CHAPTER 9

MODELING THE GLOBAL OCEANS WITH THE ECOPATH SOFTWARE SUITE: A BRIEF REVIEW AND APPLICATION EXAMPLE[1]

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The life sciences have reached a new era, that of the "big new biology" (Thessen and Patterson 2011). Ecology is following a similar path and has turned into a data-intensive science (Michener and Jones 2012). As demonstrated by this atlas and the mountain of data its completion entailed, this is also the case for marine biology and fisheries science. Indeed, our work is increasingly relying on large preexisting datasets, allowing new insights on phenomena visible mainly or only at global scales (e.g., Pauly 2007; Christensen et al. 2009; see also chapter 8).

However, data sharing in marine and fisheries biology is still not as extensive as in the historical "big" sciences, such as oceanography, meteorology, and astronomy, where massive data sharing is the norm (Pauly 1995; Edwards 2010; Thessen and Patterson 2011). The open-access principle of sharing information online for free has been increasingly applied to publications, but much less to data, mainly because of issues with recognition and sense of data ownership (Zeller et al. 2005; Vision 2010; Thessen and Patterson, 2011). Although incentives for digitization of nondigital materials have been growing, existing repositories have been estimated to represent less than 1% of the data in ecology (Reichman et al. 2011; Thessen and Patterson 2011).

GATHERING INFORMATION FOR AND FROM ECOPATH WITH ECOSIM MODELS

In aquatic ecology, the Ecopath with Ecosim (EwE) modeling approach has been widely applied to inform ecosystem-based management (e.g., Jarre-Teichmann 1998; Christensen and Walters 2004, 2011; Plaganyi and Butterworth 2004; Coll and Libralato 2012), since its original development in the early 1980s (Polovina 1984) and its relaunch in the early 1990s (Christensen and Pauly 1992). The EwE modeling approach was developed primarily as a tool to help fisheries management and answer "what if" questions about policy that could not be addressed with single-species assessment models (Pauly et al. 2000; Christensen and Walters 2004; 2011). The EwE software is user-friendly, free (under the terms of the GNU General Public License), and downloadable online (www.ecopath.org). Thus, hundreds of EwE models representing aquatic (and some

