950 can be estimated from a logistic function,

$$F_t = \frac{C_{1950}}{C_{max}} \cdot K \cdot (1 - e^{-K \times (W_t - a_0)})^3$$

where C_{1950} is the catch for the species in 1950, C_{max} is the maximum annual catch during 1950–2004 for the species, a_0 is the weight at recruitment to the fishery, here assumed to be 0.1·W_∞ With this, we can now estimate the number at age (N_t) as,

$$N_t = N_{t-1} \cdot e^{-(M_t + F_t)/12}$$

by setting $N_1 = 1$ as we only need relative numbers and biomass. The biomass of the age class is estimated as

$$B_t = N_t \cdot W_t$$

For the species (i), we sum up, to get $B_i = \sum_t B_t$, $M_i = \sum_t M_t \cdot B_t$, and, $F_i = \sum_t F_t \cdot B_t$. Next, we want to integrate over species within a functional group. For this, we assume that the contribution of the individual species (i) can be based on their contribution to catches. We acknowledge that this is a very rough assumption, assuming the same catchability and targeting for all species within a group, but see this as the only possible first assumption. It will be possible to modify this assumption later; this is only a first step. We thus estimate the functional group production/biomass ratio (P/B, year^{-1}) from,

$$\frac{P}{B} = \sum_i \left[\frac{C_{i,1950}}{F_i} \cdot (F_i + M_i) \right] / \sum_i \left(C_{i,1950}/F_i \right)$$

which is simply a weighted average of $F_i + M_i$, with each (i) weighed by $C_{i,1950}/F_i$.

2.5. Maximum fishing mortality rates

We estimate an overall natural mortality rate (M, year^{-1}) for each exploited fish species based on Pauly (1980),

$$\ln M = -0.2107 + 0.4627 \cdot \ln T + 0.6757 \cdot \ln K - 0.0824 \cdot \ln W_\infty$$

where T is the ambient temperature (°C), K is the von Bertalanffy curvature parameter (year^{-1}), and W_∞ is the asymptotic weight (g). We weigh the exploited species by their overall catch over time to obtain a weighted natural mortality rate for each exploited functional group.

For each functional group, we then set the maximum allowable fishing mortality, F_{lim}, to four times the natural mortality rate obtained from the Pauly equation. We use F_{lim} as a reference point in Ecosim, so that if the estimated fishing mortality (obtained using a 'conditioned on catch' model forcing procedure where $F = (observed\ catch)/(model\ biomass)$ exceeds F_{lim} we limit the fishing mortality to this reference value. This ensures a smooth decline in population size (but not immediate collapse) even if B_{1950} has been underestimated during early steps of the time series fitting procedure. That fitting procedure then seeks to move the population out of the 'crash zone'.

2.6. Primary productivity

Ecosim models are sensitive to changes in ecosystem productivity, and we have generally found a need to include both fisheries impact and temporal change in system productivity to reproduce historic abundance trends in ecosystems (Christensen and Walters, 2005). It is therefore extremely important to include changes in system productivity in the models throughout the simulation period. While global, spatial estimates are available from satellites for the recent decade, we do, however, need to use models to obtain estimates going back in time to the start of our simulation, i.e. to 1950, just like we need models to go forward to evaluate impact of climate changes. Fortunately such models are being developed in response to the need to evaluate the impact of climate change, and we here include four different models, though we have only used one set of data to date for the actual simulations conducted.

We used two different modeling approaches to simulate primary production. The first approach uses an empirical model to estimate chlorophyll based on physical properties. This technique, described in detail in Sarmiento et al. (2004), fits observed SeaW-iFS (http://oceancolor.gsfc.nasa.gov/SeaWiFS/) chlorophyll data to a function of sea surface temperature, sea surface salinity, maximum winter mixed layer depth, and growing season length for different biogeochemical provinces (Longhurst, 1998), and then uses the empirical fits to predict chlorophyll under varying physical conditions. The resulting chlorophyll values were converted to primary production values based on three different algorithms: Carr (2002), Marra et al. (2003), and Behrenfeld and Falkowski (1997). All three algorithms estimate primary production as a function of surface chlorophyll, light, and temperature. The second modeling approach used was a lower trophic level biogeochemical model run within a coupled atmosphere ocean general circulation model (Dunne et al., in preparation).

Our intention for including four different primary production series (as a starter) is to be able to evaluate different scenarios for how future fish production may be impacted by climate change. We see this as an important use of the database-driven ecosystem models.

The primary production estimates were available on a 1° latitude by 1° longitude basis, with coastal cells excluded. We estimated primary production by LME by averaging the monthly primary production estimates over all cells with estimates within a given LME. We further estimated the average annual primary production by LME by averaging the monthly estimates within each year. In the averaging we did not consider that the cells had variable sizes; since coastal cells were excluded, all cells within an LME will have similar size.

The primary production estimates were obtained as mg Chl m^{-3} day^{-1}; we assumed this pertained to a water column of 50 m, and that the average chlorophyll content in phytoplankton was 2.6% by weight of organic carbon (Riemann et al., 1989). We next converted the estimate of g carbon m^{-2} to g wet weight m^{-2} based on a conversion factor of 1:9 (Pauly and Christensen, 1995). We note that the conversion factors used will have negligible impact on the simulations performed here; what is important is not the overall level of system productivity, but how productivity changes over time. We consider it safe to assume that the conversion factors are not time varying, and that they, therefore, have little impact on the overall results.

From the sources above we estimated total primary production as well as standing stock of phytoplankton (from the SeaWiFS chlorophyll estimates) for use as biomass measures, and from the ratio of the two we obtained production/biomass ratios to use for the individual LMEs. In Ecosim simulations, we forced the biomass over time to match the selected series, and also fixed the production/biomass ratio over time, so that modeled total primary production would follow the selected series closely.

