Trophic modelling of the Peruvian upwelling ecosystem: Towards reconciliation of multiple datasets ☆

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A B S T R A C T

In the 1980s, personnel from the Instituto del Mar del Peru collaborated with foreign experts to reconstruct time series of (1) catch and biomass of the Peruvian anchovy *Engraulis ringens* back to 1953, along with parallel time series of (2) abundance of anchovy predators and competitors, and (3) abiotic parameters indicative of the dynamics of the Peruvian upwelling system. This contribution documents an attempt to build an ecosystem model of the Peruvian upwelling ecosystem and recreate the observed biomass trends through the period 1953–1984, using the Ecopath with Ecosim (EwE) software. The time series of biomass, particularly of Peruvian anchovy and its various predators, are not reproduced by the EwE model based solely on the original parameters. Instead, to model the anchovy abundance fluctuations caused by El Niño and other oceanographic events, it is necessary to include mechanisms that were not part of the original description of the ecosystem, which focused on mass-balance. For example, a switch between large and small phytoplankton appears to be required to induce the observed abundance shifts between sardine and anchovy. Similarly, a 'mitigating' relationship must be assumed between bonito (*Sarda chilensis*) and seabirds for the 1965 collapse of seabirds to be reproduced by the model. Mechanisms of this sort, here proposed in a very tentative fashion, will have to be firmly established and quantified before a model can successfully explain both the older data series (1953–1984) as done here, and eventually the new series on the Peruvian upwelling system that became available only recently. With a total of now over 50 years of data, this would represent one of the best documented marine ecosystems in the world, matching its status as one of the most productive.

1. Introduction

In the 1980s, personnel of the Instituto del Mar del Peru (IMARPE) collaborated with foreign experts to construct long (30+ years) monthly time series of catch and biomass of the Peruvian anchovy *Engraulis ringens*, along with time series of abundance of anchovy predators and competitors, and abiotic parameters indicative of the dynamics of the Peruvian upwelling system. These time series, which spanned the years 1953 to the mid-1980s, were documented in two 'data-rich' edited volumes (Pauly, 1993), which presented most of the data upon which the analyses in their chapters were based (see Pauly and Tsukayama, 1987; Pauly et al., 1989). The volume's contributions, while representing the state-of-the-art in fish population dynamics at the time (Cushing, 1988) and leading to a fair description of the Peruvian anchovy

population responses to environmental variability, did not allow for any measure of predictability.

Simultaneous efforts at constructing an 'anchovy-centred' model of the Peruvian ecosystem based on coupled differential equations (Jarre et al., 1991; Jarre-Teichmann, 1992) failed. Instead, modelling emphasis shifted to trophic mass-balance (Ecopath) models, for which predecessors existed, notably the model of Walsh (1981). These models could be parameterized for using the data in the above-cited books and other literature (Jarre et al., 1991; Jarre-Teichmann and Pauly, 1993). They provided snapshots of the ecosystem and were useful in that they quantified the food web and documented the main energy pathways leading to anchovy production; but again, they did not allow for predictions.

This contribution has two goals. The first one is to build on previous modelling efforts with the extensive data gathered over 30 years to verify how they could be used directly to reconstruct the observed changes in biomass, and make these results usable by the scientific community. This has now become possible thanks to the Ecopath with Ecosim (EwE) software, which can fit the model to reference time series data (Christensen and Walters, 2005). The second goal is to revisit the original time series (1953–1984)

in an attempt to provide a different perspective by going back in time and identify critical processes with today's perspective. In doing so, we intend to explore various mechanisms that may be involved and suggest avenues for future research. It is the use of time series to fit a model and the inclusion of mechanisms of interactions that will allow us to move towards evaluating hypotheses about what caused the variations in anchovy biomass. In addition, the use of a long time series provide a better basis to evaluate current events with a larger breadth of experience, going back earlier in time, and thus avoid shifting baselines (Pauly, 1995). We then discuss how to construct a dynamic model potentially capable of making useful predictions for fisheries management.