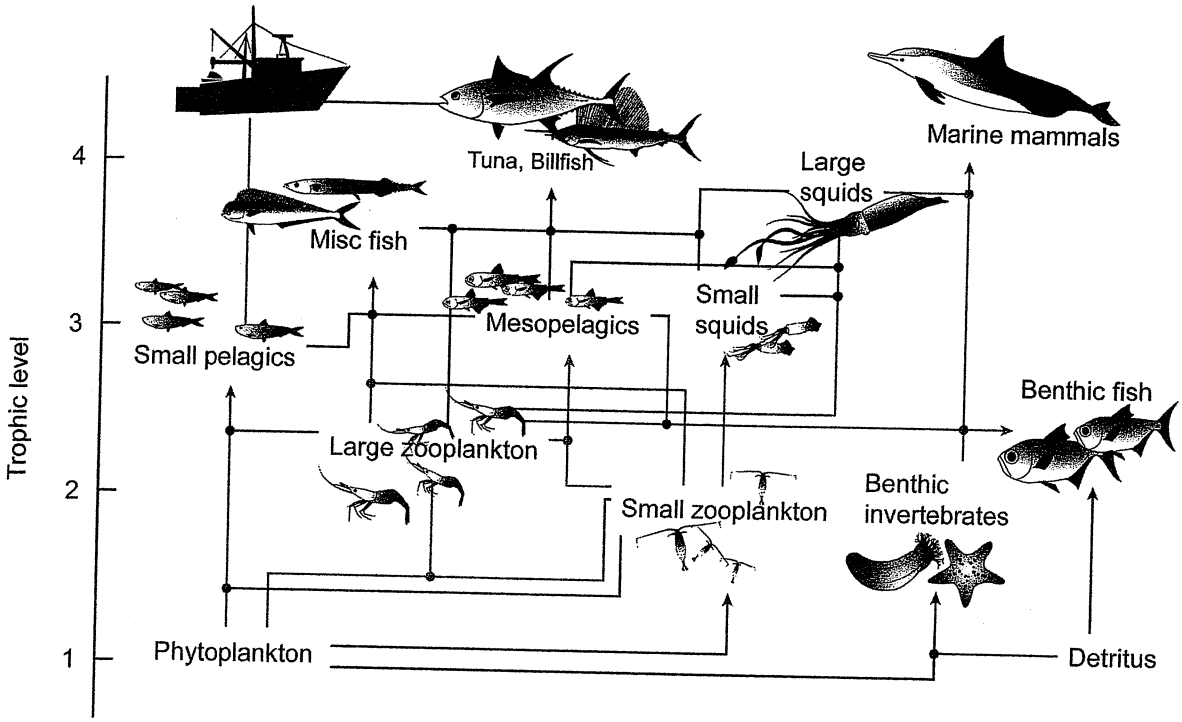

Figure 9.1. Flowchart of an Ecopath ecosystem model with a low number of groups. (Adapted from Pauly and Christensen 1993.)

terrestrial) ecosystems have been developed and published worldwide. The foundation of the EwE modeling approach is an Ecopath model, which creates a static mass-balanced snapshot of the resources in an ecosystem and their interactions, represented by trophically linked biomass "pools" (figure 9.1). The key principles and equations of EwE are presented in box 9.1, and more details can be found in the EwE online user guide (Christensen et al. 2008).

By formalizing available knowledge on a given ecosystem, EwE helps elucidate its structure and functioning and thus may be seen as an important source of mutually compatible data (Walters et al. 1997). Indeed, building an EwE model requires the collection, compilation, and harmonization of various types of information: descriptive data on species abundance, diet composition, and catch; computed data on species production and consumption; and the biomass trends resulting from various exploitation scenarios. Several meta-analyses based on smaller sets of EwE models have been performed, focusing either on theoretical ecology and ecological concepts (e.g., Christensen and Pauly 1993a; Pérez-España and Arreguín-Sánchez 1999, 2001; Gascuel et al. 2008; Arreguín-Sánchez 2011) or on ecosystems and species of particular interest (e.g., Pauly et al. 1999, 2009; Christensen et al. 2003a, 2003b). However, only few meta-analyses based on a large collection of EwE models have been published (e.g., Christensen 1995; Coll et al. 2012; Pikitch et al. 2012; Heymans et al. 2014).

Global Overview of EwE Applications and Presentation of a Meta-Analysis Case Study

EcoBase is an online information repository of EwE models published in the scientific literature, developed with the intention of making the models discoverable, accessible, and reusable to the scientific community (ecobase.ecopath.org). Details on the structure, usage, and capabilities of EcoBase can be found in the report introducing EcoBase (Colléter et al. 2013), which is available online. Colléter et al. (2013) first aimed to give a global overview of the applications of the Ecopath with Ecosim modeling approach in the scientific literature, using metadata gathered on the 435

BOX 9.1. ECOPATH KEY PRINCIPLES AND EQUATIONS

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The foundation of the EwE modeling approach is an Ecopath model (Polovina 1984; Christensen and Pauly 1992), which creates a static mass-balanced snapshot of the resources in an ecosystem and their interactions, represented by biomass "pools" linked by grazing or predation. The modeled food web is thus represented by "pools" or functional groups (i), which can be composed of species or groups of species that are ecologically similar or represent different age groups (or "stanzas") of a species. For each group, the Ecopath software solves two balancing equations: one to describe the production (equation 9.1), the other the energy balance (equation 9.2):

$$B_i \times \left(\frac{P}{B}\right)_i = \sum_{j=1}^{N} B_j \times \left(\frac{Q}{B}\right)_j \times DC_{ji} + \left(\frac{P}{B}\right)_i \times B_i \times (1 - EE_i) + Y_i + E_i + BA_i \quad (9.1)$$