Primary production estimates were missing for some of the inland seas, and for those we followed a prioritized list where we used the Carr estimates if available. If not, we used the Marra et al. estimates, the Behrenfeld and Falkowski estimates, or, finally, the Dunne et al. estimates. In all cases, we used the annual primary production estimates to drive the ecosystem models, as we are not evaluating seasonal match-mismatch, and the monthly estimates will likely add more noise than signal.
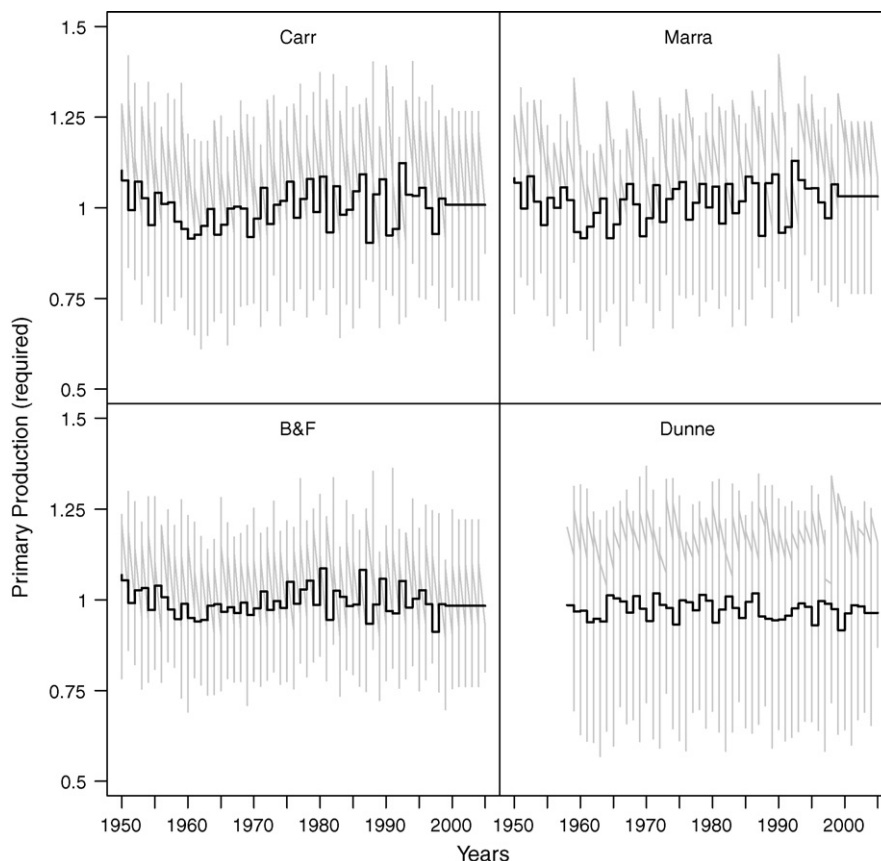
An example of the primary production estimates is shown in Fig. 1 for the Humboldt Current LME. It is noteworthy that at the scale of the LME, which stretches from northern Peru to the south tip of Chile, there is relatively little inter-annual variability, even though this area is strongly influenced by periodic El Niño/La Niña Southern Oscillations events. There were, e.g., El Niño events in 1976–1977, 1982–1983, 1986–1987, 1991–1994, and 1997–1998. We actually see stronger temporal variation in other LMEs, e.g., the Gulf of Mexico.

2.7. Zooplankton

The biomass estimates are based on a map of zooplankton abundance in the upper 100 m of the world's oceans, published by FAO (1972, 1981), and based on the work of Bogorov et al. (1968). The original map was digitized by the *Sea Around Us* project, and the original estimates in mg m^{-3} (wet weight) were re-expressed in t km^{-2}. We apply the estimates of zooplankton biomass to the upper 100 m of the water column, and assume that abundances at greater depths are negligible.

2.8. Benthos

Biomass estimates for two size-categories of benthos, macro-benthos and meio-benthos are from a spatial GIS-layer developed at the Conservation Biology Marine Institute, Bellevue WA, USA in cooperation with the *Sea Around Us* project (Peters-Mason et al., unpublished data). Peters-Mason et al. evaluated 28 publications with geo-referenced estimates of meio-fauna (0.1–1 mm, $N = 184$ samples, notably foraminiferans, nematodes, and harpacticoid copepods) and macro-fauna (1–10 mm, $N = 140$ samples, notably polychaetes, crustaceans, and mollusks). Samples of larger benthos ('mega-fauna', notably cnidarians, crustaceans and echinoderms) were too sparse in the literature to allow derivation of global estimates. We extract estimates of benthos abundance from this source with a half-degree by half-degree resolution globally, and sum the abundance by LME. No information about temporal trends in benthos abundance was available at the scale of interest, and we

Fig. 1. Primary production estimates (relative) for the Humboldt Current (LME 13) for the time period 1950–2004. Estimates are expressed relative to the 1950 values, and are based on the methods of Carr (2002), Marra et al. (2003), Behrenfeld and Falkowski (1997), and Dunne et al. (in preparation) Darker lines indicate annual, lighter monthly values.

therefore let the abundance and productivity patterns be estimated from the time-dynamic simulations.

2.9. Mesopelagics

A combined spatial biomass of small and large mesopelagic fishes was obtained from the information provided by Gjøsaeter and Kawaguchi (1980) based on extensive trawl-surveys in the world oceans. The maps were digitized and validated by Lam and Pauly (2005). The derived GIS-layer is incorporated in the *Sea Around Us* database, and we extract estimates by half-degree and sum up to the LME-level for all LMEs.

2.10. Marine mammals

We used published reconstructions of marine mammal population estimates and trends for all extant species of marine mammals with an exploitation history (Christensen and Martell, 2005; Christensen, 2006). This work included creation of a global database of marine mammal whaling, sealing and bycatch/discards estimates, and we combined this database with a spatial database of marine mammal distribution and relative abundance, covering all marine species (Kaschner, 2004; Kaschner et al., 2006).

Combining the estimates of abundance by species by year, and the relative species distributions we obtain estimates of the spatial abundance of marine mammal species by year. For each spatial cell we sum up the abundance to the LME-level, and thus obtain species-weighted marine mammal abundance by LME. We are currently not allocating the catch database of marine mammal kills to spatial cells, because the whaling database as implemented does not have the required spatial information, and we are thus unable to estimate mortality by LME by year. Instead, we force marine mammal abundance directly in the Ecosim model runs, i.e. we provide that abundance as a 'known' biomass time series from which time series Ecosim predictions of marine mammal food consumption and impact on prey are generated. We assume that the trend has been the same throughout the species' distribution area.

