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Models of the World's Large Marine Ecosystems





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GEF/LME global project Promoting Ecosystem-based Approaches to Fisheries Conservation and Large Marine Ecosystems

UNESCO 2008

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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 database developed as part of the Sea Around Us project. The models are formulated using the Ecopath with Ecosim modeling approach and software, and are made available to GEF/LME projects for further development. 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. The biggest hurdles at present to further model development and validation are insufficient time series trend information, and data on spatial fishing effort. We will be further developing the models, as this is one of the major activities of the Sea Around Us project, and encourage GEF/LME projects to participate in the process, notably by enriching the models through addition of more local and regional data. We here use the models to summarize information about fisheries catch and value in the LMEs.

Acknowledgements

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Supporting organizations







United Nations Educational, Scientific and Cultural Organization



Foreword

Today there is a growing need for tools to apply the ecosystem approach towards the sustainable management of ocean and coastal resources. The scientific community is actively engaged in the development of models and indicators to use the ecosystem approach in fishery management, aquaculture planning and more broadly in the integrated management of coastal zones.

This Report, which represents hundreds of hours of work by dozen of scientists, is the continuation of the work of UNESCO and its IOC on the development and application of the ecosystem approach to the ocean and coastal zones. The immediate precedent was the work carried out by the Joint IOC–SCOR Working Group 119, co-chaired by Philippe Cury and Villy Christensen, culminating in the Symposium on Quantitative Ecosystem Indicators for Fisheries Management held the 31 March–3 April 2004 in UNESCO headquarters .

The ultimate goal of the IOC-SCOR Joint Working Group 119 was to develop a methodology to evaluate changes in states and processes of marine ecosystems, from an environmental, ecological and fishery perspectives. The Working Group defined generic indicators, formulated in mathematical or statistical terms, that can be applied to specific marine environments, single-species fisheries, assemblages of exploited fish populations or to full marine ecosystems. The methodology also determined the range of statistical or ecological validity of the indicators and when to apply them to specific data-sets or multispecies models.

This report is an incremental step towards the development of quantitative indicators at the ecosystem level, by providing new definitions of reference points aimed at building a bridge between scientific results, societal needs, and an effective Ecosystem Approach to management.

We ambition this to be used as a reference by managers and researchers, in support of sustainable, science-based, sound ocean and coastal development as requested by the WSSD Implementation Plan. As Executive Secretary of the Intergovernmental Oceanographic Commission I would like to dedicate this publication to the memory of Dr.Umit Unluata, former Head of the Ocean Sciences Section of our Commission, for the guidance and leadership he provided by throughout this study.

Patricio A. Bernal

Assistant Director General of UNESCO
IOC Executive Secretary
Intergovernmental Oceanographic Commission

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 Revkjavik 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 actually being used for management in more than a few of the LMEs. We attribute this to a combination of factors, of which lack of experience may be more important than lack of data. Indeed, ecosystem modeling 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 feed 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. The many training courses we have conducted around the world serves as good examples of building capacity for ecosystem modeling. We have realized, however, that training alone does not suffice: there is considerable work involved in the three steps described above, and we here report on how we can assist GEF/LME projects through what we call 'database-driven ecosystem model generation'. We describe how we link into a large number of spatial and temporal databases describing the world's oceans, their resources, and how we exploit the resources. We extract data from these databases, and use these data to modify a generic ecosystem model in order to obtain an ecosystem models for each of the 66 LMEs in the World's oceans. We further describe how we analyze the LME models to derive estimates for the fish production.

Model Methodology

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: 1993). Polovina examined Polovina, ecosystem models then in use for fisheries research (notably Andersen and Ursin, 1977; and 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 for production (and, again, by deduction 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 models being published (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), and this was a necessary requirement for making it possible to program 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.

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. The project is designed to document how we exploit the oceans living resources, the consequences of the exploitation, and what can be done to improve ocean conditions (Pauly, 2007). As part of this we have developed spatial databases for catches, effort, and prices, and other based information related to productivy and harvesting (see below). 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 large marine ecosystems.

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 of the aspects that have direct relevance for the model construction.

Functional groups and basic parameters

Ecopath, and also the time-dynamic Ecosim model (Walters et al., 1997; Walters et al., 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 (notably 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 groups of species.

To develop the database-driven models we have cooperated with FishBase (www.fishbase.org) 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 not using 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 demersals. bathypelagics, pelagics. bathydemersals, benthopelagics, reef fishes, sharks, rays, and flatfishes. We separate invertebrates into cephalopods, other molluscs, krill, shrimps, lobsters and crabs, jellyfishes, zooplankton, megabenthos. macrobenthos, meiobenthos, and corals, soft corals, sponges, etc. Marine mammals are split into baleen whales, toothed whales, dolphin and porpoises,

and pinnipeds (seals and sea lions), while we here aggregate all seabirds in one functional groups. Primary producers are included as phytoplankton and benthic plants.

An overview of the functional groups is presented in Table 1, which also shows the basic (default) input parameters for all groups as well as indicating the parameters that are supplied as part of the database-driven model-generation.

Ecotrophic efficiencies (EE), in Table 1 for the exploited species are used only for initial parameterization. Once the model-generation procedure is past the initial step, the EE input has provided a start biomass, which subsequently will be changed to ensure that the population does not crash over time when observed catches are removed from it, and in order to fit the biomass better in the random optimization search process, described below.

Table 1. Functional groupings and basic input parameters for the LME models. *B is biomass* (*t·km*²), *P/B* and *Q/B* are the production/biomass and consumption/biomass ratios (both year¹), *EE is the* (dimensionless) ecotrophic efficiency, *P/Q* the (dimensionless) production/consumption ratio. The proportion of the consumption that is excreted or egested was set to 0.2 for all groups, apart from zooplankton where 0.4 was used. The 'e' indicates that the parameter is estimated as part of the mass-balance calculations of Ecopath (or the multi-stanza calculations for the large pelagics), '-' 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.' for 'not-applicable' indicates that the parameter is not defined. While an input biomass is supplied for group 3, it may be increased as part of the mass-balance calculations where the biomass is insufficient to meet demands, notably by fisheries.

	Group name	В	P/B	Q/B	EE	P/Q
1	Pelagics small	е	0.9 (*)	-	8.0	0.25
2	Pelagics medium	е	0.5 (*)	-	8.0	0.25
3	Pelagics large	е	0.3 (*)	-	8.0	0.20
4	Demersals small	е	1.5 (*)	-	8.0	0.25
5	Demersals medium	е	0.6 (*)	-	8.0	0.2
6	Demersals large	е	0.3 (*)	-	8.0	0.15
7	Bathypelagics small Bathypelagics	*	0.5 (*)	-	-	0.25
8	medium	е	0.3 (*)	-	0.8	0.2
9	Bathypelagics large	е	0.1 (*)	-	8.0	0.2
10	Bathydemersals small Bathydemersals	е	0.5 (*)	-	0.95	0.2
11	medium	е	0.3 (*)	-	0.7	0.2
12	Bathydemersals large	е	0.1 (*)	-	0.85	0.25

13	Benthopelagics small Benthopelagics	е	0.6 (*)	-	0.95	0.25
14	medium	е	0.4 (*)	-	0.9	0.25
15	Benthopelagics large	е	0.2 (*)	-	0.9	0.25
16	Reef fish small	е	1.0 (*)	-	8.0	0.25
17	Reef fish medium	е	0.6 (*)	-	8.0	0.2
18	Reef fish large	е	0.3 (*)	-	0.5	0.15
19	Sharks small medium	е	0.5 (*)	-	0.9	0.2
20	Sharks large	е	0.2 (*)	-	0.2	0.15
21	Rays small medium	е	0.4 (*)	-	0.6	0.2
22	Rays large	е	0.2 (*)	-	8.0	0.15
23	Flatfish small medium	е	0.8 (*)	-	0.9	0.25
24	Flatfish large	е	0.3 (*)	-	0.9	0.15
25	Cephalopods	е	2.0	10	0.7	-
26	Shrimps	е	2.5	-	0.7	0.3
27	Lobsters crabs	е	2.0	-	0.9	0.3
28	Jellyfish	0.5	10	40	е	-
29	Molluscs	е	2.0		0.8	0.3
30	Krill	е	5.0		0.9	0.25
31	Baleen whales	*	0.03	*	е	-
32	Toothed whales	*	0.05	*	е	-
33	Pinnipeds	*	0.15	*	е	-
34	Birds	*	0.1	*	е	-
35	Megabenthos	е	3.0	-	0.8	0.3
36	Macrobenthos	*	10	-	е	0.35
37	Corals	0.1	1.0	1.5	е	-
	Soft corals, sponges,					
38	etc	2	0.2	1	е	-
39	Zooplankton other	е	30	120	0.9	-
40	Phytoplankton	*	*	n.a.	е	n.a.
41	Benthic plants	2	10	n.a.	е	n.a.
42	Meiobenthos	4	40	-	е	0.4
43	Dolphins porpoises		0.08	*	е	-
44	Detritus	100	n.a.	n.a.	е	n.a.