$$Q_i = P_i + R_i + UA_i \quad (9.2)$$

where N is the number of groups in the model, B the biomass, P/B the production rate, Q/B the consumption rate, DC_{ji} the diet matrix representing the fraction of prey i in the diet of predator j, E the net migration rate, BA the biomass accumulation, Y the catches, EE the ecotrophic efficiency (i.e., the fraction of production that is used in the system), R the respiration, P the production, Q the consumption, and UA the unassimilated consumption because of egestion and excretion. The quantity (1 – EE) × P/B is the "other mortality" rate unexplained by the model.

Thus, the Ecopath model assumes the trophic network to be in a steady state during the reference period (usually 1 year), and consequently mass-balance occurs, where the production of the group is equal to the sum of all predation, nonpredatory losses, exports, biomass accumulations, and catches (see equation 9.1). Assuming there is no export and no biomass accumulation, and that the catches *Y* are known, only three of the four parameters *B*, *P/B*, *Q/B*, and *EE* have to be set initially for each group. The remaining parameter can be calculated by the software. The diet composition of each group is needed, that is, the percentage of the prey items in the diet of the group; rough initial diet composition estimates can be obtained from FishBase (www.fishbase.org) and SeaLifeBase (www.sealifebase.org).

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Polovina, J. J. 1984. Model of a coral reef ecosystem, Part I: ECOPATH model and its application to French Frigate Shoals. *Coral Reefs* 3: 1–11.

EwE models registered in EcoBase. We focused on the objectives of the EwE-based studies, the complexity and scope of the models, and the general characteristics of the modeled ecosystems and noted the complementary use of EcoTroph in EwE models (box 9.2). Based on the year of publication of the models, we also analyzed the evolution of the EwE applications over the past 30 years.

We present an application example detailed in Christensen et al. (2014), based on 200 models and a method that has been previously applied to the North Atlantic, Southeast Asia, and West Africa (Christensen et al. 2003a, 2003b, 2004). Therein, the 200 EwE models in figure 9.2 were used to provide snapshots of how much life there was in the ocean at given points in time and space. Christensen et al. (2014) then evaluated how the environmental conditions at each point relate to environmental parameters, from which they developed a multiple regression model to predict biomass trends. Finally, they used global environmental databases to predict the spatial distribution of fish biomass. This allowed Christensen et al. (2014) to predict the biomass trends for

BOX 9.2. ECOTROPH: A TOOL TO ANALYZE FISHING IMPACTS ON AQUATIC FOOD WEBS

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EcoTroph is a modeling approach articulated around the idea that an ecosystem can be represented by trophic spectra, representing the distribution across trophic levels, of biomass, production, catches, fishing mortalities, and so on. That is, ecosystems are viewed as biomass flowing from lower to higher trophic levels, through predation and ontogenetic processes (Gascuel 2005; Gascuel and Pauly 2009). Thus, the ecosystem biomass present at any given trophic level may be estimated from two simple equations, one describing biomass flow, the other their kinetics, which quantifies the velocity of biomass transfers toward top predators.

Modeling biomass flows as a quasiphysical process enables us to explore aspects of ecosystem functioning that complement EwE analysis. It provides users with simple tools to quantify fishing impacts at an ecosystem scale and a new way of looking at ecosystems. It also provides tools and indicators to analyze fishing fleets' interactions at the ecosystem level (Gasche and Gascuel 2013). EcoTroph can be used either in association with an existing Ecopath model or as a stand-alone application, especially in data-poor environments. It runs either as a plug-in of the EwE software or as an R-package (Colléter et al. 2013).

EcoTroph has also been used in specific case studies to assess the current fishing impacts at the ecosystem scale. High trophic levels have been found globally overexploited, for instance, in the Guinean EEZ (Gascuel et al. 2011), or the Bay of Biscay (Lassalle et al. 2012).