2. Methods

This model of the Peruvian ecosystem encompasses the coast of Peru between latitudes 4 and 14°S, to 40 nm offshore on average (Jarre et al., 1991) for a total area of 82,000 km^2, and corresponding to the main distribution area of the North-Central stock of Peruvian anchovy. During the period considered here, 1953–1984, anchovy population and catch fluctuated enormously. Major episodes were: (1) onset of the anchovy fisheries in the early 1950s, (2) the increase of anchovy biomass in the late 1950s and 1960s, (3) collapse of the fishery in the early 1970s, and (4) a period of low anchovy catch and biomass. Other species fluctuated similarly, though for several groups (e.g., sea birds and bonito), this was a one-way trip, with high biomasses in the early 1950s coinciding with the onset of the 1973 El Niño, and low biomasses in the 1980s (Muck, 1989b), from which they never recovered.

2.1. The model

Mass-balanced trophic models assign the main species within an ecosystem to functional groups (single species or of a group of ecologically similar species), and account for their (1) biomass (in metric tonnes per square km, t · km^{-2}) (2) diet (percentage in biomass or volumes), (3) prey consumption per year, per unit of biomass (4) natural and fishing mortality per year, (5) rate accumulation of biomass per year, and (6) net migration. The principle behind this ecosystem modelling approach is that energy is conserved and must be accounted for on a yearly basis (see Walters et al., 1997). Ecosim is a tool for dynamic simulations based on an Ecopath model, whose static representation provides some of the initial-state Ecosim parameters (Walters et al., 1997; Pauly et al., 2000). Ecosim uses a system of differential equations to describe the changes in biomass and flow of biomass within the system over time, by accounting for changes in predation, consumption and fishing rates (Walters et al., 1997; Christensen et al., 2005). Thus, the rate of change of biomass of group i (B_i) is described by

$$\frac{dB_i}{dt} = g_i \sum_j Q_{ji} - \sum_j Q_{ij} + I_i - (m_i + F_i + e_i)B_i \tag{1}$$

where g_i is the net growth efficiency (year^{-1}); Q_{ji} and Q_{ij} are the consumption rate (year^{-1}) of group j by group i and the consumption of group i by group j, respectively (year^{-1}); I_i is the immigration flow in t · km^{-2}; m_i is non-predation mortality (year^{-1}); F_i is fishing mortality (year^{-1}); and e_i is emigration rate (year^{-1}) (Christensen and Walters, 2004).

Ecopath with Ecosim (EwE) allows the fitting of the model to time series of abundance and catch, and thus allow to evaluate how well the model replicates observed behaviour through time. The time series are used to tune the model. EwE models are generally not 'validated' in the classical sense of using one dataset to tune the model, and using another set of independent data for the validation process. This is not an inherent model problem,

but rather a systematic lack of data for most ecosystems. Ecosim is able to incorporate multiple stanzas (ontogenic stages) representing different life history stages of species of special interest (anchovies and sardines in these models). The stanzas of a species are linked and their respective production per unit of biomass (P/B year^{-1}), consumption per unit of biomass (Q/B year^{-1}), and growth calculated from a baseline estimate for a reference group (the adults in our case). Growth for each stanza is calculated from von Bertalanffy growth curves, and a stable survivorship through ages within stanzas is assumed, while natural and fishing mortality is allowed to vary between stanzas (Christensen et al., 2005).

The functional predator–prey relationship is based on the foraging arena theory, which divides the biomass of all prey into vulnerable and invulnerable pools (Walters and Kitchell, 2001). The transfer rate between these two pools (here called 'vulnerability') can range from one to infinity with higher rates implying that the behaviour of both the prey and the predator have less effects on limiting predation rates. A large vulnerability value also means that the predator initial biomass is low compared to its carrying capacity, and that a change in predator biomass will cause a corresponding change in the mortality rate of its prey. The system will thus be more stable when a predator is close to its carrying capacity, and more variable when it is far from it.

Vulnerability values can be specified for each predator–prey pair. Due to uncertainty about how this parameter might change between prey species and to reduce the number of parameters that needs to be estimated, we chose to assume that the vulnerability setting is the same for all species of prey consumed by a given predator. This functional predator–prey response equation predicts changes in diet composition due to changes in relative availability of prey and alternative prey, but it does not allow switching of the diet to new prey that were not consumed initially. Switching between prey items included in the diet can be accommodated.