We use an assumed diet composition for each functional group (see Appendix 1 for details). For each LME, however, we modify the diets through an automated procedure where we extract diet data for fish from FishBase, for invertebrates from SeaLifeBase (see www.sealifebase.org), for marine mammals from Kaschner (2004), and for marine birds from Karpouzi (2005). We refer to these sources for details.

Production rates for exploited groups

To obtain a weighted production/biomass ratio (total mortality rate, Z) 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_{\bullet} at age (t, months) based on the von Bertalanffy growth equation,

$$W_{\mathfrak{g}} = W_{\mathfrak{m}} \times (1 - e^{-K \times \mathfrak{g}})^{3} \tag{1}$$

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,

$$M_{\mathfrak{g}} = M_{\mathfrak{g}} \times W_{\mathfrak{g}}^{W_{\mathfrak{g}}} \tag{2}$$

where M_{w} is 3.08 at latitudes <30°, 3.13 at latitudes between 30° and 60°, and 1.69 at higher latitudes. The values for M_{w} are -0.21, -0.309 and -0.292 for the same latitudes, respectively. For each LME we estimate the mean latitude of all cells, 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,

$$F_{t} = \frac{C_{1980}}{C_{max}} \times K \times \left(1 - e^{-K \times \left[KW\right]_{t} - \omega_{0}\right)}\right)^{3}$$
(3)

where \P_{1800} is the catch for the species in 1950, $\P_{max} = 1$ is the maximum catch for the species, \P_{n} is the weight at recruitment to the fishery, here assumed to be $\P_{n} = 1 \times W_{n}$. With this, we can now estimate the number at age (N_{ϵ}) as,

$$N_{c} = N_{c-1} \times e^{-\frac{M_{C} + F_{C}}{12}} \tag{4}$$

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

$$\mathbf{E}_{t} = \mathbf{N}_{t} \times \mathbf{W}_{t} \tag{5}$$

For the species (i), we sum up, to get

$$\mathcal{E}_t = \sum_{v} \mathcal{B}_v, M_t = \sum_{v} M_v \times \mathcal{B}_v,$$

and,

$$P_t = \sum_{v} P_v \times B_v.$$

We next want to integrate over species within a functional group, and for this assume that we can weigh the contribution of the individual species (i) based on their contribution to catches. We thus estimate the functional group production/biomass ratio, (P/B), year-1) from,

$$\frac{F}{B} = \sum_{t} \frac{\left[\frac{C \mathbb{I}_{t4980}}{F_{t}}\right) \times (F_{t} + M_{t})}{\sum_{t} \left[\frac{C \mathbb{I}_{t4980}}{F_{t}}\right)}$$
(6)

Which is simply a weighted average of $\mathbb{A}_{t} + \mathbb{A}_{t}$, with each I weighed by

$$\frac{C_{t,1980}}{F_t}$$

Maximum fishing mortality rates

We estimate an overall natural mortality rate (M , year⁻¹) for each exploited species based on Pauly (1980),

$\ln M = -0.2107 + 0.4627 \times \ln T + 0.6757 \times \ln K - 0.0824 \times \ln W$

(7)

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_{limit} , to four times the natural mortality rate obtained from the Pauly equation. We use F_{limit} 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_{limit} we limit the fishing mortality to this reference value. This is necessary to cause smooth decline in population size (but not immediate collapse) when size (but not immediate during early steps of the time series fitting procedure. That fitting procedure then seeks to move the population out of the crash zone.

Primary Productivity

As described elsewhere. EwE models are sensitive to changes in ecosystem productivity, and we are finding that we generally have 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 through 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 impact of climate change, and we here include four different models, though we have only used one to date for the actual simulations conducted.

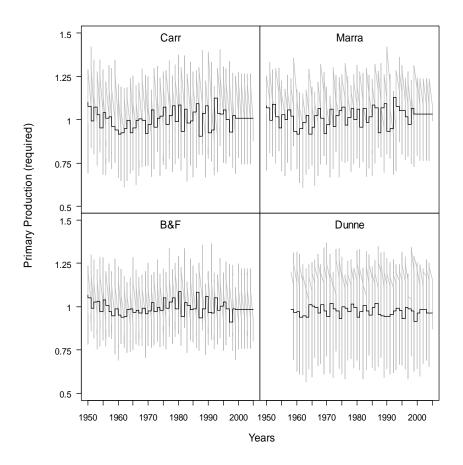
We used two different modeling approaches to simulate primary production. The first approach uses an empirical model to estimate chlorophyll based on physical properties. This technique, described in detail in Sarmiento et al. (2004), fits observed SeaWiFS chlorophyll data to a function of sea surface temperature, sea surface salinity, maximum winter mixed layer depth, and growing season length for different biogeochemical provinces, 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 prep.).

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 meters, and that the average chlorophyll content in phytoplankton was 2.6% 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 conversions 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 conversions 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 runs, 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.

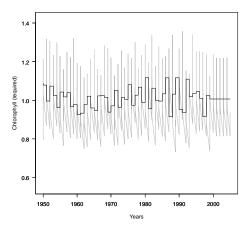
Figure 1. Primary production estimates (relative) for the Humboldt Current (LME 13) for the time period 1950-2004. Estimates are expressed relative to the 1950 values, and are based on the methods of Carr (2002), Marra et al. (2003), Behrenfeld and Falkowski (1997), and Dunne et al. (in prep.) Darker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



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 (1) if available. If not we used the Marra et al. estimates (2), the Behrenfeld and Falkowski estimates (3), or, finally, the Dunne et al. estimates (4). 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 Figure 1 (and chlorophyll estimates in Figure 2) 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 variation in other LMEs, e.g., the Gulf of Mexico.

Figure 2. Chlorophyll estimates (relative) for the Humboldt Current (LME 13) for the time period 1950-2004. The darker line indicates annual values, lighter lines monthly.



Zooplankton

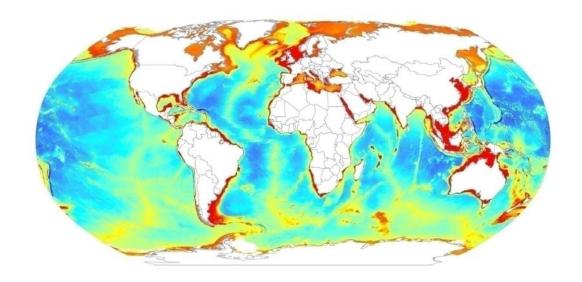
The biomass estimates are based on a map of zooplankton abundance in the upper 100 m of the world's oceans, published by FAO (1972; 1981), and based on the work of V.G. Borogov et al. (1968). The original map was digitized by the *Sea Around Us* project, and the original estimates in mg·m⁻³ (wet weight) were re-expressed in t·km⁻². We apply the estimates of zooplankton biomass

to the upper 100 meter of the water column, and assume that abundances at greater depths are negligible.

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

Figure 3. Macrobenthos biomass as estimated by Peters-Mason et al. (unpublished data) Red (darker) colors indicate higher biomass expressed per unit area.

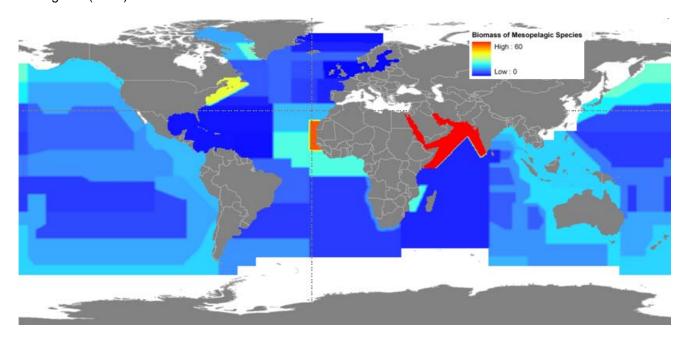


Mesopelagics

A combined spatial biomass of small and large mesopelagic fishes was obtained from the information provided by Gjøsaeter and Kawaguchi (1980) based on extensive trawlsurveys in the world oceans. The maps were

digitized and validated by Lam and Pauly (2005). The derived GIS-layer (Figure 4) 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.

Figure 4. Mesopelagic biomass in the world's oceans based on trawl surveys as reported by Gjøsaeter and Kawaguchi (1980).



Marine mammals

Line Bang Christensen reconstructed marine mammal population estimates and trends for all extant species of marine mammals with an exploitation history (Christensen and Martell, 2005; Christensen, 2006), see Figure 5 and Figure 6 for examples. This work (which was part of the Sea Around Us project) included creation of a global database of marine mammal whaling, sealing and bycatch/discards estimates. The work was conducted in cooperation with Jordan Beblow of the Sea Around Us, and with Kristin Kaschner, who developed a spatial database of mammal distribution and marine abundance for all marine species as part of her Ph.D. thesis, another Sea Around Us activity (Kaschner, 2004).

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 enough 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.

Figure 5. An example of a marine mammal population dynamics, here for North Pacific sei whales. The solid line indicates the most likely population trajectory (the median of the posterior), the stippled lines the 95% confidence interval, the vertical lines the catches applied, and the dots the abundance estimates to which the analyses are tuned. From (Christensen, 2006).