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Lassalle, G., D. Gascuel, F. Le Loc'h, J. Lobry, G. Pierce, V. Ridoux, B. Santos, J. Spitz, and N. Niquil. 2012. An ecosystem approach for the assessment of fisheries impacts on marine top predators: the Bay of Biscay case study. *ICES Journal of Marine Sciences* 69: 925–938.

higher-trophic-level predatory fish (i.e., the larger predatory "table fish") and for the lower-trophic level prey fish, such as small pelagics (e.g., sardines, anchovies, capelins), which are used mainly for fishmeal and oil. Given the recent controversy over whether "fishing down the food web" is a phenomenon actually occurring in nature (Pauly et al. 1998; see also www.fishingdown.org) or a sampling artifact with no or little relation to the underlying ecosystem structure, we contribute here to this discussion by evaluating how the biomass of high-trophic-level species has changed relative to the biomass of low-trophic-level species.

APPLICATIONS OF THE EWE MODELING APPROACH

The 435 Ecopath or EwE models in Ecobase were used to tackle a wide range of ecological issues; notably, 87% of the models were developed to answer questions about ecosystem functioning, 64% to analyze fisheries, 34% to focus on particular species of interest, and 11% to consider environmental variability (the percentages add to more than 100 because models may have more than one purpose). Less than 10% of the models focused on marine protected areas (MPAs), pollution (e.g., Booth and Zeller 2005), or aquaculture. The model module that identifies the keystone species (or groups) in

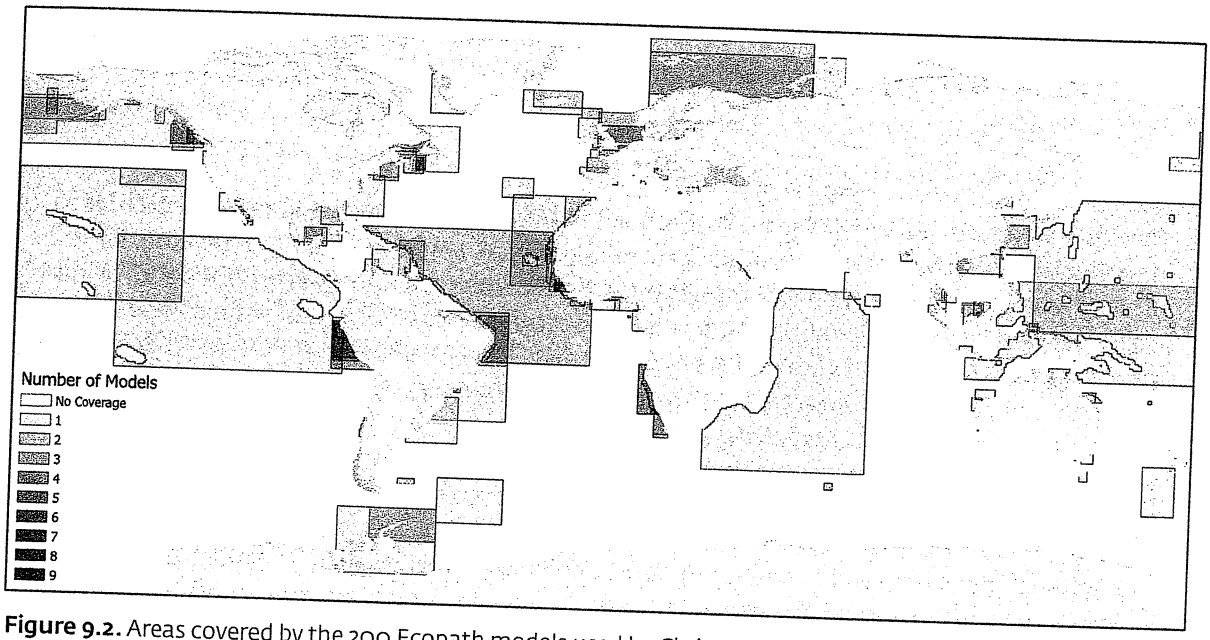

Figure 9.2. Areas covered by the 200 Ecopath models used by Christensen et al. (2014) to estimate historic changes in the biomass of fishes with high (≥3.5) and low (<3.5) trophic levels in the world ocean (see text).

ecosystems, based on Libralato et al. (2006), was used in 11% of the models, whereas the Ecotracer plug-in for tracking pollutants has been applied in less than 1% of the models (but see chapter 13).