In addition to the direct trophic relationships mentioned above, it is possible in Ecosim to account for indirect, non-trophic relationships, called 'mediation', that result from a third species modifying the trophic relationship between two other species. The relationships can be negative when increase in biomass of the third species results in a prey becoming less accessible to the predator (i.e., decrease of the vulnerability of the prey to the predator). Conversely, it can be positive, when an increase in the third species abundance increases the vulnerability of the prey to its predator. In the present paper, we explored the hypothesis that bonito feeding activities, which will tend to drive small pelagic fishes to the surface, will tend to make them more vulnerable to seabird predation, similar to the situation described by Au et al. (1999). Other studies have shown that tuna species drive sardines and other schooling fish to surface waters making them available to boobies (Anderson and Ricklefs, 1987).

Environmental influence on the productivity of the ecosystem was also included in the model to improve the fit to time series. The influence of environmental factors is generally included in the model by using a climate index to directly influence the production of primary producers. We assume that the large quantities of nutrients lifted into the euphotic zone by strong upwelling results in the production of larger phytoplankton cells such as diatoms (Iriarte and González, 2004), which in turn favours the production of large zooplankton (calanoids and euphausids) (Alheit and Niquen, 2004). Thus, indices of oceanic changes were included in the model and modified the productivity of diatoms and benthic macrophytes. We added mediation between diatoms and dinoflagellates so that large populations of diatoms would use the nutrients that would otherwise go to small phytoplankton. We used this mediation as a simple proxy for more complex dynamics in which dinoflagellates are favoured over diatoms in less turbulent and warmer temperatures (van der Lingen et al., 2006).

2.2. Data

We structured our model based on the 1950 model presented by Jarre et al. (1991), which was composed of 16 functional groups of organisms including anchovy (*E. ringens*) and sardines (*Sardinops sargax*) and their piscine predators bonito (*Sarda chiliensis*), mackerel (*Scomber japonicus*), horse mackerel (*Trachurus murphyi*), and hake (*Merluccius gayi*), and other consumers, the guano birds, and pinnipeds (Table 1). Guano birds included the cormorant (*Phalacrocorax bougainvillii*), booby (*Sula variegata*), and pelican (*Pelecanus thagus*); the pinnipeds species are the fur seals (*Arctocephalus australis*) and sea lions (*Otaria byronia*). We completed the structure with additional groups: demersal fish (three groups instead of one), other pelagic fish (small and large instead of one group), and invertebrates to include all of the reported catches (Table 1). To this basic structure, we added larval stanzas for sardine and anchovy, and included predation by adult sardine and anchovy on each other's larvae.

Moreover, it soon became obvious that more details in plankton groups needed to be included to account for the respective feeding preferences of sardines and anchovies, as in Jarre-Teichmann (1992). Phytoplankton was divided in two groups, dinoflagellates and diatoms, to account for the fact that sardines are efficient feeders on smaller organisms (which includes cyclopoid copepods) while anchovy prefer calanoids, euphausids and chain-forming diatoms (Jarre-Teichmann, 1992; van der Lingen, 1994). Time series data for zooplankton biomass (Carraso and Lozano, 1989) was assigned to large zooplankton as the sampling has been carried out with a 300 μm plankton net.

Estimates of P/B and Q/B were taken from Jarre-Teichmann (1992) for most species. As a starting point, groups not described in her model, (e.g., demersals and 'other pelagic fishes') were attributed estimates based on values generally used for the species in question (Table 1). Diet data were based mainly on Jarre-Teichmann (1992) and completed with information from the literature (Table 2). The fractional diet of anchovy, originally assumed to be

composed mainly of diatoms (Jarre-Teichmann, 1992, see her Table 2), was compared with a revised estimate suggested by the reanalysis of Espinoza and Bertrand, 2008, and set at 0.39 diatoms, 0.60 for large zooplankton and 0.01 to other items. This forced a change of the biomass of large zooplankton, which had to be increased to $50 \text{ t} \cdot \text{km}^2$ to re-establish mass-balance.