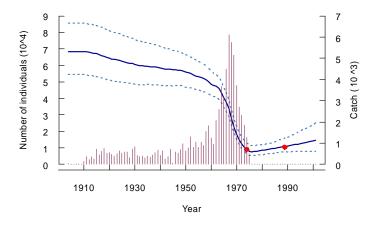
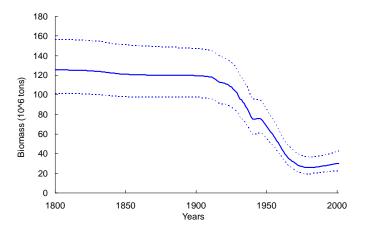


Figure 6. Decline in the global biomass of marine mammals, all species combined. The solid line is the median, and the dotted lines represent the 95% confidence interval. From Christensen (2006).



We obtain estimates of annual consumption for marine mammal species based on estimated ratios consumption/biomass and species abundance estimates, and for each LME summed up by species to obtain the total consumption by the marine mammal biomass. 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 baleens.

$$\frac{Q}{B} = 8 \times 30 \times 1.66 \overline{W}^{0.889} / \overline{W}$$
(8)

where \overline{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),

$$\frac{Q}{B} = \frac{363 \times 317 \, \overline{W}^{0.714}}{(\overline{W} \times 1207)} \tag{9}$$

For otariids (eared seals),

$$\frac{Q}{B} = \frac{363 \times 320 \, \overline{W}^{0.714}}{(W \times 1134)} \tag{10}$$

And for other pinniped species,

$$\frac{Q}{B} = \frac{363 \times 200 \, \overline{W}^{0.714}}{(\overline{W} \times 1134)} \tag{11}$$

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

Marine birds

Vasiliki Karpouzi developed a global database of seabird distribution, abundance, and utilization, (see Figure 7) for her M.Sc. as part of the *Sea Around Us* project (Karpouzi, 2005; Karpouzi et al., 2007). From this source, we obtained spatial estimates of marine bird abundance by species, (a summary of which is presented in Figure 8, as well as estimates of food consumption by marine birds.

Figure 7. Areas of the world for which at least one seabird population size estimate was available. From Karpouzi (2005).

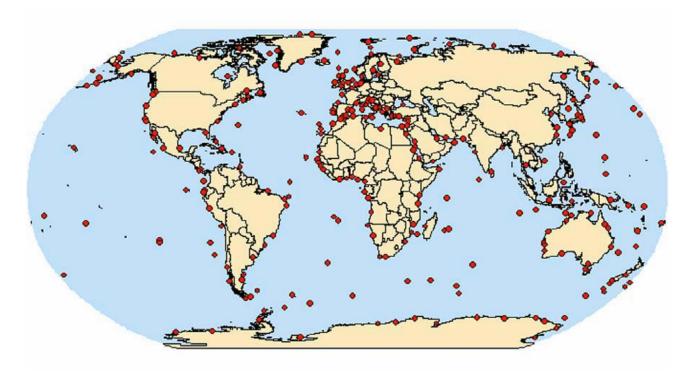
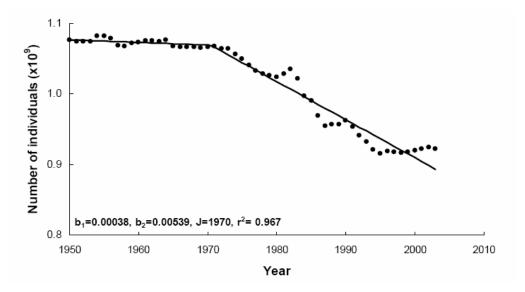


Figure 8. Trend of overall population size of the world's seabirds during 1950-2003. Numbers are in billions, the fitted piecewise regression model has parameters as indicated on the figure, and P<0.01. From Karpouzi (2005).



A noteworthy finding from Karpouzi's studies is an indication that the abundance of marine birds globally has been declining over the period since 1970, i.e. during the period where industrialized fishing pressure has intensified, see Figure 8.

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

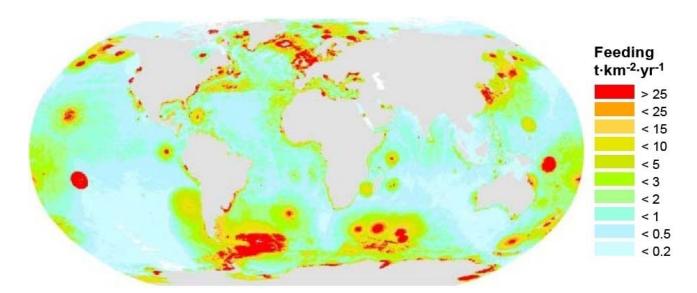
$$DFI = \frac{ER}{\sum_{j} DC_{j} \times ED_{j}} \times \frac{1}{AE}$$
 (12)

where ER is the energy requirement (obtained from Table 2), 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.

Table 2. Allometric equations used for calculation of Basal and Field Metabolic Rates (BMR and FMR, in kJ·day⁻¹), assumed to represent energy requirements during the non-breeding and breeding season, respectively. Body mass (g) is represented by m. For Anseriformes the 'All seabirds' expression was used. From Karpouzi (2005).

Order	BMR	FMR	
Charadriiformes	BMR=2.149·m	0.718 FMR=11.49∙m	
Pelecaniformes	BMR=1.392·m	FMR=3.90·m	
Procellariiformes	BMR=2.763·m	FMR=22.06·m	
Sphenisciformes	BMR=1.775·m	FMR=21.33·m	
All seabirds	0.719 BMR=3.201·m	FMR=16.69·m	

Figure 9. Map of predicted global food consumption rate of all seabirds combined for an average year in the 1990s. For comparison, fisheries catches rarely exceed 30 t·km⁻²·year⁻¹. From Karpouzi (2005).



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 Appendix 2 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.

Abundance trends for marine populations

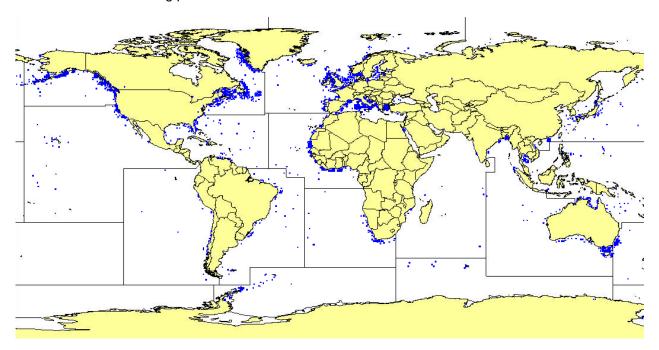
We have developed a database with more than 2600 trends for marine populations with focus on fish species. The trends are from a variety of sources and represent survey estimates, estimates from assessments, as well as fisheries-dependent estimates such as commercial CPUE series. The database has so far been under development for three years and the development has been partly funded through the current activity; see Figure 10 for an overview of trend data locations.

The trend database is important for fitting the time-dynamic LME models, notably with regards to assessment of compensatory responses to fishing (density-dependence), and 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 area 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 for LMEs, they do provide a starting point that goes beyond what we most often have seen for LME 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.

Figure 10. World map indicating with dots the locations of the 2600+ population trend datasets available for the Ecosim model tuning procedure.



Fisheries

Catches

The Sea Around Us project studies the impact of fisheries on the world's marine ecosystems. To this end, the project uses a web-based 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). The data are freely available in table and summary form from the project website, and are meant to support studies of global fisheries trends and the development of sustainable, ecosystembased 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.

Fishing effort

Ecosim performance at explaining 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 and lacking in spatial resolution (Gelchu, 2006; Alder et al.,

2007). We are currently expanding on the effort estimation procedures and expect to have more detailed, spatial effort measures available at the end of 2008 or early 2009 (Watson et al., 2006a; b; Watson et al., in prep). 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.

Prices and cost of fishing

Rashid Sumaila and co-workers have developed a global price database as part of the Sea Around Us project (Sumaila et al., 2007). The database includes all catch categories (typically at the species-level), and gives nominal and real (standardized to 2000) prices by country for 1950 onwards. We calculate average price by functional groups from this database, expressed as real prices for 2000, see Table 3, 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 modelling complex.

Table 3. Average real prices by functional groupings are for year 2000, here not weighted by species composition, area, or country. In the individual LME models the actual prices used are weighted based on species composition in landings.