We obtain estimates of annual consumption for marine mammal species based on estimated consumption/biomass ratios and species abundance estimates, and for each LME summed up by species to obtain the total consumption by the marine mammal biomass. The consumption/biomass (Q/B, year^{-1}) estimates are based on an assumption of baleens feeding eight months a year. Based on Reilly et al. (2004), we have for baleen whales,

$$\frac{Q}{B} = \frac{8 \cdot 30 \cdot 1.66 \bar{W}^{0.559}}{\bar{W}}$$

where $\bar{W}$ indicates average individual weight (kg).

For toothed whales and dolphins we use an empirical equation developed by Hunt et al. (2000), as modified by Piroddi (2008),

$$\frac{Q}{B} = \frac{365 \cdot 317 \bar{W}^{0.714}}{\bar{W} \cdot 1207}$$

For otariids (eared seals),

$$\frac{Q}{B} = \frac{365 \cdot 320 \bar{W}^{0.714}}{\bar{W} \cdot 1134}$$

And for other pinniped species,

$$\frac{Q}{B} = \frac{365 \cdot 200 \bar{W}^{0.714}}{\bar{W} \cdot 1134}$$

where the last three equations are described in more detail by Piroddi (2008).

2.11. Marine birds

We used a global database of seabird distribution, abundance, and utilization (Karpouzi, 2005; Karpouzi et al., 2007), to obtain spatial estimates of marine bird abundance by species, as well as estimates of food consumption by marine birds. Details about the approximation approach is presented by Christensen et al. (2008).

The daily food intake (DFI) for marine birds was estimated based on the bioenergetic model of the ICES Working Group on Seabird Ecology (ICES, 2000), expressing DFI for each bird species as

$$\text{DFI} = \frac{\text{ER}}{\sum_j \text{DC}_j \times \text{ED}_j} \cdot \frac{1}{\text{AE}}$$

where ER is the energy requirement, DC_j is the fraction that each prey species j contributes to the bird's diet, ED_j is the energy density of prey j, and AE is the mean assimilation efficiency for the bird (assumed to be 0.75). See Karpouzi (2005) for details of the calculations.

Based on diet information collated by Karpouzi (2005), we derive estimates for 24 prey types of how to allocate the bird diet composition (prey composition) to the functional groups used in the present study (see Christensen et al., 2008 for details). For each LME, we used the relative bird species abundance by year to calculate annual consumption and biomass as well as an initial diet for 1950, i.e. bird abundance was treated as a forcing variable like marine mammal abundance.

2.12. Abundance trends for marine populations

We have developed a database with more than 2600 trends for marine populations with focus on fish species. The trends are from a variety of sources and represent survey estimates, estimates from assessments, as well as fishery-dependent estimates such as commercial CPUE series. The vast majority of trend series are from temperate areas, but we have taken care to increase the spatial coverage, and we, e.g., have a fair representation from the western and southern Africa. The trend database is important for fitting the time-dynamic LME models, notably with regards to assessment of compensatory responses to fishing (density-dependence). This aspect is very important for evaluating carrying capacity of LMEs to support future fisheries.

We extract trends for the LMEs by functional group by first selecting all trend series for which the taxon is allocated to the given functional group in the *Sea Around Us* taxon database, and which are from the same FAO statistical area (www.fao.org) as the given LME. All trend series are geo-referenced, and we weigh the series by a squared inverse distance weighting to the LME (border nearest the trend location, to obtain a weighted trend series by functional group by LME.

While the trend series derived in this manner are only to be considered a first attempt at providing comprehensive time series information, they do provide a starting point that goes beyond what we most often have seen for ecosystem models. We emphasize though, that it is very important to thoroughly search and evaluate all sources of information for a given LME as part of the modeling process.

2.13. Fisheries

2.13.1. Catches

The *Sea Around Us* project studies the impact of fisheries on the world's marine ecosystems. To this end, the 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). Summary data are freely available from the project website, and are meant to support studies of global fisheries trends and the development of sustainable, ecosystem-based fisheries policies. For the present study, we link directly to the underlying spatial catch dataset, enabling analysis with (rule-based) spatial resolution, albeit here summed up to the LME-level. The catches are available online at www.seaaroundus.org.

2.13.2. Fishing effort

Ecosim's ability to explain historical abundance trend patterns is typically best in cases where historical fishing impacts can be estimated from changes in historical fishing efforts, rather than by subtracting historical catches from model biomasses over time (which often causes dynamic instability in the model equations). At present, the effort measures we have access to are quite tentative (Gelchu and Pauly, 2007) or lacking in resolution (Alder et al., 2007). We are currently expanding on the effort estimation procedures (Watson et al., 2006a,b), and expect to have more detailed, spatial effort measures available by the end of 2009. For the present study, we have been unable to use effort estimates to drive the modeling as the available estimates have too little detail with regard to fleet definitions to be able to determine the diversity of fleets needed to capture changes in target species over time. We therefore do not use effort as a model driver here; instead we use only the catch estimates by target groups and years to drive the models over time.

2.13.3. Prices and cost of fishing

A global ex-vessel price database has been developed as part of the *Sea Around Us* project (Sumaila et al., 2007, available online at www.seaaroundus.org). The database includes all catch categories (typically at the species-level), and gives nominal and real (standardized to year 2000) prices in US$ by country for 1950 onwards. We calculate average price by functional groups from this database, expressed as real prices for 2000, based on the species catch composition in the individual LMEs. We have access to regional prices by the functional groupings (see www.seaaroundus.org) used for the model, and will consider using these in subsequent iterations of this modeling complex.

Work on populating cost estimates for the various fisheries is presently underway in connection with the further development of the ex-vessel price database. We recognize that the cost of fishing is very different in various parts of the world, while the prices of export-quality fish commodities are of a more global character. This has implications for what price/cost structure to use for the individual, spatial regions in the forward-looking simulations. This will need further consideration in the next round of simulations. For the time being, we use a global price average in the models, not country-specific prices from the countries fishing in the individual LMEs. All catches are allocated to countries fishing, and as we have country-specific ex-vessel prices, we will use these in coming iterations of the ecosystem models.