The EcoTroph plug-in (see box 9.2 and figure 9.3) has also been little applied to date (2% of the models), but several of these applications focused on the effects of MPAs on the food web of ecosystems (Albouy et al. 2010; Colléter et al. 2012; Valls et al. 2012). In particular, Colléter et al. (2014) showed that the potential exports from small MPAs are of the same order of magnitude as the catch that could have been obtained inside the reserve, and Guénette et al. (2014), who used EcoTroph to assess the contribution of an MPA to the trophic functioning of a larger ecosystem, showed that the MPA of the Banc d'Arguin, in Mauritania, supports about 23% of the total production and 18% of the total catch of the Mauritanian shelf ecosystem, and up to 50% for coastal fish.

About three fourths of the 435 EwE models include between 10 and 40 functional (or taxonomic) groups, with 32% (141 models) including 10 to 20 groups. Overall, the numbers of groups range from 7 to 171 groups, but only 5 models include between 75 and 100 groups, and 2 models include more than 100 groups; 31% of

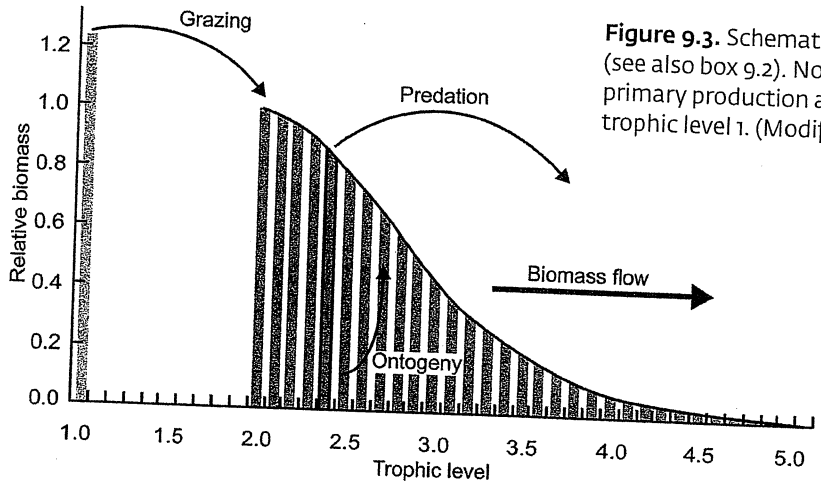

Figure 9.3. Schematic representation of EcoTroph (see also box 9.2). Note that the food web is fueled by primary production and recycled detritus entering at trophic level 1. (Modified from Gascuel et al. 2008.)

the models include groups corresponding to stanzas (age groups). Time dynamic (Ecosim) versions were developed for 41% of the models and spatially explicit (Ecospace) versions for 7% of the models.

About 70% of the models refer to a time period between 1980 and 2009, with 37% (159 models) corresponding to the 1990s. About three fourths of the models represent a time period lasting from 1 to 5 years, with 44% (192 models) corresponding to 1 year, which is the classical temporal scale of Ecopath models. The longest time period represented by a model is 40 years. The spatial extent covered by the models varies widely, from 0.005 km^2 to 34,640,000 km^2. However, model area does not exceed 1,000,000 km^2 for most models, and about half of the models cover an area ranging from 10,000 to 1,000,000 km^2. About 90% of models use wet weight as a unit (of which 88% express it in t/km^2), 5% carbon weight, and 4% dry weight. Only 4 models used calories (or joules) as a unit, and 1 used nitrogen (see chapter 13). Almost all models use year as a time unit, and only 10 models used day, month, or season.