Group name	Real price (\$US/kg)	No.	Group name	Real price (\$US/kg)
	0.76		Flatfish, small	2.17
Pelagics, small		23	medium	
Pelagics, medium	1.83	24	Flatfish, large	4.90
Pelagics, large	3.82	25	Cephalopods	0.85
Demersals, small	1.78	26	Shrimps	5.19
Demersals, medium	1.73	27	Lobsters, crabs	5.19
Demersals, large	2.43	28	Jellyfish	0.50
	Pelagics, small Pelagics, medium Pelagics, large Demersals, small Demersals, medium	Group name price (\$US/kg) 0.76 Pelagics, small Pelagics, medium 1.83 Pelagics, large 3.82 Demersals, small 1.78 Demersals, medium 1.73	Group name price (\$US/kg) No. 0.76 0.76 Pelagics, small 23 Pelagics, medium 1.83 24 Pelagics, large 3.82 25 Demersals, small 1.78 26 Demersals, medium 1.73 27	Group nameprice (\$US/kg)No.Group name0.76Flatfish, smallPelagics, small23mediumPelagics, medium1.8324Flatfish, largePelagics, large3.8225CephalopodsDemersals, small1.7826ShrimpsDemersals, medium1.7327Lobsters, crabs

7	Bathypelagics, small	2.34	29	Molluscs	2.29
8	Bathypelagics, medium	2.34	30	Krill	0.50
9	Bathypelagics, large	2.61	31	Baleen whales	-
10	Bathydemersals, small	1.00	32	Toothed whales	-
11	Bathydemersals, medium	1.39	33	Seals	-
12	Bathydemersals, large	3.50	34	Birds	-
13	Benthopelagics, small	1.76	35	Megabenthos	-
14	Benthopelagics, medium	2.69	36	Macrobenthos	-
15	Benthopelagics, large	2.04	37	Corals	-
		3.58		Soft corals, sponges,	-
16	Reef fish, small		38	etc.	
17	Reef fish, medium	2.69	39	Zooplankton, other	-
18	Reef fish, large	3.60	40	Phytoplankton	-
19	Sharks, small medium	0.84	41	Benthic plants	-
20	Sharks, large	0.85	42	Meiobenthos	-
21	Rays, small medium	1.01	43	Dolphins, porpoises	-
22	Rays, large	0.42	44	Detritus	-

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 is 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 countryspecific 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.

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-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 (Figure 11). We consider this tuning required 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.

Figure 11. Modeling process for the LME models.

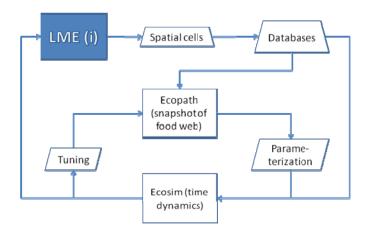
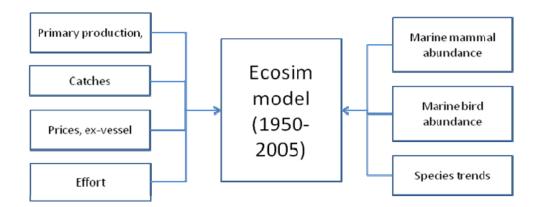


Figure 12. Time series extraction from databases for time-dynamic Ecosim runs for each of the World's 66 LMEs.



For each LME model, we extract time series information from a range of sources as explained above, and illustrated in Figure 12. 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 spatial ½° latitude by ½° longitude 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:
 - 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 0.01 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.
 - Chlorophyll estimates are (after conversion) used to force the phytoplankton biomass.
- Check model for mass balance.
 - If any of the ecotrophic efficiencies, (EE, indicating the proportion of production that is 'used' in the system mainly for catches and predation), exceeds unity then:
 - For pinnipeds the predation estimate can be heavy, 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 residuals (SS) for Table 4.
 - 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}).

- 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 4 again.
- Fit the model to the time series data using a Matyas search (random optimization) procedure (Christensen and Walters, MS) 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 c.v.
 - When a better fit (lower SS) is obtained, resample the parameters from a normal distribution with a band around the last better 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.
- Save the model
- Move to the next LME.

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 catch series. Given that we force the catches in Ecosim to match the time series catches, 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 it cannot, 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, estimated based on the assumption that fishing mortality equalled natural mortality in the year with maximum catches were assigned a weight of 1. Each such biomass contributes $(B_i - B_i)^{r} \wedge 2$ to the fitting SS, where B_i is model predicted biomass for whatever year had maximum catch, and B_i is the catch-based prior

estimate $M_i = \max_{M_i} M_i$.

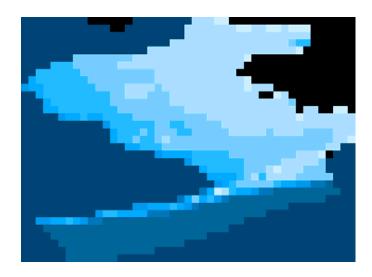
Spatial models

Given that most of the information available for the database-driven model generation is available on a spatial basis, typically at the half-degree latitude by half-degree longitude level, we opted to create preliminary spatial models based on the dynamic Ecospace model of EwE (Walters et al., 1999). For each LME, we thus produce a base map based on depth information, (e.g., Figure 13; we populate it with information about primary productivity (presently only in form of a static map, but we will, in future iterations, add monthly and annual primary productivity fields that can be used as drivers for Ecospace).

We have not yet added spatial catches to the Ecospace time series, though these can be extracted from the *Sea Around Us* catch database, and used for evaluation of the Ecospace runs. Also, we do not yet have estimates of detailed, spatial effort patterns available, but we will have this within the next six months.

The spatial model is thus rather rudimentary, but can serve as a starting point for refinement by the individual GEF/LME projects as part of their modeling activities, or for that matter by individual research groups in the various LMEs.

Figure 13. Spatial model of LME number 1, the East Bering Sea, as obtained through the database-driven model generation approach. Grid cell size is half degree latitude by half degree longitude, and there are estimates of spatial catches, primary production, etc. (see above) available for the spatial models. Habitats are based on depth strata, indicated by darker colors for deeper areas. The darkest color indicates cells outside the LME area, while black indicates land.



Results and Discussion

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 vield from high-latitude systems. This is our use 'generic' connected to of а production/biomass (P/B) factor for many functional groups. We have partly remedied this by using P/B-estimates based on Lorenzen (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.

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 focusing attention on poor model fits (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: see Figure 14 for an example of one of the diagnostic plots we use for manual tuning.

In this example there are numerous time series for biomass (indicated by the coloured circles on the biomass plot) indicating a downward trend over time. This trend is picked up well by Ecosim (the line on the plot), and we see from the second plot (mortality) that the downward trend in the early 1970s may be associated with predation increase, rather than catches, which only increased some years later.

In the development of the automatic fitting procedure, we were confronted with numerous logical problems, but we have 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 procedure rule-based fittina to 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 4 we review the sum of squared 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 typically correspond to fitting 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, we, as part of the random optimization-fitting procedure vary both the initial biomasses and vulnerabilities (Christensen and Walters, MS). 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).

Figure 14. 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) indicated by the circles on the first plot, which also shows the Ecosim biomass trajectory as a line. The yield plot shows that Ecosim (line) used the reported catches (circles) to drive the simulations.

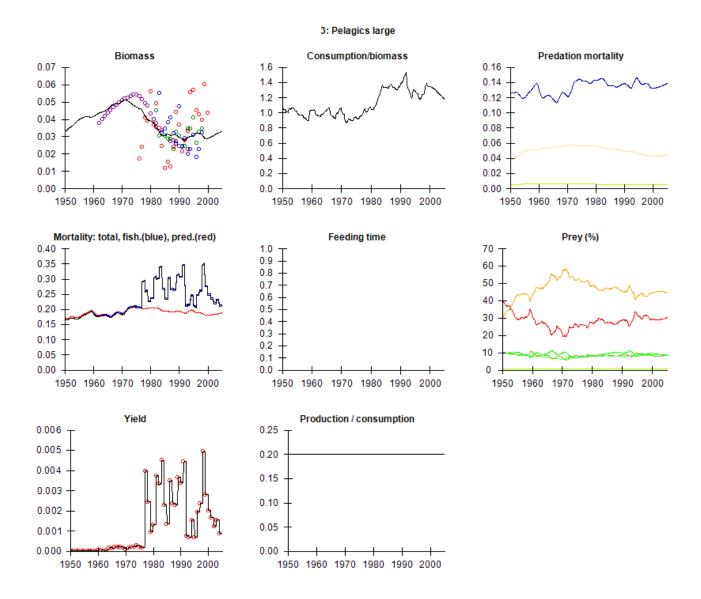


Table 4. Residuals from the time series fitting of LME models. Numbers indicate, by LME, the summed squared residuals (log observed/predicted) before fitting, after fitting, and the ratio of after/before, indicating how much the fitting procedure improved the fit. Fitting is done by fitting one vulnerability parameter for each consumer group with time series as well as the initial 1950-biomasses.