2.13.4. Database-driven model generation

We have developed an approach that relies on a number of databases, spatial and temporal, to construct ecosystem models using an automated procedure. We call this approach 'database-
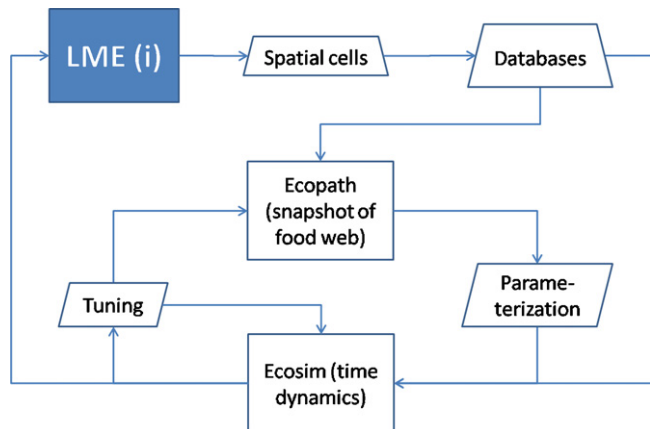
Fig. 2. Modeling process for the LME models.

driven ecosystem model generation', and have described aspects of many of the databases we build on above.

Based on the database-parameterized Ecopath models for each of the LMEs, we have developed a modeling process to represent time-dynamics and to tune the models to the time series data (Fig. 2). For each LME, we identify the spatial cells within it, and search a series of databases (as described above) for information about these cells. This information is passed to the static Ecopath model, and the time-dynamic Ecosim model. The Ecopath model is then balanced, Ecosim is run with time series, and the tuning may impact both Ecopath and Ecosim parameters. We consider this tuning necessary for evaluating carrying capacity, as well as for any other study that seeks to evaluate the potential impact of changes in fishing pressure or environmental productivity.

For each LME model, we extract time series information from a range of sources as explained above, and illustrated in Fig. 3. In summary form, the method for extracting the data, parameterizing the model, and fitting it to time series data follows a stepwise approach, most easily explained in pseudo-code form:

- Read information assigning all 1/2° latitude by 1/2° longitude spatial cells to LMEs, and read size of all cells.
- Read how all exploited species are assigned to taxonomic categories.
- Extract real ex-vessel prices by taxonomic unit (typically species), and by year, 1950–2004.
- Do the following steps for each of the 66 LMEs:
- Open a generic Ecopath model; copy and rename it to indicate the current LME number, e.g., LME1.
- Make a list of all cells included in the current LME.
- Read Ecopath parameters for these cells; set EE to be estimated for groups with data, and add remarks to the model. This is initially for:

Fig. 3. Time series extraction from databases for time-dynamic Ecosim runs for each of the World's 66 LMEs.

- ○ Mesopelagic biomass.
- ○ Macro- and meio-benthos biomass.
- ○ Zooplankton biomass.
- Read catches for each cell by taxonomic unit (typically species) and by year.
  - ○ Assign catches to functional groups.
  - ○ Sum up catches over all cells by functional groups.
  - ○ Calculate total ex-vessel price over all cells by functional groups.
  - ○ Calculate average ex-vessel price.
  - ○ Add the catches for the first year as landings estimates in the Ecopath model.
  - ○ Store time series of catches for use in Ecosim.
  - ○ We currently do not use the time series of prices.
- Read effort estimates.
  - ○ Our current effort estimates show too little detail. We therefore omit this step at present.
- Read marine mammal information.
  - ○ Estimate consumption rates.
  - ○ Estimate marine mammal abundance by year from distributions and population trends.
  - ○ Estimate marine mammal diet and consumption/biomass ratio for the first year from total consumption by prey species over all cells.
- Read marine birds information.
  - ○ Sum up biomass by year.
  - ○ Sum up consumption for each prey species and estimate diet and consumption/biomass ratio.
- Read fish diets from FishBase and diet for other species from SeaLifeBase.
  - ○ Allocate species information to functional groups.
  - ○ Calculated average diet for functional groups with information.
- Add a tentative biomass (as a prior estimate of absolute biomass) to the time series data set used for Ecosim fitting for each of the exploited groups, based on the assumption that the fishing mortality in the year with maximum catch corresponds to the natural mortality.
- Check if there are any groups that lack biomass estimates, and have neither catch nor predators.
  - ○ For such groups, Ecopath cannot estimate biomasses, and the biomass is initially set to 0.001 t km^{-2}.
- Run Ecopath; load Ecosim scenario, and read time series information obtained above.
- Read primary production and chlorophyll estimates.
  - ○ We currently have included four approaches for estimating primary production, and for each of these we include monthly and annual estimates as forcing functions.
  - ○ One of the series is used to force the production/biomass ratio for phytoplankton (order of selection described earlier).
  - ○ Chlorophyll estimates are (after conversion) used to force the phytoplankton biomass.
- Check model for mass balance.
  - ○ If any of the ecotrophic efficiencies (indicating the proportion of production that is 'used' in the system—mainly for catches and predation), exceeds unity then:
    - Predation on pinnipeds can be overestimated; if so reduce the contribution of pinnipeds to their predators' diets.
    - For groups where we calculate EE based on other basic input, change this to an assumed EE of 0.95 and calculate P/B instead.
  - ○ Repeat this procedure until the model is balanced.
- Run Ecosim and store the initial model log residuals (SS) between observed and estimated series (Table 3).
  - ○ Check if there are any groups that are 'crashing' (i.e. end biomass <start biomass/100), or whose catch is lower than in the Ecosim data time series (F has exceeded F_{lim}).
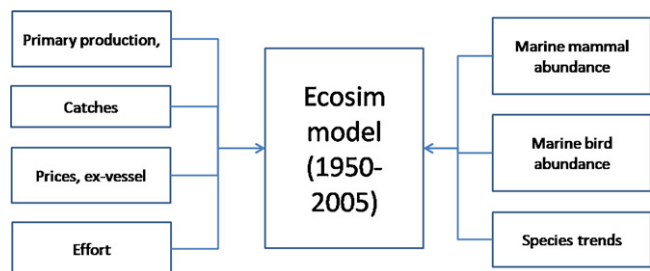
Table 3

Residuals from the time series fitting of LME models. The ratio, by LME, indicates the ratio between the summed squared log residuals (log observed/predicted) before and after fitting, indicating how much the fitting procedure improved the fit. Fitting is done by fitting one vulnerability parameter and the initial 1950-biomass for each consumer group with time series.