The biomass time series for anchovy (1953–1984), obtained from virtual population analysis, were taken from Pauly et al. (1989). The biomass time series used here for the other species are documented in Muck (1989b). Fishing mortality series were calculated as the ratio catch/biomass. Catches, mainly based on data supplied by Peru to FAO, were obtained from the *Sea Around Us Project* database (Watson et al., 2004, see http://www.seaaroundus.ca), assuming that catches from the study area accounted for 80% of the total catch of Peru as the study area represents about 80% of the total coastline. In absence of biomass data for added demersal and pelagic groups, we derived the biomass estimates from the catch data using a stock reduction analysis (Kimura, 1985). Catches, assumed to be known quantities, are subtracted from the simulated stock size for each time step. This approach is very sensitive to the estimate of initial biomass (or production/biomass ratio – P/B); if it is too low, there will not be enough production ($B*P/B$) estimated over time and this will cause the population to crash. In the fitting, this is seen as an indication that the initial biomass (or P/B) is too low and should be increased.

The biomass time series of bonito and anchovy were rescaled to avoid values of the ratio catch/biomass higher than 1 year^{-1} in the 1970s. In addition, to balance the model, the 1953 anchovy biomass was increased to $75 \text{ t} \cdot \text{km}^{-2}$ from an initial value of $68 \text{ t} \cdot \text{km}^{-2}$ to increase the available production ($B*P/B$) to meet the demands and notably those of the predators.

Time series of biomass and catch were used to fit the model for the period 1950–1984. The model was driven with fishing mortality and fitted by varying the vulnerability settings such as to obtain predicted biomass and catch trajectories similar to those observed for the various fish groups, sea birds and pinnipeds. The model was

Table 1
Parameters of the balanced model and vulnerabilities (Vuln.) used as the basic scenario (#1).

	Group name	Trophic level	Biomass (t · km^{-2})	P/B (year^{-1})	Q/B (year^{-1})	EE	P/Q	Vuln.
1	Pinnipeds	**3.39**	0.0044	0.09	28.0	**0.890**	**0.00**	4.82
2	Birds	**3.40**	0.56	0.04	62.0	0.000	**0.00**	2.00
3	Sharks	**3.91**	**0.58**	0.20	**1.0**	0.100	0.20	1.50
4	Rays	**3.77**	**0.42**	0.50	**2.5**	0.050	0.20	3.16
5	Bonito	**3.47**	7.87	0.20	**1.0**	**0.266**	0.20	3.00
6	Mackerel	**3.18**	2.80	0.85	10.0	**0.112**	0.09	1.00
7	Horse mackerel	**3.30**	12.68	0.85	10.0	**0.038**	0.09	1.00
8	Anchovy larvae	**2.00**	0.23	7.00	102.0	**0.015**	0.07	2.00
9	Anchovy	**2.22**	75.00	1.80	15.0	**0.958**	0.12	1.00
10	Sardine larvae	**3.00**	0.04	7.00	98.0	**0.390**	0.07	1.19
11	Sardine	**2.98**	20.00	1.80	12.0	**0.486**	0.15	1.00
12	Pelagic S	**3.08**	**8.36**	1.80	**7.2**	0.900	0.25	1.00
13	Pelagic L	**3.61**	**2.25**	0.10	**0.5**	0.100	0.20	1.78
14	Hake	**3.33**	3.28	0.30	**1.5**	**0.110**	0.20	1.00
15	Demersal L	**3.80**	**0.89**	0.20	**1.0**	0.100	0.20	2.00
16	Demersal M	**3.32**	**3.08**	0.50	**2.5**	0.300	0.20	1.17
17	Demersal S	**3.20**	**5.23**	0.90	**4.5**	0.900	0.20	4.82
18	Cephalopods	**3.38**	**0.69**	2.00	10.0	0.700	**0.20**	1.12
19	Shrimps	**2.79**	**1.99**	2.50	**16.7**	0.900	0.15	1.57
20	Lobster crab	**2.81**	**1.99**	2.00	**13.3**	0.900	0.15	1.01
21	Macrobenthos	**2.41**	**38.29**	3.00	**12.0**	0.500	0.25	1.04
22	Meiobenthos	**2.06**	8.00	9.00	**45.0**	0.507	0.20	1.74
23	Lg zoopl	**2.10**	16.00	20.00	**100.0**	0.824	0.20	1.08
24	Sm. zoopl	**2.00**	25.00	40.00	**200.0**	0.633	0.20	10.00
25	Dinoflagellates	**1.00**	71.00	70.00	–	**0.879**	–	–
26	Diatoms	**1.00**	55.00	70.00	–	**0.797**	–	–
27	Macroalgae	**1.00**	19.72	12.50	–	**0.613**	–	–
28	Detritus	**1.00**	900.00	–	–	**0.147**	–	–

Parameters **in bold** were estimated by Ecopath; the vulnerabilities were estimated in Ecosim.