LME	Before	After	Ratio (%)	LME	Before	After	Ratio (%)
1	90757	217	0.2	34	42931	203	0.5
2	65584	1295	2.0	35	35666	183	0.5
3	87422	1440	1.6	36	46993	322	0.7
4	66266	3155	4.8	37	46594	5	0.0
5	80364	1856	2.3	38	34411	41	0.1
6	173535	4647	2.7	39	85817	110	0.1
7	107316	959	0.9	40	55706	26	0.0
8	99045	1015	1.0	41	102595	650	0.6
9	101890	212	0.2	42	92571	97	0.1
10	47431	116	0.2	43	70540	1831	2.6
11	94130	3	0.0	44	74387	133	0.2
12	98368	169	0.2	45	69051	267	0.4
13	96782	1391	1.4	46	110081	127	0.1
14	97493	797	0.8	47	63789	12	0.0
15	56104	241	0.4	48	41579	38	0.1
16	70172	1543	2.2	49	91060	101	0.1
17	75251	17	0.0	50	101346	174	0.2
18	87831	986	1.1	51	111675	115	0.1
19	246105	2264	0.9	52	53169	1650	3.1
20	53122	2225	4.2	53	93228	0	0.0
21	118819	1672	1.4	54	0	0	0.0
22	188938	1812	1.0	55	12	9	71.7
23	87764	1055	1.2	56	0	0	
24	213343	5635	2.6	57	0	0	
25	290131	13230	4.6	58	38	0	0.0
26	105924	1565	1.5	59	85354	3254	3.8
27	66903	593	0.9	60	146590	1740	1.2
28	80657	1	0.0	61	2	0	0.0
29	142769	1301	0.9	62	82909	79	0.1
30	84529	1235	1.5	63	532	467	87.9

31	85405	353	0.4	64	24	0	0.0
32	44465	8	0.0	65	402	202	50.1
33	72169	145	0.2	66	115377	2536	2.2

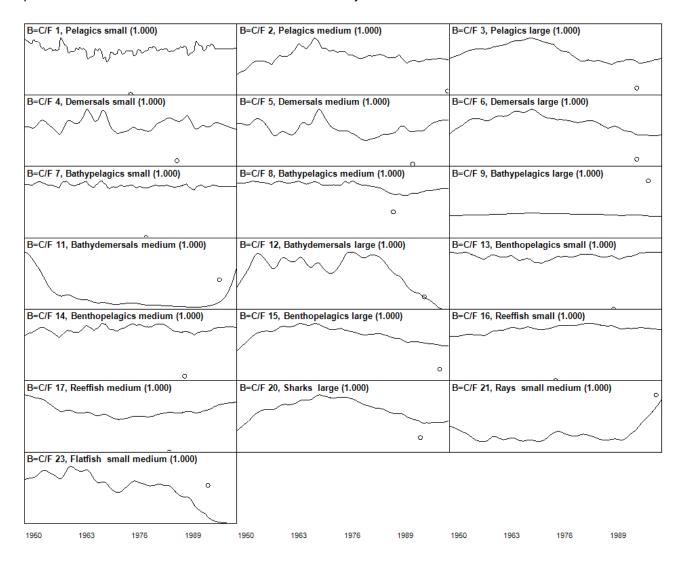
For manual model fitting, Ecosim provides important diagnostics in the form of a plot showing all the time series fits in a model. We here give an example of such a plot comparing population trend time series with Ecosim

predictions for the New Zealand Shelf model (LME 46) in Figure 15. The numbers in brackets after the plot titles indicate the time series weight, while the initial numbers in the titles indicate functional group numbers.

Figure 15. Time series fits for biomasses on the New Zealand Shelf (LME 46). Lines indicate the Ecosim estimates and dots 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.