LME	Ratio (%)	LME	Ratio (%)
1	0.2	34	0.5
2	2.0	35	0.5
3	1.6	36	0.7
4	4.8	37	0.0
5	2.3	38	0.1
6	2.7	39	0.1
7	0.9	40	0.0
8	1.0	41	0.6
9	0.2	42	0.1
10	0.2	43	2.6
11	0.0	44	0.2
12	0.2	45	0.4
13	1.4	46	0.1
14	0.8	47	0.0
15	0.4	48	0.1
16	2.2	49	0.1
17	0.0	50	0.2
18	1.1	51	0.1
19	0.9	52	3.1
20	4.2	53	0.0
21	1.4	54	0.0
22	1.0	55	71.7
23	1.2	56	n.a.
24	2.6	57	n.a.
25	4.6	58	0.0
26	1.5	59	3.8
27	0.9	60	1.2
28	0.0	61	0.0
29	0.9	62	0.1
30	1.5	63	87.9
31	0.4	64	0.0
32	0.0	65	50.1
33	0.2	66	2.2

○ If there are such problem groups, then gradually increase the biomass of the groups in question, while ensuring that no other group in the system becomes unbalanced because of increased predation pressure.

○ Iterate a gradual biomass increase until every group is capable of having produced observed catches without collapsing completely.

• Run Ecosim and store the SS for Table 3 again.

• Fit the model to the time series data using a random optimization procedure (Matyas search, in preparation) now incorporated in EwE6.

○ Set initial wide bounds for the biomass, P/B (and hence Q/B as Q/B here is estimated from P/B), and vulnerabilities.

○ Sample each parameter based on a narrow coefficient of variation.

○ When a better fit (lower SS) is obtained, resample the parameters from a normal distribution with a band around the last 'best fit' parameters.

○ Iterate until there have been at least 10,000 iterations, and continue until there has not been a better fit in the last 1000 iterations.

• Open the spatial- and time-dynamic Ecospace model.

○ Create a base map for the LME with habitat definitions based on depth strata.

○ Extract spatial primary production estimates and store these.

○ The Ecospace models are not described in this contribution, but are included with the data files.

• Save the model

• Move to the next LME.

2.14. Time series weighting for SS

The random optimization search procedure for parameter estimates that better fit historical abundance trend data relies upon improving a sum of squares fitting criterion, SS. For fitting relative abundance data, the SS term for each abundance trend series is a sum over time of squared deviations between observed trend index value and predicted index value, where the predicted index value is a scaling or catchability coefficient (evaluated at its conditional maximum likelihood value) times modeled biomass. When several time series contribute sums of values over time to the overall SS, the weight W of individual time series are estimated from the inverse spatial distance from the LME, raised to the third power. If the distance is more than 40 half-degree cells or if the time series is from another FAO area, it is not used. Further, we halved the weight if the method used for estimating the relative abundance time series is fishery-dependent, while we doubled the weight if the time series is from an assessment. The weights are scaled so that the average trend time series weight for each LME-model is 1.

For catches, we used a high weighting factor (10) for all time series. Given that we force the catches in Ecosim to match the time series catches (thus, by default, the observed catch = simulated catch), this factor should not contribute to the SS calculation, unless Ecosim for some reason cannot match the forced catch. This can either be because the population has crashed, or because the estimated fishing mortalities exceed a set maximum. If the simulation cannot match the catch, then the high weighting factor will penalize the model parameter values leading to the poor match, by assigning those values a high SS value.

'Prior' biomasses for each of the exploited groups were obtained based on the assumption that fishing mortality equaled natural mortality in the year with maximum catch; these estimates were assigned a weight of 1. Each such biomass contributes $(B_i - \hat{B}_i)^2$ to the fitting SS, where B_i is model predicted biomass for whatever year had maximum catch, and $\hat{B}_i$ is the catch-based prior estimate, $\hat{B}_i = \max C_i / M_i$.

3. Results

3.1. Model parameters

A notable finding from this first round of database-driven ecosystem model generation is that the initial approach (where we use 'generic' parameters for many of the basic input parameters for the Ecopath model) will need to be substantially improved. We find from trial runs of the EwE policy optimization procedure, for instance, that it tends to overestimate potential yield from high-latitude systems. This is connected to our use of a 'generic' production/biomass (P/B) factor for many functional groups. We have partly remedied this by using P/B-estimates based on the Lorenzen-model (1996), but find that further work is required. In the next iteration of the procedure, we intend to test the empirical equation of Gascuel et al. (2008) for estimation of P/B as a function of trophic level and mean water temperature.

It is also clear that we need more detailed estimates of fleet effort to improve the drivers for the time-dynamic simulations.