Table 2
Diet composition used in the balanced model as it was in scenario 1, and the sources of information for each functional group.

	Prey/predator	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
	Source	1	1	2	2	1	3	3	4	5	4	6	2	2	1	2	2	2	4	4	4	4	1	1	4
1	Pinnipeds	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
2	Birds	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
3	Sharks	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
4	Rays	–	–	0.012	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
5	Bonito	–	–	0.012	–	–	–	–	–	–	–	–	–	0.020	–	0.002	–	–	–	–	–	–	–	–	–
6	Mackerel	–	–	0.012	–	0.02	–	–	–	–	–	–	–	0.020	0.010	0.003	–	–	–	–	–	–	–	–	–
7	Horse mackerel	–	–	0.005	–	0.02	–	–	–	–	–	–	–	0.040	0.040	0.003	–	–	–	–	–	–	–	–	–
8	Anchovy larvae	–	–	–	–	–	–	–	–	–	–	0.0001	–	–	–	–	–	–	–	–	–	–	–	–	–
9	Anchovy	0.80	0.88	0.033	–	0.70	0.60	0.65	–	–	–	–	–	0.050	0.550	0.161	0.002	–	–	–	–	–	–	–	–
10	Sardine larvae	–	–	–	–	–	–	–	–	0.0001	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
11	Sardine	0.12	0.05	0.036	–	0.18	0.09	0.10	–	–	–	–	–	0.020	0.050	0.014	0.002	–	0.01	–	–	–	–	–	–
12	Pelagic small	0.02	0.18	0.071	–	0.08	–	–	–	–	–	–	–	0.090	0.010	0.054	0.052	0.02	0.05	–	–	–	–	–	–
13	Pelagic large	–	–	0.012	–	–	–	–	–	–	–	–	–	–	–	0.008	–	–	–	–	–	–	–	–	–
14	Hake	0.01	–	0.012	–	–	–	–	–	–	–	–	–	–	0.020	0.002	–	–	–	–	–	–	–	–	–
15	Demersal large	–	–	0.012	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
16	Demersal medium	0.02	–	0.036	–	–	–	–	–	–	–	–	–	–	0.002	0.080	–	–	–	–	–	–	–	–	–
17	Demersal small	0.03	0.05	0.102	0.167	–	–	–	–	–	–	–	–	–	0.008	0.139	0.134	0.03	0.05	–	–	–	–	–	–
18	Cephalopods	–	–	0.012	0.056	–	–	–	–	–	–	–	–	0.060	–	0.100	0.007	–	–	–	–	–	–	–	–
19	Shrimps	–	–	0.340	0.222	–	–	–	–	–	–	–	–	0.230	–	0.133	0.100	0.10	0.10	–	–	–	–	–	–
20	Lobster crab	–	–	0.238	0.222	–	–	–	–	–	–	–	–	–	–	0.170	0.046	0.10	0.05	–	–	–	–	–	–
21	Macrobenthos	–	–	0.060	0.333	–	–	–	–	–	–	–	0.200	0.233	0.030	0.103	0.160	0.30	0.34	0.05	0.5	–	–	–	–
22	Meiobenthos	–	–	–	–	–	–	–	–	–	–	–	–	0.233	–	0.042	0.180	0.20	–	0.40	0.1	–	0.01	–	–
23	Large zooplankton	–	–	–	–	–	–	0.14	–	0.192	–	–	0.466	–	0.280	–	0.100	–	–	–	–	–	–	–	–
24	Small zooplankton	–	–	–	–	–	0.25	0.11	–	–	1	0.97	0.285	–	–	0.002	0.120	0.10	0.40	0.30	–	0.35	0.10	0.1	–
25	Dinoflagellates	–	–	–	–	–	–	–	–	–	–	0.02	–	–	–	–	–	–	–	–	–	0.10	0.10	0.2	0.8
26	Diatoms	–	–	–	–	–	0.05	–	1	0.800	–	–	–	–	–	–	0.060	0.05	–	–	–	0.10	–	0.7	0.2
27	Macroalgae	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.023	–	–	–	–	0.25	0.10	–	–
28	Detritus	–	–	–	–	–	–	–	–	0.070	–	0.02	0.050	–	–	0.004	0.055	0.10	–	0.25	0.4	0.25	0.79	–	–
29	Import	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–