B Baleen whales (1.000)	B Toothed whales (1.000)	B Pinnipeds (1.000)
Bulletin Milales (1.000)	DECESSION WINDER (1.000)	**************************************
B Delphine persoine (1 000)	######################################	
B Delphins, porpoises (1.000)	14 Pseudocyttus maculatus (New Ze (2.164)	15 Barracouta (BAR) Thyrsites atu (0.0182)
		·
15 Barracouta (BAR) Thyrsites atu (0.0146)	22 Elephant Fish (ELE) Callorhinc (0.00438) 🚓	15 Gemfish (SKI) Rexea solandri (0.0416)
000	_	
12 Ling (LIN) Genypterus blacodes (0.00886)	3 New Zealand and South-west pac (0.00528)	3 New Zealand and South-west pac (0.00276)
over over over over over over over over	000000000000000000000000000000000000000	**************************************
3 New Zealand and South-west pac (0.00383)	26 South East Fisheries (SEF) of (0.000161)	11 South-eastern Australia contin (0.000319)
600,000	~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~	~ ~ /
2 South-eastern Australia contin (0.000323)	21 New South Wells, Australia sha (0.000324)	21 New South Wells, Australia sha (0.000327)
20 Shark by-catch in New Zeland t (0.00727)	27 Spiny lobster in Gisbore, West (0.0732)	29 Paua (PAU 7) Marlborough Halio (0.695)
		<u></u>
5 Red Gurnard (GUR) Chelidonicht (0.361)	5 Red Gurnard (GUR) Chelidonicht (0,0555)	6 Snapper (SNA) Ragrus auratus (0.361)
	~~~	Constitution of the second
20 Spiny Dogfish (SPD) Squalus ac (0.0109)	6 Evolution of a stock assessmen (0.695)	3 MULTIFAN-CL: a length-based, a (0.00334)
800 8	8	3 WOLTHANCE: a status based, a (0.00034)
B Phytoplanton, from Chlorophyll (1.000)	8 Biomass estimation of orange r _c (19.47)	
	0	
1950 1963 1976 1989	1950 1963 1976 1989	1950 1963 1976 1989

**Figure 16.** Estimates of biomasses for each of the exploited groups on the New Zealand Shelf (LME 46). These estimates are based on an assumption that a biomass can be obtained from an assumed catch / natural mortality ratio in the year with maximum catches. They serve to provide a penalty for the optimizations if the biomasses should move too far away from this indicated biomass.



The fits are perfect for the marine mammals in Figure 15 (first four plots) since for these groups we force Ecosim to use the biomasses from the 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 biomass 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, and this is currently the focus of our work.

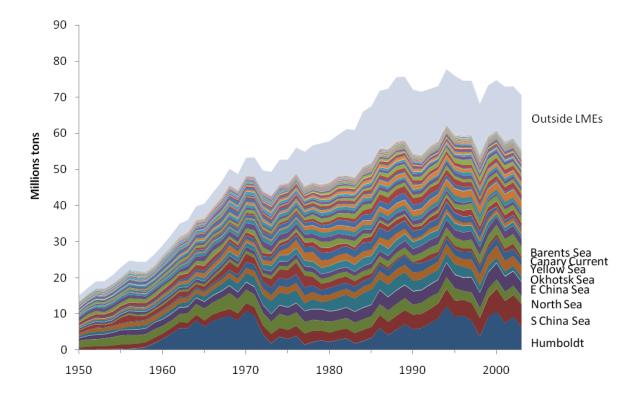
#### LME catches

Indications are that the global fisheries catches have been steady or decreasing since the 1980s as reported by Watson and Pauly (2001). We

compare this to the situation in the part of the oceans included in the 66 currently defined LMEs in Figure 17, which is based on the LME models and derived from cell-specific (½° latitude by ½° longitude) catches from the Sea Around Us database. We see from this that the LME catches have been stagnant since the mid 1980s. It is also evident from the figure that the vast majority (80-90%) of the World's fisheries catches come from the LME areas.

Overall, the catches are dominated by the small-to midsize pelagics, (e.g., anchoveta, herring, mackerel), large benthopelagics (notably cod), and demersals. Invertebrates play a relative minor role in the catches by weight (Figure 18).

**Figure 17.** Annual fisheries landings (million tons) in the world's LMEs. The largest catches are in the Humboldt current, represented mainly by Peruvian anchoveta. The LMEs contribute 80-90% of the global landings, the remaining indicated here in grey as 'Outside LMEs'.



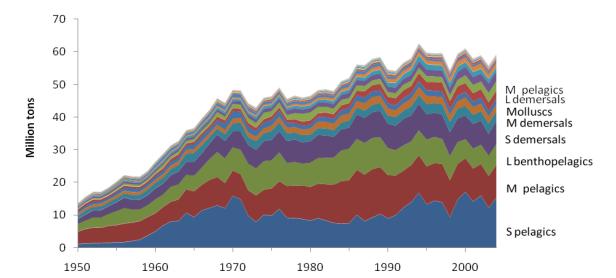


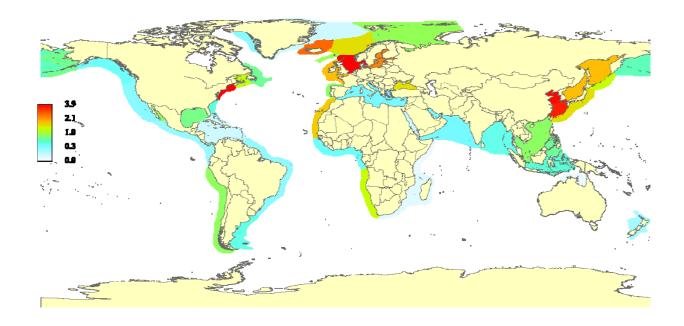
Figure 18. Annual landings (million tons) in the world's LMEs arranged by functional groups.

If we look closer at how the LME-catches are distributed over time and space, we can further compare the 1980 and 2004-situation; see Figure 19 and Figure 20. In 1980, the highest yielding LMEs (by unit area) were in the North Atlantic and Northwest Pacific, while Chinese waters and the Humboldt Current were dominating by 2004. The highest catch levels have more than doubled

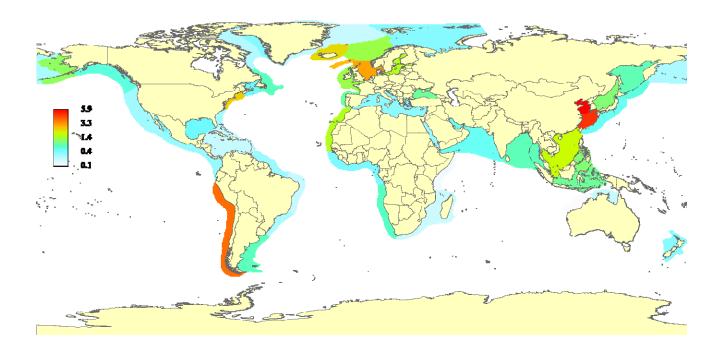
over the period, but many ecosystems have actually experienced a decline, e.g., for the Northeast US Shelf, and the Gulf of Mexico.

We saw from Figure 17 that the LME catches have been stagnant since the mid-1980s. This is in spite of massive increase in fishing effort since then, see, e.g., Alder et al. (2007).

**Figure 19.** Catches (t-km⁻²-year⁻¹) in the world's LMEs in 1980 as obtained from the LME models and based on the *Sea Around Us* catch database.



**Figure 20.** Catches (t-km⁻²-year⁻¹) in the world's LMEs in 2004 as obtained from the LME models based on the *Sea Around Us* catch database.



#### Value of LME fisheries

We estimated the ex-vessel value of the fisheries in the world's LMEs from the ecosystem modeling, based on the *Sea Around Us* catch and price databases, and express the value over time as real prices (i.e., accounting for inflation) for 2000. The values are based on the actual species composition in the catches, and can thus be seen to indicate how much we would be able to get for the catches today if we fished like we did then.

Examining the value over time in Figure 21, we see a striking feature. The ex-vessel value reached a level of US\$60 billion in the early 1970s, and it has remained at or below that level since then, with the average since 1990 being \$56 billion. In spite a five-fold increase in effective fishing effort globally from 1970 to 1995 (Gelchu and Pauly, 2007), the value of the catches has declined, not increased. The reason is of course that massive overexploitation leads to lower catches as well as a less valuable catch composition, among other due to fishing down the food web (Pauly et al., 1998).

This is illustrated in Figure 22, where the functional groups are arranged after their contribution to summed value over time. Medium-sized pelagics, (e.g., herring, mackerel) followed by large benthopelagics (notably cod), top the list overall, while it is shrimp that now dominated the value sheet globally.

Overall, we find that invertebrates currently contribute 42% of the value of the LME fisheries, which by far exceeds their contribution to the catches (see Figure 18), indicating that we actually prefer invertebrates to fish.

The contribution to overall ex-vessel value is quite variable between LMEs, and indeed the top eight of the 66 LMEs contribute half of the total value, summed over time. The "LME-8" are, surprisingly perhaps, (47) East China sea, 11%; (36) South China Sea, 8.6%; (48) Yellow Sea, 8.6%; (52) Okhotsk Sea, 4.7%; (49) Kuroshio Current, 4.6%; (50) Sea of Japan/East Sea, 4.3%; (22) North Sea, 3.7%; and (32) the Arabian Sea, 3.5%.

**Figure 21.** Annual ex-vessel value (US\$, billion) of the fisheries in each of the world's 66 LMEs calculated using year 2000 real prices.

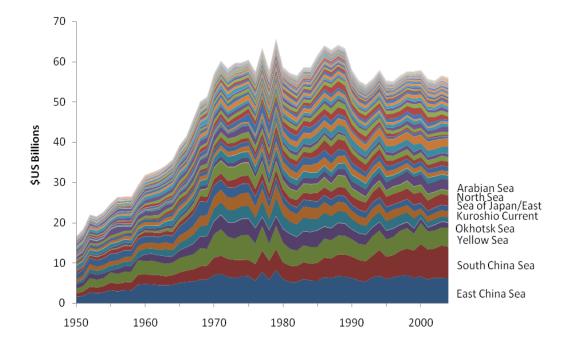
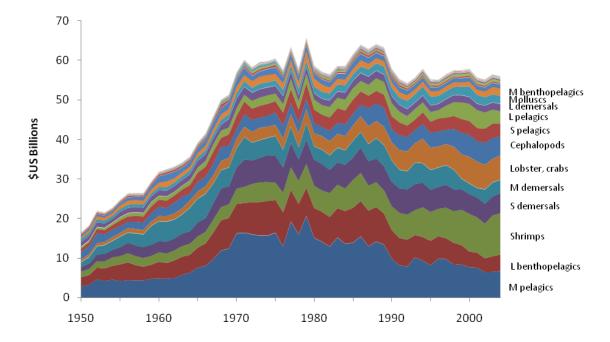


Figure 22. Annual fisheries ex-vessel value (US\$, billion) by functional groups in the world's LMEs.

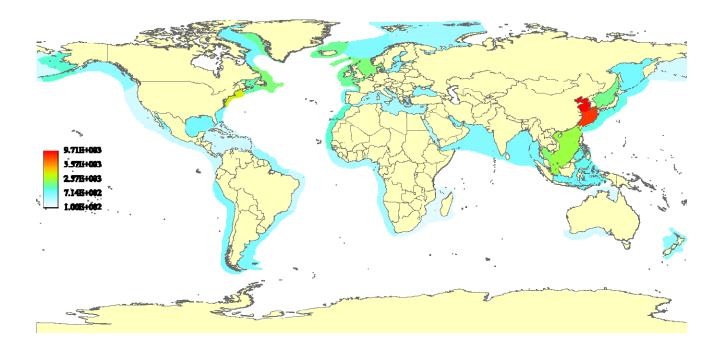


We show in Figure 23 the ex-vessel value per square kilometer for 2004. This can be seen as a 'real-estate' value, expressing how much revenue that is being earned for each square kilometer. Values reach up to close to \$10,000 per km² per year in the Yellow Sea, an order of magnitude higher than for most other areas.

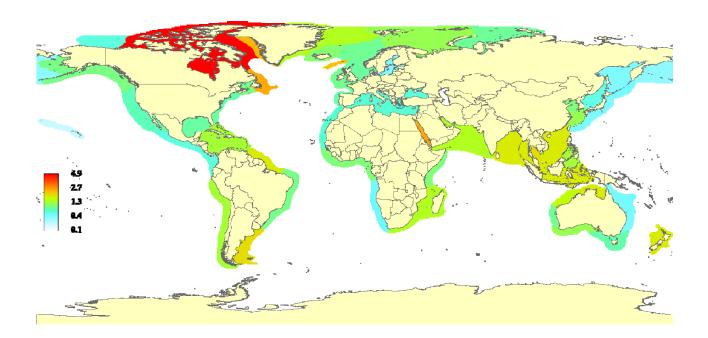
When comparing the catches in 2004 relative to the catches in 1980, we find that the value has declined for 38 out of the 63 LMEs with catches.

Notable is that all North Pacific LMEs have seen declined catch value over the period. The more doubling value in catch for Newfoundland-Labrador Shelf is initially surprising, given the collapse of the cod fisheries. The cod fisheries were, however, already at a low level, and the catch values in the 1960s and 1970s clearly exceed the current values. The relatively large increases in parts of the Arctic are based on very low catch levels.

**Figure 23.** Ex-vessel fisheries value (US\$ km⁻²·year⁻¹) by LME in 1980 calculated using year 2000 real prices.



**Figure 24.** Ratio of ex-vessel value in 2004 relative to the value in 1980, calculated based on real prices for year 2000.



#### **Conclusion and Recommendations**

Large Marine Ecosystems face serious threats throughout the world, one of the dominating being overfishing caused by excessive effort capability. 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 of GEF/LME projects. 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 for GEF/LME projects by developing capabilities for database-driven ecosystem model generation. We encourage

GEF/LME projects 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 GEF/LME projects to also emphasize the economical and social aspects of the fish produce chain. We here, could only evaluate the ex-vessel importance of the fisheries, but given information from throughout the fishing sector, ecosystem models combined with economical value chain modeling can be used to evaluate how food security, and economic and social parameters will be impacted by fisheries management decisions.

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## **Appendices**