3.2. Time series fitting

The present study represents a first attempt to automate the model time series fitting procedure. Over the last years, we have worked with numerous ecosystem models and fitted these models to time series data (see Christensen and Walters, 2005), but this has always been done with careful inspection of the models, and with a qualified eye evaluating the tactics of the fitting by focus-
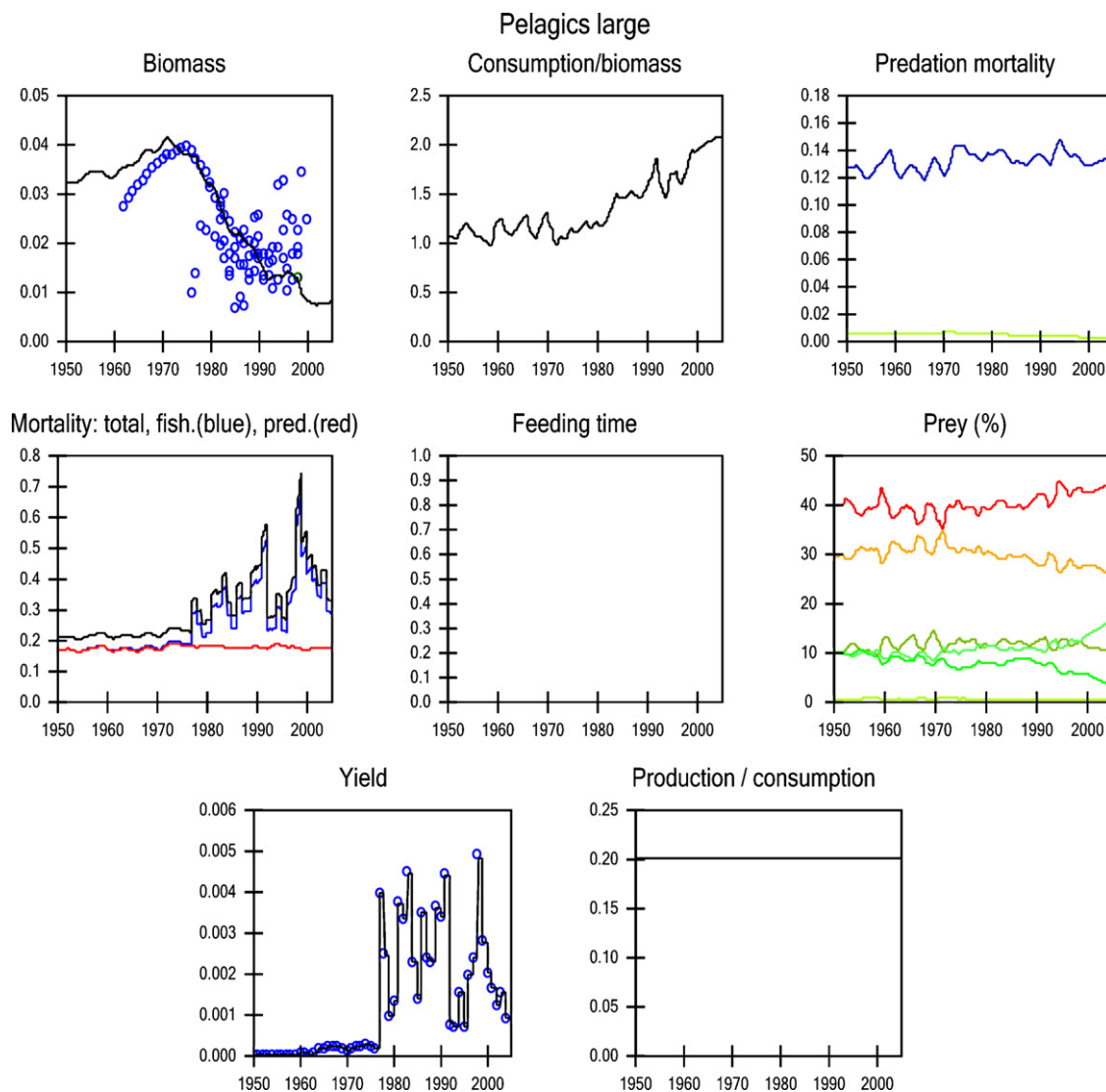
Fig. 4. Ecosim time plot for the large pelagics on the New Zealand Shelf (LME 46). There are numerous time series of biomass (for various species in various places, unit t km^{-2}) indicated by the circles on the first plot, which also shows the Ecosim biomass trajectory as a line. The yield plot (unit t km^{-2} year^{-1}) shows that Ecosim (line) used the reported catches (circles) to drive the simulations. Mortality, consumption/biomass, and predation mortality are rates (year^{-1}), and prey diets are relative measures. Predators and prey identities are not indicated, but available in the model output.

ing attention on poor model fits. When doing this, we look for model time series that diverge greatly from data; then ask why that divergence has occurred, and modify the Ecosim parameters and time series inputs accordingly. In the manual fitting, emphasis is on careful examination of how individual groups react in the model.

We present an example of some of the diagnostic plots showing how the time-series biomass trend data affect simulated outputs from Ecosim (Fig. 4). In this example there are numerous relative time series (small circles) for biomass indicating a downward trend over time. This trend is picked up well by Ecosim (the line on the plot), and we see that the downward trend from the early 1970s is likely associated with increased catches, rather than predation mortality.

The development of the automatic fitting procedure has now reached a state where the model fits are beginning to be comparable to many manually conducted model fits, and we know that we can improve the procedure further through inclusion of additional rules. We have taken great care to make the fitting procedure rule-based to ensure reproducibility, to enable us to develop finer scale ecosystem models, and to be able to continuously update the

models as more data become available. A manual element in the fitting procedure would make this impossible.

In Table 3 we review the sum of squared log residuals (SS) fitting criterion for the individual LME models before the automated time series fitting, after the fitting, and the ratio between the two. For 60% of the models the automated procedure has reduced the SS with 99% or more, while the average reduction is 98.6%. The low SS values after fitting indicates that we have been able to fit several or most relative abundance time series quite well.