The best-represented ecosystem types are continental shelves (32% of the models), bays and fjords (14%), open oceans (13%), and freshwater lakes (8%); 49% of the models are located in the tropics, 44% in temperate areas, and only 7% in high latitudes (see figure 9.2). EwE models have been developed to study aquatic ecosystem worldwide, with some regions better covered than others. Overall, the northern and central Atlantic Ocean are the regions with the highest proportion of EwE models. All FAO areas (figure 2.1) have at least one model, but five areas have about 40 models each: the northeast Atlantic and the eastern central Atlantic comprise 10% of the models each, and the western central Atlantic, the northwest Atlantic, and the Mediterranean and Black Sea comprise 9% of the models each. The Humboldt Current, the Gulf of Alaska, the Mediterranean, and the Guinea Current are the Large Marine Ecosystems (LMEs; see www.seaaroundus.org/data/#/lme/) with the highest number of models (at least 5% each). Three LMEs have no EwE model representing them: the Osyashio Current, the East Siberian Sea, and the Laptev Sea. Overall, few EwE models have been developed for the Indian Ocean and for Antarctic waters.

Recently developed models tend to be less aggregated and thus more complex, although highly aggregated models are still being published. In the first decade of the development of the EwE modeling approach, the total number of groups defined in the models ranged from seven to twenty-seven. Over time, the number of groups has expanded, up to sixty-seven groups in the past decade (excluding the few outlier models). The median is about fifteen groups between 1984 and 1993, and it is about thirty groups between 2004 and 2014. In contrast, the time period represented by the models tends to decrease over time; thus the median number of years represented by the models ranged from 3 years in 1984–1993 to 1 year in 2004–2014. The areas covered by the models have expanded toward very large areas, and the median area has shifted accordingly, from about 1,000 km^2 in 1984–1993 to about 100,000 km^2 in 1994–2014.

Fish Biomass in the World Ocean: A Century of Decline

Using 200 EwE models, each providing a snapshot of how much life there was in the ocean at given points in time and space, Christensen et al. (2014) evaluated trends in biomass of fish separately for higher-trophic-level predatory fish ("table fish") and for the lower-trophic-level prey fish. Their results suggest that the biomass of predatory fish has declined strongly (and significantly) over the last hundred years. For the 200 models, covering the period from 1880 to 2010, they evaluated how the conditions at each point relate to environmental parameters and other variables, and they obtained the multiple regression in table 9.1. The multiple coefficient of determination (R^2) they obtained is 0.70, indicating that the model they derived explains 70% of the variation in the dataset. The predictor variables are all highly significant apart from the factorial

Table 9.1. Parameter coefficients and associated test statistics for multiple linear regressions to predict the global marine biomass of predatory fishes. R^2 is 0.70; the *t* values are the ratios of an estimate and its standard error, and *p* (>|*t*|) indicates the probability of obtaining a larger *t* value; all but *p* values are significant ($\alpha = 0.001$).

Variable	Estimate	*t* value	*p* (>|*t*|)	Significant
Intercept	24.2500	54.8	<0.001	Yes
Year	−0.0151	−69.7	<0.001	Yes
log(distance)	−0.1008	−28.0	<0.001	Yes
log(prim. prod.)	1.1040	142.8	<0.001	Yes
Temperature	−0.0608	−69.6	<0.001	Yes
Upwelling index	0.0002	42.4	<0.001	Yes
FAO 18	0.0978	2.0	0.041	No
FAO 21	0.6361	19.9	<0.001	Yes
FAO 27	0.7966	28.4	<0.001	Yes
FAO 31	0.0605	1.7	0.091	No
FAO 34	−0.1952	−6.0	<0.001	Yes
FAO 37	−0.4279	−8.4	<0.001	Yes
FAO 41	1.0460	31.0	<0.001	Yes
FAO 47	0.6778	18.2	<0.001	Yes
FAO 48	1.1660	32.8	<0.001	Yes
FAO 57	1.1920	26.1	<0.001	Yes
FAO 61	1.1250	35.6	<0.001	Yes
FAO 67	1.5880	51.4	<0.001	Yes
FAO 71	1.2270	36.1	<0.001	Yes
FAO 77	0.4832	14.9	<0.001	Yes
FAO 87	0.3341	9.7	<0.001	Yes