**Appendix 1.** Diet compositions for the generic LME model. Actual diet compositions used for the individual LME models were modified based on diet data for fish (from FishBase), invertebrates (from SeaLifeBase), marine mammals (Kaschner, 2004), and marine birds (Karpouzi, 2005). Column headings (numbers) indicate consumers, names are listed in rows.

	Prey \ predator	1	2	3	4	5	6	7	8	9	10	11
1	Pelagics small		0.1	0.4			0.02			0.2		
2	Pelagics medium			0.295						0.1		
3	Pelagics large			0.005								
4	Demersals small			0.1		0.6	0.6					
5	Demersals medium						0.1					
6	Demersals large											
7	Bathypelagics small								0.3	0.3		
8	Bathypelagics medium									0.2		
9	Bathypelagics large											
10	Bathydemersals small											0.2
11	Bathydemersals medium											
12	Bathydemersals large											
13	Benthopelagics small			0.1			0.06					
14	Benthopelagics medium											
15	Benthopelagics large											
16	Reeffish small											
17	Reeffish medium											
18	Reeffish large											
19	Sharks small medium											
20	Sharks large											
21	Rays small medium											
22	Rays large											
23	Flatfish small medium											
24	Flatfish large											
25	Cephalopods		0.01									
26	Shrimps					0.01	0.01				0.01	0.01
27	Lobsters crabs						0.01					
28	Jellyfish											
29	Molluscs				.01							
30	Krill	0.05	0.1	0.1				0.05	0.1	0.1		
31	Baleen whales											
32	Toothed whales											
33	Pinnipeds											
34	Birds											
35	Megabenthos				0.15	0.2	0.2				0.44	0.49
36	Macrobenthos											

37 38	Corals Softcorals sponges etc									
39	Zooplankton other	0.8	0.79	0.3		0.95	0.6	0.1	0.1	
40	Phytoplankton	0.15								
41	Benthic plants									
42	Meiobenthos			.395	0.19				0.4	0.2
43	Dolphins porpoises									
44	Detritus			0.15					0.05	0.1

## Appendix 1. continued

	Prey \ predator	12	13	14	15	16	17	18	19	20	21	22
1	Pelagics small				0.1			0.05	0.1	0.2		
2	Pelagics medium									0.2		
3	Pelagics large									0.01		
4	Demersals small				0.1		0.1	0.1	0.1			0.05
5	Demersals medium				0.05				0.1	0.1		0.05
6	Demersals large											
7	Bathypelagics small											
8	Bathypelagics medium											
9	Bathypelagics large											
10	Bathydemersals small	0.2										
11	Bathydemersals medium	0.2										
12	Bathydemersals large											
13	Benthopelagics small			0.02	0.02			0.01				0.05
14	Benthopelagics medium				0.1				0.1	0.1		0.05
15	Benthopelagics large											
16	Reeffish small						0.2	0.4				
17	Reeffish medium							0.2		0.05		
18	Reeffish large									0.005		
19	Sharks small medium									0.01		
20	Sharks large											
21	Rays small medium	0.02								0.01		
22	Rays large									0.001		
23	Flatfish small medium											
24	Flatfish large											
25	Cephalopods	0.05		0.05	0.05		0.05			0.05		
26	Shrimps	0.01	0.01		0.01	0.01	0.01		0.01		0.01	0.01
27	Lobsters crabs	0.01							0.05		0.01	0.01
28	Jellyfish											
29	Molluscs	0.02	0.01							0.05		0.05
30	Krill		0.05	0.05	0.1	0.1						
31	Baleen whales											
32	Toothed whales											

33 34	Pinnipeds Birds											
35	Megabenthos	0.24	0.19	0.15	0.19	0.24	0.29	0.24	0.54	0.214	0.93	0.73
36	Macrobenthos					•						
37	Corals						0.03					
38	Softcorals sponges etc						0.02					
39	Zooplankton other	0.05	0.7	0.68	0.28	0.65	0.2				0.05	
40	Phytoplankton											
41	Benthic plants											
42	Meiobenthos						0.1					
43	Dolphins porpoises											
44	Detritus	0.2	0.04	0.05								

## Appendix 1. continued

Pelagics small		Prey \ predator	23	24	25	26	27	28	29	30	31	32	33
3         Pelagics large           4         Demersals small         0.05         0.0316         0.0993           5         Demersals medium         0.05         0.0316         0.0993           6         Demersals large         0.01         0.0889           7         Bathypelagics small sarge         0.01         0.01           8         Bathypelagics large         0.01         0.01           10         Bathydemersals small         0.01         0.01           11         Bathydemersals large         0.01         0.01           12         Bathydemersals rege         0.01         0.0316         0.093           14         Benthopelagics small         0.001         0.0316         0.093           15         Benthopelagics medium         0.01         0.01         0.093           15         Benthopelagics medium         0.01         0.01         0.093           15         Benthopelagics medium         0.01         0.01         0.01           16         Reeffish small         0.01         0.01         0.01           17         Reeffish medium         0.01         0.01         0.01         0.01           20         Sharks large	1	Pelagics small			0.01						.0735	0.2	.0891
Demersals small   0.05   0.25   0.316   0.093     Demersals medium   0.05   0.05   0.316   0.093     Demersals large   0.0889   0.01     Bathypelagics small   0.0889   0.01     Bathypelagics medium   0.01   0.01     Bathydemersals medium   0.01   0.01     Bathydemersals medium   0.001   0.016   0.01     Bathydemersals medium   0.001   0.0316   0.093     Bathydemersals large   0.001   0.0316   0.093     Bathydemersals large   0.001   0.0316   0.0993     Bathydemersals large   0.001   0.0316   0.0993     Benthopelagics small   0.001   0.0316   0.0993     Benthopelagics large   0.01   0.016   0.016     Reeffish small   0.001   0.0316   0.016     Reeffish large   0.01   0.016   0.016     Rays small medium   0.2   0.2     Rays small medium   0.2   0.016   0.0574   0.16     Cephalopods   0.1   0.0574   0.16     Cephalopods   0.1   0.0574   0.16     Cobsters crabs   0.01   0.01   0.01     Cobsters crabs   0.01   0.01   0.01     Cobsters crabs   0.01   0.01   0.01     Cobsters crabs   0.01   0.01   0.01   0.01   0.01   0.01   0.01   0.01   0.01   0.01   0.01   0.01   0.01   0.01   0.01   0.01   0.01   0.01   0.01   0.01   0.01   0.01   0.01   0.01   0.01   0.01   0.01   0.01   0.01   0.01   0.01   0.01   0.01   0.01   0.01   0.01   0.01   0.01   0.01   0.01   0.01   0.01   0.01   0.01   0.01   0.01   0.01   0.01   0.01   0.01   0.01   0.01   0	2	Pelagics medium									.0735	0.3	.0891
5         Demersals medium         0.05         .0316         .0993           6         Demersals large         .0889	3	Pelagics large											
6       Demersals large         7       Bathypelagics small       .0889         8       Bathypelagics medium       0.01         9       Bathypelagics large       0.01         10       Bathydemersals small       .001         11       Bathydemersals medium       .001         12       Bathydemersals large       0.01         13       Benthopelagics small       .0001         14       Benthopelagics medium       .0316       0.1         15       Benthopelagics large       .001       .0316       0.0         16       Reeffish small       .001       .001         17       Reeffish large       .001       .001         20       Sharks small medium       .02         21       Rays small medium       .02         22       Rays large       .001         23       Flatfish small medium       .02         24       Flatfish large       .001         25       Cephalopods       .01         26       Shrimps       .001         27       Lobsters crabs	4	Demersals small	0.05	0.25							.0316		.0993
7       Bathypelagics small       .0889         8       Bathypelagics medium       0.01         9       Bathypelagics large       0.01         10       Bathydemersals small	5	Demersals medium		0.05							.0316		.0993
8       Bathypelagics medium       0.01         9       Bathypelagics large       0.01         10       Bathydemersals small       0.01         11       Bathydemersals medium       0.01         12       Bathydemersals large       0.01         13       Benthopelagics small       0.001         14       Benthopelagics large       0.0316       0.1         15       Benthopelagics large       0.01       0.01         16       Reeffish small       0.01       0.01         17       Reeffish large       0.01       0.01         19       Sharks small medium       0.0       0.0         20       Sharks large       0.0       0.0         21       Rays small medium       0.2         22       Rays large       0.01         23       Flatfish small medium       0.2         24       Flatfish large       0.01         25       Cephalopods       0.1         26       Shrimps       0.01         27       Lobsters crabs	6	Demersals large											
9       Bathypelagics large       0.01         10       Bathydemersals small	7	Bathypelagics small									.0889		
Bathydemersals small   Bathydemersals medium   Bathydemersals large   D.001   D.011   D.0012   D.0013   D.0014   D.0015   D.001	8	Bathypelagics medium										0.01	
11       Bathydemersals medium         12       Bathydemersals large       0.01         13       Benthopelagics small       0.001       .0316       .0993         14       Benthopelagics medium       .0316       0.1       .0993         15       Benthopelagics large       0.01       .01       .0993         16       Reeffish small	9	Bathypelagics large										0.01	
Bathydemersals large	10	Bathydemersals small											
13       Benthopelagics small       0.001       .0316       .0993         14       Benthopelagics medium       .0316       0.1       .0993         15       Benthopelagics large       0.01       .01       .001         16       Reeffish small <td>11</td> <td>Bathydemersals medium</td> <td></td>	11	Bathydemersals medium											