Even if the reduction is quite impressive for many models, we note that this is usually because the models with high initial SS will have a number of groups that 'crashed'. Once a crash happens, the SS will shoot up (since the SS calculation heavily penalizes inability to explain historical catch data due to collapse in simulated population size to levels too low to have produced the catch). Avoiding such crashes will therefore have a disproportionally large impact on the SS compared to what subsequent fitting may provide. The reduction is mostly obtained by increasing the start biomass for the impacted group, but we also provide other diagnostics and remedies as described in the methodology section. Notably, as part of the random optimization-fitting procedure we vary both the ini-
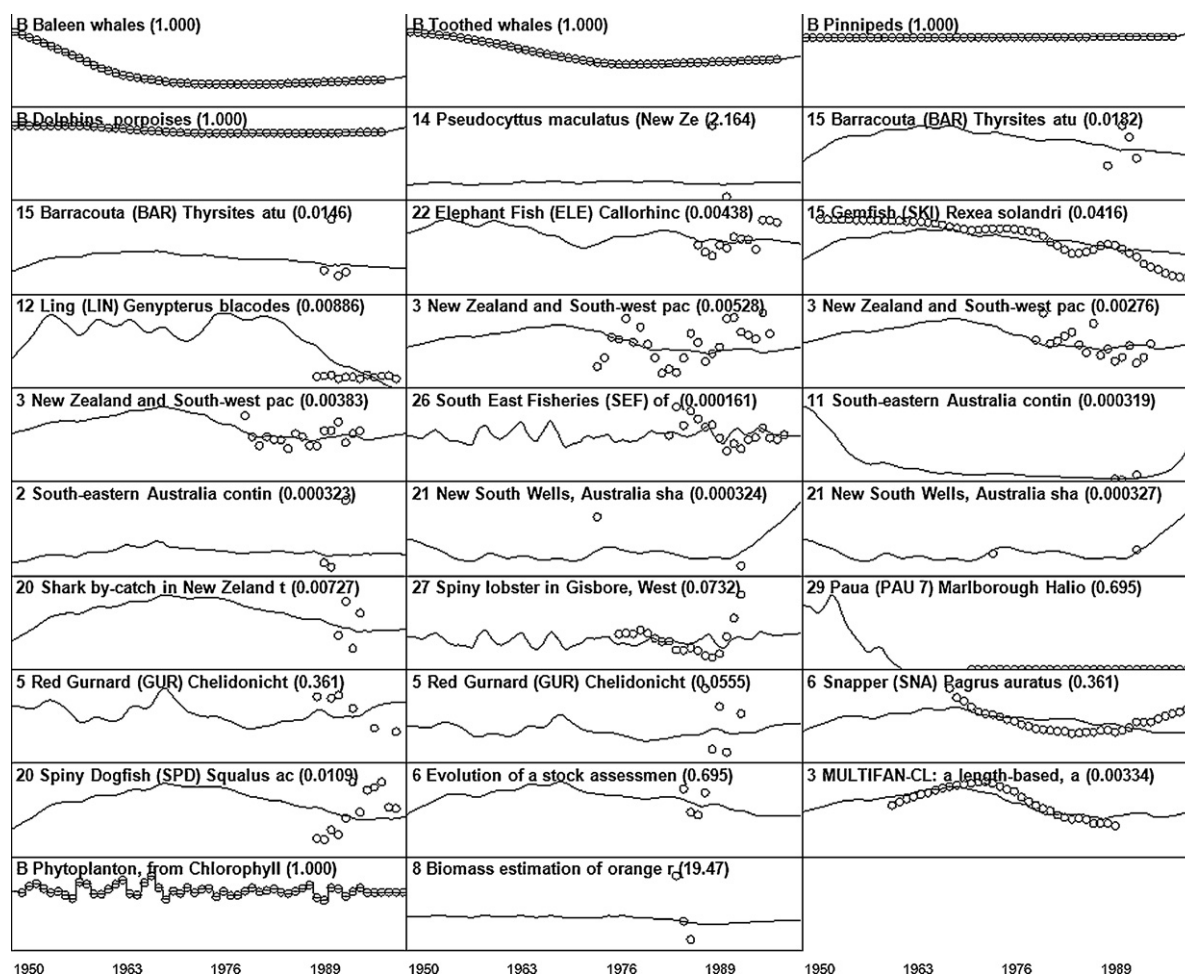
Fig. 5. Time series fits for relative biomasses on the New Zealand Shelf (LME 46). Lines indicate the Ecosim estimates, and dots indicate the time series data used for fitting the model. The time series are applied to a single group, and hence, may supply diverging information. The phytoplankton biomass trend is used to force the simulations. The values in brackets indicate time series weights, while the initial numbers indicate functional group numbers.

tial biomasses and vulnerabilities. The procedure may thus find that a lower initial biomass can be used for a group, if the group is assumed to be closer to its carrying capacity (i.e. to be taking a higher proportion of the prey potentially available to it).

For manual model fitting, Ecosim provides important diagnostics in the form of a plot showing all the time series fits in a model. We here give an example of such a plot comparing population trend time series with Ecosim predictions for the New Zealand Shelf model (LME 46) in Fig. 5. The fits are perfect for the marine mammals in Fig. 5 (first four plots) since for these groups we force Ecosim to use biomasses from the estimated time series; the same is the case for the phytoplankton (bottom row). For the other groups the fits are of variable quality, and it is clear that the fitted parameter values generally are not very capable of reproducing variation in the population trend series. However, tight fits should not be expected due to variance in the observed data and because the trends are for individual species, while the Ecosim simulations are for functional groups including numerous species.

In this initial iteration of the database-driven ecosystem models, we have used catches to drive the Ecosim simulations. For groups where we have no trend series, this may cause the groups' biomass to be too stable over time; the initial biomass may be overestimated as this reduces the risk of the group crashing due to high catches. If, for such groups, the catches decrease over time, this may well result in the groups' biomasses being estimated to increase due to perceived lower fishing pressure. It may well be, in reality, that the fishing pressure stays high, and that the catches decline because of

lower biomass. We cannot avoid such cases given our quite limited number of population trend series, and this serves to (1) strengthen the case for using fishing effort to drive the simulations, and (2) illustrate why we do not currently want to use the models for predictions about how the ecosystems may react to future changes in fishing pressure. To do so calls for improved detailed estimates of spatial fishing effort.

3.3. Biomass of fishes in the world's LMEs

We use the 66 LME models to obtain a first estimate of the total biomass in 1950 of fishes in the world's LMEs, see Fig. 6. The term 'fishes' is here defined as being represented by functional groups 1–24 in Table 2. The biomass is estimated so as to be sufficient to support the catches obtained in the LMEs from 1950 to 2004, while accounting for predator demand through the food web as well.

We estimate the total biomass of fish in the LME areas to 1.1 billion tonnes. There are to our knowledge only two other estimates of fish biomass, one, estimating the total fish biomass to approximately 1 billion tonnes based on size spectra (Jennings et al., 2008), the other, which is based on the approach presented there estimates the global fish biomass to approximately 2 billion tonnes (Wilson et al., 2009).