1. Jarre-Teichmann (1992); 2. Adapted from Fishbase; 3. Modified from Jarre-Teichmann (1992) to balance the model; 4. Assumed; 5. From Jarre-Teichmann (1992) and Rojas de Mendiola (1989); 6. From Jarre-Teichmann (1992) and Konchina (1992).

first fitted manually to identify where possible solutions were most likely. Formal fitting to the time series was then performed using a non-linear search procedure, allowing vulnerabilities to be modified. We used the knowledge gained in the manual fitting to start the search procedure with different initial parameters to avoid being caught in local optimal solutions. The criterion was a weighted sum of squares of deviations (SS) between the logarithms of observed and predicted biomasses and catches.

3. Results

Given the well known link between El Niño events and anchovy biomass, it was no surprise that fitting the model to time series based on vulnerabilities alone did not lead to good fit to the biomass and catch series of anchovies and sardines (Fig. 1, Basic fit). The only two functional groups that were reasonably well fitted were bonito and pinnipeds. The decrease in bonito seems mainly linked to fishing, although predicted catches were slightly lower than observed. Pinnipeds have been dramatically overexploited since before 1950, their abundance has increased steadily during the study period. All models and fitting strategies suggested that given their initial biomass and production, their abundance had to increase during the study period. The total sum of squares (SS) for this scenario was 206. In the following scenarios, we will monitor the trends in biomass and landings of the species of interest, anchovies, sardines, bonito and seabirds.

Several productivity indicators were successively added in the model, including sea surface temperature, surface NO_3 concentration and flux, upwelling and turbulence (Pauly and Tsukayama, 1987; Pauly et al., 1989) (Table 3), but the index of turbulence off the coast near Trujillo (Mendo et al., 1987) was retained as providing the best fit to the anchovy abundance time series. The turbulence index is calculated as the cube of wind velocity (Mendo et al., 1987). With turbulence index in the model, catches and biomasses of anchovies increased slightly, but they did not reach the peaks observed in the 1960s for anchovies and in the 1980s for sardines (Fig. 1, scenario 1; SS = 188). Note that birds were not influenced directly by the turbulence index.

We tried to recreate the observed decrease in birds using the mediation between bonito and birds which increased the vulnerability of anchovy to guano birds in the presence of bonito (Fig. 2). Considering this mechanism became necessary to model a situation where seabirds were experiencing lower abundance as a consequence of their 'competitors', large pelagics, being fished down (see Methods section). Without this mediation effect, the model behaves so that less large pelagics means more small pelagics and hence more food for the seabirds, which then results in higher seabird abundance. In the present model, the mediation caused the bird and bonito biomass' to decrease in parallel (Fig. 1, scenario 2, SS = 171). Ecosim predicted a decline in guano birds but it did not match observations in steepness and in timing. The reduction of bird predation on anchovy, although small compared to that inflicted by other predators, still allowed anchovy biomass to increase slightly at the end of the study period.