14       Benthopelagics medium       .0316       0.1       .0993         15       Benthopelagics large       0.01         16       Reeffish small           17       Reeffish medium            18       Reeffish large             19       Sharks small medium	12	Bathydemersals large										0.01	
15       Benthopelagics large       0.01         16       Reeffish small       0.01         17       Reeffish medium       0.01         18       Reeffish large       0.01         19       Sharks small medium       0.01         20       Sharks large       0.01         21       Rays small medium       0.2         22       Rays large       0.01         23       Flatfish small medium       0.2         24       Flatfish large       0.01         25       Cephalopods       0.1       .0574       0.1         26       Shrimps       0.01       0.01         27       Lobsters crabs       0.01       0.01	13	Benthopelagics small			0.001						.0316		.0993
16       Reeffish small         17       Reeffish medium         18       Reeffish large         19       Sharks small medium         20       Sharks large         21       Rays small medium         22       Rays large         23       Flatfish small medium         24       Flatfish large         25       Cephalopods         0.1       .0574         26       Shrimps         0.01       .001         27       Lobsters crabs	14	Benthopelagics medium									.0316	0.1	.0993
17       Reeffish medium         18       Reeffish large         19       Sharks small medium         20       Sharks large         21       Rays small medium         22       Rays large         23       Flatfish small medium         24       Flatfish large         25       Cephalopods         26       Shrimps         0.01         27       Lobsters crabs	15	Benthopelagics large										0.01	
18       Reeffish large         19       Sharks small medium         20       Sharks large         21       Rays small medium         22       Rays large         23       Flatfish small medium       0.2         24       Flatfish large       0.01         25       Cephalopods       0.1         26       Shrimps       0.01         27       Lobsters crabs	16	Reeffish small											
19 Sharks small medium 20 Sharks large 21 Rays small medium 22 Rays large 23 Flatfish small medium 24 Flatfish large 25 Cephalopods 26 Shrimps 27 Lobsters crabs  28 Sharks small medium 29 0.01 20 0.01 20 0.01 20 0.01 20 0.01 20 0.01	17	Reeffish medium											
20       Sharks large         21       Rays small medium         22       Rays large         23       Flatfish small medium         24       Flatfish large         25       Cephalopods         0.1       .0574         26       Shrimps         0.01         27       Lobsters crabs	18	Reeffish large											
21       Rays small medium         22       Rays large         23       Flatfish small medium       0.2         24       Flatfish large       0.01         25       Cephalopods       0.1       .0574       0.1         26       Shrimps       0.01       0.01         27       Lobsters crabs       0.01       0.01	19	Sharks small medium											
22       Rays large         23       Flatfish small medium       0.2         24       Flatfish large       0.01         25       Cephalopods       0.1         26       Shrimps       0.01         27       Lobsters crabs	20	Sharks large											
23       Flatfish small medium       0.2         24       Flatfish large       0.01         25       Cephalopods       0.1       .0574       0.1         26       Shrimps       0.01       0.01         27       Lobsters crabs	21	Rays small medium											
24       Flatfish large       0.01         25       Cephalopods       0.1       .0574       0.1         26       Shrimps       0.01       0.01         27       Lobsters crabs       .0574       .0574	22	Rays large											
25       Cephalopods       0.1       .0574       0.1         26       Shrimps       0.01       0.01         27       Lobsters crabs       .0574       0.1	23	Flatfish small medium		0.2									
26 Shrimps 0.01 0.01 27 Lobsters crabs	24	Flatfish large										0.01	
27 Lobsters crabs	25	Cephalopods		0.1							.0574	0.1	
	26	Shrimps	0.01	0.01									
28 Jellyfish 0.02	27	Lobsters crabs											
•	28	Jellyfish						0.02					

29	Molluscs	0.05										
30	Krill			0.1					0.05		0.249	0.114
31	Baleen whales											
32	Toothed whales											
33	Pinnipeds										.0005	
34	Birds											
35	Megabenthos	0.64	0.29			0.2		0.05		0.580		0.311
36	Macrobenthos											
37	Corals											
38	Softcorals sponges etc											
39	Zooplankton other	0.15	0.1	0.789			8.0	0.1	0.7			
40	Phytoplankton								0.1			
41	Benthic plants											
42	Meiobenthos	0.1			0.1	0.5		0.35				
43	Dolphins porpoises											
44	Detritus			0.1	0.9	0.3	0.18	0.5	0.15			

## Appendix 1. continued

	Prey \ predator	34	35	36	37	38	39	42	43
1	Pelagics small	0.2							0.149
2	Pelagics medium	0.05							0.149
3	Pelagics large								
4	Demersals small	0.2							.0648
5	Demersals medium	0.05							.0648
6	Demersals large								
7	Bathypelagics small	0.11							
8	Bathypelagics medium								
9	Bathypelagics large								
10	Bathydemersals small								
11	Bathydemersals medium								
12	Bathydemersals large								
13	Benthopelagics small	0.1							.0648
14	Benthopelagics medium	0.04							.0648
15	Benthopelagics large								
16	Reeffish small								
17	Reeffish medium								
18	Reeffish large								
19	Sharks small medium								
20	Sharks large								
21	Rays small medium								
22	Rays large								
23	Flatfish small medium	0.04							

24	Flatfish large								
25	Cephalopods	0.1							0.443
26	Shrimps								
27	Lobsters crabs								
28	Jellyfish								
29	Molluscs								
30	Krill								
31	Baleen whales								
32	Toothed whales								
33	Pinnipeds								
34	Birds								
35	Megabenthos		0.02						
36	Macrobenthos		0.2						
37	Corals								
38	Softcorals sponges etc								
39	Zooplankton other		0.05	0.3	0.5	0.5			
40	Phytoplankton			0.2	0.1	0.1	0.9	0.5	
41	Benthic plants		0.01						
42	Meiobenthos		0.05	0.1					
43	Dolphins porpoises								
44	Detritus		0.67	0.4	0.4	0.4	0.1	0.5	

**Appendix 2.** Prey items for marine birds. Each prey type is assigned to a function group based on taxonomic code, and from this an overall assignment by prey group was derived in the last column by assigning equal weighting to all prey types. Derived from information in Karpouzi (2005) and the 'Sea Around Us' database.

No	Taxon code	Common name	Functional group	Prey group	Functional group
1	500124	Sandlances	4	Ammodytes	4
2	600004	Anchoveta	1	Anchovies	1
	600066	European anchovy	1		
	601659	Argentine anchoita	1		
	601661	Cape anchovy	1		
	601663	Japanese anchovy	1		
	601664	Californian anchovy	1		
3	400218	Silversides	1	Atherinidae	1
4	600047	Garpike	2	Beloniformes	2
	600303	Pacific saury	2		
	601084	Atlantic saury	2		
5	600252	Capelin	1	Capelin	1
6	500661	Jack mackerels	2	Carangidae	2 (5/6)
	502102	Scads	2		14 (1/6)
	600368	Pacific jack mackerel	2		
	600372	Greenback horse mackerel	14		
	601278	Mediterranean horse mackerel	2		
	601365	Atlantic horse mackerel	2		
7	390002	Squids	25	Cephalopods	25
	590010	Common squids	25		
8	400384	Crocodile icefishes	5	Channichthyidae	5
9	600024	Atlantic herring	2	Clupeidae	1 (2/3)
	601350	European pilchard	1		2 (1/3)
	601357	European sprat	1		
	601455	Round herring	1		
	601456	Whiteheads round herring	1		
	601477	South American pilchard	2		
40	601520	Pacific herring	2	Danamada	00
10	100345	Natantian decapods	26	Decapods	26
	490046	Northern shrimps	26 26		
	590096 690005	Penaeus shrimps	26		
11		Akiami paste shrimp Flyingfishes	1	Exocoetidae	1
11 12	400206 100039	Marine fishes	4	Fish, other	4
13	400440		23	Flatfish	23
13	500618	Righteye flounders Soles	23	1 14111511	23
	600516	Greenland halibut	23		
14	500654	Hakes	15	Gadids	5 (3/13)
14	600031	Blue whiting	14	Caulus	6 (4/13)
	600069	Atlantic cod	15		14 (1/13)
	600308	Pacific cod	6		15 (5/13)
	600315	Saffron cod	5		10 (0/10)
	600318	Alaska pollock	15		
	600319	Polar cod	5		
	600313	Southern blue whiting	15		
	600329	Patagonian grenadier	15		
	600510	Okhostk atka mackerel	5		

					,
	601343	Saithe	6		
	601825	Blue grenadier	6		
	602020	Red codling	6		
15	501132	Tropical goatfishes	4	Goatfishes	4
16	690016	Antarctic krill	30	Krill	30
	690274	Norwegian krill	30		
17	400185	Grenadiers or rattails	14	Macrouridae	14
18	400167	Lanternfishes	7	Myctophidae	7
19	600467	Patagonian toothfish	12	Nototheniidae	1 (1/7)
	600468	Marbled rockcod	15		5 (2/7)
	600472	Antarctic silverfish	1		12 (1/7)
	604702	Yellowbelly rockcod	5		14 (1/7)
	607039	Antarctic toothfish	15		15 (2/7)
	607041	Humped rockcod	5		
	607045	Grey rockcod	14		
20	502724	Pacific salmon	15	Oncorhynchus	15
21	300060	Perch-likes	4	Perch-like	2 (2/14)
	400304	Cardinalfishes	16		3 (1/14)
	400359	Mullets	5		4 (1/14)
	400362	Wrasses	16		5 (1/14)
	500705	Seabreams and porgies	14		6 (1/14)
	600063	European seabass	6		11 (1/14)
	600117	Chub mackerel	2		14 (4/14)
	600118	Atlantic mackerel	2		15 (1/14)
	600364	Bluefish	3		16 (2/14)
	600395	Redbait	11		
	600489	Snoek	15		
	600706	Striped seabream	14		
	600889	Axillary seabream	14		
	612918	Common warehou	14		
22	400277	Sculpins	4	Scorpaeniformes	4 (2/3)
	500144	Gurnards	11		11 (1/3)
	500495	Sea robins	4		
23	501135	Redfishes	5	Sebastes	5
24	400160	Lizardfishes	5	Synodontidae	5