The biomass estimate for global LMEs can be compared to a total annual catch of approximately 60 million tonnes per year since the mid-1980s, the vast majority of which was obtained from within the LMEs. While this may seem to indicate a low exploitation pressure
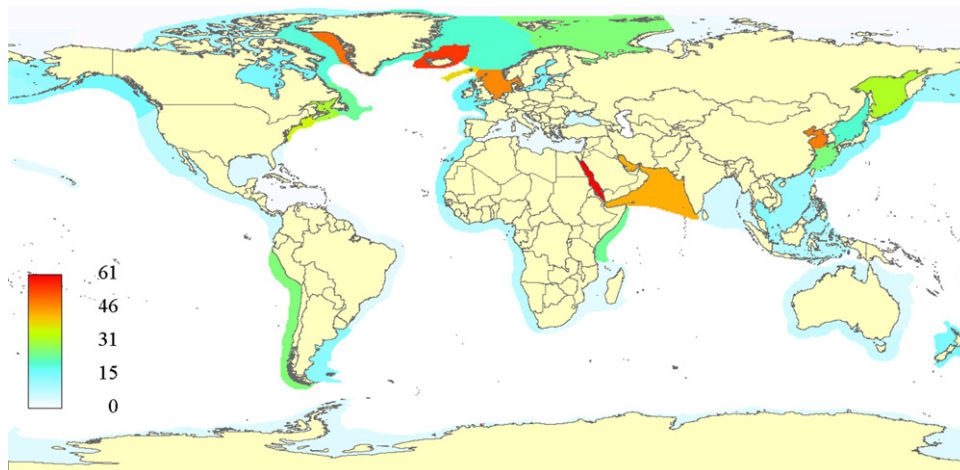
Fig. 6. Fish biomass in the world's LMEs, expressed in t km^{-2}. The biomass estimates includes mesopelagics, which reportedly are especially abundant around the Arabian peninsula.

Table 4
Fish biomass (10^3 t km^{-2}) by functional groups in the world's 66 LME in 1950. The catch column gives the current catches by functional group (10^3 t km^{-2} year^{-1}). The ratio is the catch/biomass ratio, and is included to indicate that the major part of the fish biomass is represented by groups that are of little commercial interest.

		Biomass (1950)	Catch (2000)	Ratio
1	Pelagics small	88,796	17,123	0.193
2	Pelagics medium	63,821	10,187	0.160
3	Pelagics large	14,469	1501	0.104
4	Demersals small	203,221	7245	0.036
5	Demersals medium	36,877	2915	0.079
6	Demersals large	23,944	1625	0.068
7	Bathypelagics small	440,863	10	0.000
8	Bathypelagics medium	682	85	0.125
9	Bathypelagics large	85	0	0.000
10	Bathydemersals small	4667	3	0.001
11	Bathydemersals medium	3020	93	0.031
12	Bathydemersals large	3165	121	0.038
13	Benthopelagics small	44,529	37	0.001
14	Benthopelagics medium	68,980	2423	0.035
15	Benthopelagics large	79,481	5903	0.074
16	Reef fish small	9629	270	0.028
17	Reef fish medium	3797	588	0.155
18	Reef fish large	663	62	0.093
19	Sharks small medium	467	8	0.017
20	Sharks large	1869	240	0.128
21	Rays small medium	2841	198	0.070
22	Rays large	379	43	0.113
23	Flatfish small medium	5392	651	0.121
24	Flatfish large	2444	181	0.074

(catch/biomass ratio) we note that the biomass is dominated by fish groups of little or no commercial interest (Table 4). No less than 58% of the estimated total biomass is thus represented by small demersals (group 3) and small bathypelagics (group 7), both with asymptotic lengths of less than 30 cm, and both with no or only minimal potential commercial interest given their sparse densities (Pauly et al., 1998a).

We here abstain from presenting estimates of temporal trend in biomass, primarily for lack of reliable, detailed estimates of fishing effort over time and space. Development of such is a priority for further development of the approach reported on here.

4. Discussion

We are presenting a new approach to modeling, and this raises a pertinent question: what is it good for? We regard it a major advantage that by making the model construction database-driven we enrich the models with information that likely would not otherwise have been used for the model construction. We are also making it much easier to get started with the modeling process by presenting a draft model for improvement.

We consider the models of appropriate quality for use to address large-scale issues, such as for instance how marine ecosystems biodiversity and productivity may be impacted by policy questions, e.g., in connection with UNEP's Global Environmental Outlook series. For more local use, i.e., for use of the individual LME-models, we see the models providing a well-defined starting point, but one, which should be enriched through local data from the LME. Notably, we do not supply effort time series, and such are very important to drive the models over time. Also, the species-resolution is very poor in the models as the functional groups are defined in a very generic manner. This poses a problem for using the models for management purposes as well as to address more specific biodiversity questions. For such use it is important to further enrich the models, and this is indeed a case where modelers should consider whether it is not better to actually develop the ecosystem models from scratch.

It is a potential danger that by automating the model construction process, the potential users may not have a full understanding of the data limitations and of what is required to use the models as part of the actual management process. We would be very hesitant to use any model for management without a thorough understanding of the model's behavior. We thus caution strongly against the direct use of the database-driven models for management purposes.

Large Marine Ecosystems face serious threats throughout the world. One important threat is that they are overfished due to excessive effort capacity. To evaluate what has happened, what is happening, and what may happen under alternative future scenarios, it is important to have ecosystem modeling as part of the toolbox for ecosystem-based management. Ecosystems models integrate a diversity of information, including ecological, economical and social considerations, and provide our best hope for expanding our understanding of how to sustainably manage the ocean's resources for our and future generations benefit.

We have taken a step for making ecosystem modeling more accessible by developing capabilities for database-driven ecosystem model generation. We encourage the scientific community to cooperate with us on developing model capabilities within the projects and to enable cooperation that will further enrich the models, and lead to their successful application.

Overall we see a need for developing better databases related to spatial effort estimation, and we encourage analysis of the economical and social aspects of the fish production chain, from sea to consumer. Given information from throughout the fishing sector, ecosystem models combined with economical value chain modeling can be used to evaluate how food security, economic and social parameters may be impacted by fisheries management decisions.

Acknowledgements

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