variable for FAO areas 18 and 31 (representing the Amerasian Arctic and the Caribbean). The signs of the predictor variable coefficients all are as expected, that is, negative for biomass, distance, and temperature and positive for primary production and the upwelling index. The model suggested that we have lost 1.5% of the biomass of higher trophic level fish per year, on average, since the late nineteenth century.

Christensen et al. (2014) examined the relationship between observed and predicted values based on the coefficients in table 9.1 and observed that the multiple regression tends to overestimate abundance at low biomasses and underestimate it at high biomasses. This suggests that the model is conservative, that is, it does not overestimate changes in biomass over time. Such results also suggest that this multiple regression model would benefit from additional variables, such as "rugosity" (i.e., depth variability within spatial cells), substrate types, and fishing effort. However, Christensen et al. (2014) did not have access to global datasets of those variables and therefore had to ignore them for the time being. The implication is not that the present study is likely to be misleading but rather that better predictions will be obtained with additional predictor variables.

Using a resampling method, Christensen et al. (2014) randomly drew 30% of the 68,939 estimates of biomass over space and time, performed a multiple regression with each subsample, and obtained a distribution for each predictor variable. They then used each of the resampled regressions and the database of environmental parameters to predict

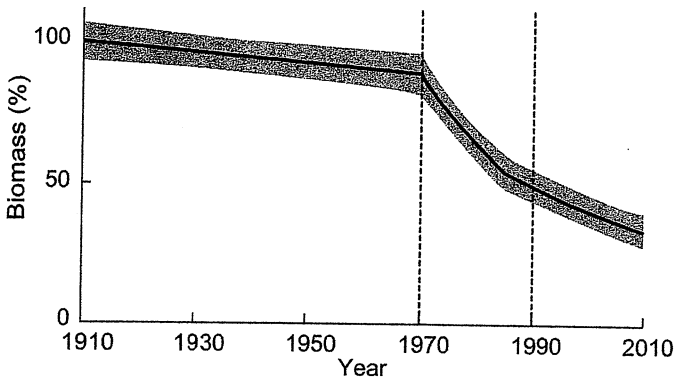

Figure 9.4. Global biomass trends for predatory fish in 1910–2010, as predicted based on 200 ecosystem models and 1,000 times random resampling of 30% of data points. The lines indicate median values and 95% confidence intervals. (Adapted from Christensen et al. 2014.)

global biomasses. Dividing the models into three time periods to increase the temporal resolution, and with the splits made in 1970 and 1990, they obtained multiple linear regressions similar to the regression reported above for the entire time period. Again the predictor variables were highly significant ($p < 10^{-16}$) and the regressions explained 66%–91% of the variability in the biomass data. Evaluating the time trends based on resampling the three regressions 1,000 times based on randomly selecting 30% of the biomass estimates for each case leads to figure 9.4.

Also, Christensen et al. (2014) estimated that the biomass of predatory fishes has declined by two thirds (66.4%, with 95% confidence intervals ranging from 60.2% to 71.2%) over the last hundred years. The decline was estimated to have been slow (10.8%, or 0.2%/year) up to 1970, then severe during 1970–1990 (41.6%, or 4.0%/year), and more slow since 1990 (14.0%, or 2.9%/year). Repeating the multiple linear regression for the entire time period and focusing on predicting the biomass of lower-trophic-level fish ($2.0 \leq TL < 3.0$) led to positive regression coefficients. The coefficient for the variable *year* (0.0085) suggested that the biomass of prey fish had been increasing over time by 0.85%/year. Over a hundred-year time period, this implies that there are now more than twice as many low-trophic-level (prey) fish in the global ocean than there were a century ago, an increase that may be caused by predation release.

CONCLUSION

The global overview of the EwE model applications showed that most models represented marine ecosystems, between 1980 and 2009, over a time period of 1 year and an area ranging from 10,000 to 1,000,000 km². The models generally include between ten and forty functional groups. Most models were built to analyze ecosystem functioning and inform fisheries management, principally in ecosystems located in the northern and central Atlantic Ocean. Half of the models were applied to tropical systems, and more than a third of the models were used to perform time dynamic simulations in Ecosim. Despite its complementarity with Ecopath, the EcoTroph plug-in has been applied to a few models only. However, EcoTroph is still a recent approach, and the development of the plug-in in R (see box 9.2) may allow a wider application.

In the first decade of its development (1984–1993), the EwE modeling approach essentially consisted of Ecopath models representing tropical marine systems, with a simple trophic structure. The initial emphasis on the tropics resulted from the development of EwE initially being centered at the International Center for Living Aquatic Resources Management (ICLARM, now WorldFish), then based in the Philippines, which was focused on developing methods for managing tropical ecosystems. In contrast, in the last two decades (1994–2014) EwE models were applied

to a wider variety of ecosystems, including polar regions, and used to analyze a wider range of research topics, including pollution, aquaculture, and MPAs. The modeling practices have evolved over the past 30 years toward Ecopath models with larger spatial scales (up to 1,000,000 km^2), shorter temporal scales (typically 1 year for Ecopath), and more complex trophic structures (up to seventy functional groups). Although Ecosim has been used in a great proportion of the EwE models (41%), the same is not true for Ecospace (7%), which is surprising considering the insights Ecospace can provide (Pauly 2002).

We believe that the standardized metadata incorporated in EcoBase and used here will be valuable to perform meta-analyses based on EwE models. Indeed, the metadata may be used as selection criteria. By applying a scoring method on these criteria, a list of models of potential interest may be obtained. The pool of selected models may then be reused in EwE-based meta-analyses. Also, the metadata presented here may serve as a template of the necessary information that should be systematically provided when publishing EwE models. Lastly, the global and synthesized overview provided here may help elucidate the usage of and interest in the EwE modeling approach. Some regions and types of ecosystems have been widely analyzed with the EwE modeling approach, and others have remained poorly studied. Notably, modeling effort should be concentrated on the Indian Ocean.

The case study adapted from Christensen et al. (2014) found a major decline in the biomass of predatory fish, that is, of the larger fish that humans tend to eat, amounting to a reduction by two thirds over the last century, thus confirming earlier results of Tremblay-Boyer et al. (2011), obtained by applying the EcoTroph model (see box 9.2) to each of the 180,000 spatial cells also used here. Figure 9.4 shows that 55% of the decline noted by Christensen et al. (2014) occurred in the last 40 years, with the decline being strongest from 1970 to 1990, before it leveled off somewhat. However, this does not mean that conditions have started to improve globally. There may be regional improvements as reported by Worm et al. (2009); however, Christensen et al. (2014) did not see them at the global level.

The material summarized here contributes to the recent discussion on whether "fishing down the food web" is a sampling artifact or something that occurs in reality. Christensen et al. (2014) estimated that the predatory fish have declined by two thirds, whereas the prey fish may have more than doubled. Such doubling is likely to be linked to predation release, that is, the mechanism whereby reduction in predator populations leads to increases in prey abundance, as documented in Myers et al. (2007). Combined, the decrease of high-trophic-level fish and the increase of low-trophic-level fish strongly suggests that fishing down the marine food web occurs at the global scale and that this can be demonstrated through a method that is less dependent on fisheries catch estimates than previous "fishing down" studies, which itself has been central to the debate about "fishing down" (see also www.fishingdown.org).

In conclusion, we believe that open access is becoming mainstream in ecology, and we built the EcoBase repository as a contribution to this trend. This study was a first step toward a global integration of EwE-based metadata, and we hope that more meta-analyses can be facilitated by the availability of EcoBase (ecobase.ecopath.org).

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NOTE

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