We tried to replicate the observed anchovy and sardine biomass trends by using the mediation and modifying the vulnerabilities. Vulnerabililities are related to the carrying capacity for a given consumer and express the factor by which the predation mortality for a given predator–prey combination can increase if there were many more predators. Low vulnerabilities means that the predator is close to carrying capacity, which results in strong density-dependence for this predator. Vulnerabilities are not completely unknown. For example, we expect a stock that has been fished down to have a high vulnerability, i.e. to be able to increase substantially the predation mortality on its prey. The manipulation of vulnerability values aim at further tuning the model and to make the functional groups respond appropriately. We used the mediation between diatoms and dinoflagellates as a proxy for their presumed competition for nutrients and light. The sigmoid relationship used resulted in less access to nutrients for dinoflagellates when diatom abundance increased, and vice-versa (Fig. 2). By itself, the mediation did not influence the biomass trends for these groups, but this changed when the vulnerabilities were adjusted. First, when the vulnerability for anchovy larvae was decreased from 2 to 1.5 (toward bottom-up control) and the vulnerability for adult anchovy was increased from 1 to 2, an increase in
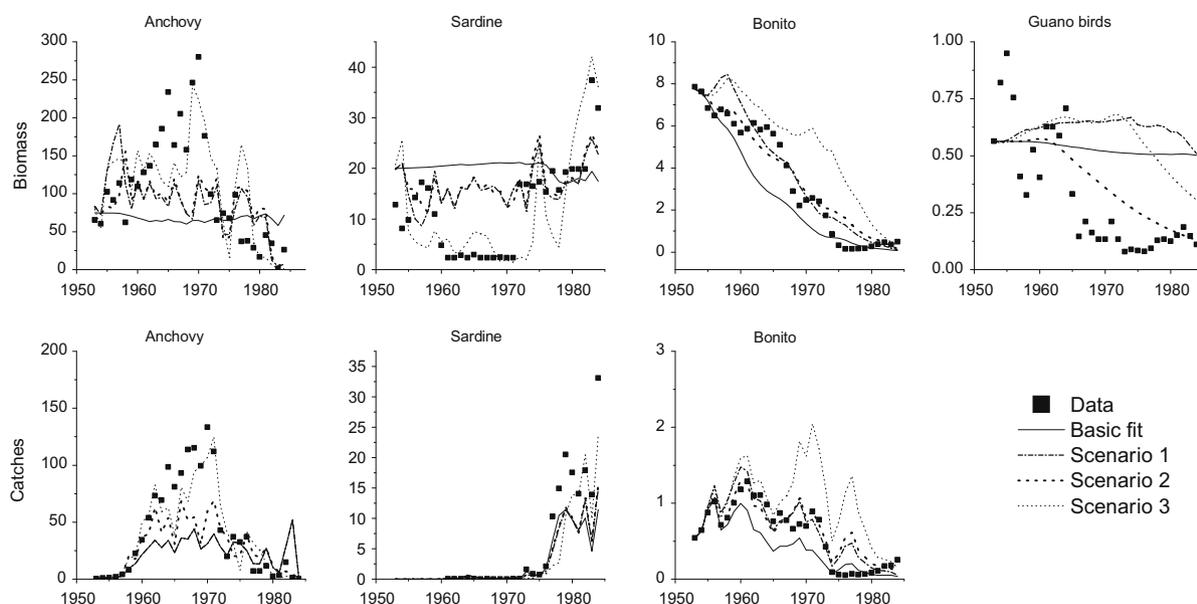
Fig. 1. Comparison of the biomass (t · km^{-2}) and catch (t · km^{-2} · year^{-1}) time series data (squares) and Ecosim predictions (lines) for four species of the Peruvian upwelling. Thin lines show the result of the basic fit changing vulnerabilities only. Dash-dot lines show the effect of including the turbulence index in the model (scenario 1). Dashed lines show the impact of adding a mediation between bonito and guano birds (scenario 2). Dotted lines show the results of adding a mediation between diatoms and dinoflagellates and modifying some vulnerability values (scenario 3; see text). There were no catches of seabirds included in the model.

Table 3
List and brief description of environmental indices used in the model. The best results were obtained using the turbulence index at Trujillo.

Index name	Unit	Description	Source
Turbulence index at Trujillo	$m^3 \cdot s^{-3}$	Cube of wind velocity	Mendo et al., (1987), Table 4
Alongshore windstress component on the sea surface index	$m^3 \cdot s^{-1} \cdot m^{-1}$ coast	Function of the northward and eastward wind and of the angle of these components from true north	Bakun and Mendelssohn, (1989), Table 1
Upwelling index at Trujillo	$m^3 \cdot s^{-1} \cdot m^{-1}$ coast	Function of Ekman's transport and the difference between the angle of the coast and that of the wind direction	Mendo et al., (1987), Table 1
Upwelling index at Callao	$m^3 \cdot s^{-1} \cdot m^{-1}$ coast	Function of Ekman's transport and the difference between the angle of the coast and that of the wind direction	Mendo et al., (1987), Table 3
Southern Oscillation Index	mbars	Mean pressure difference between Easter Island and Darwin, Australia	Brainard and McLain, (1987), Table 1
Rossby Radius	km	Measure the width of the upwelling zone based on SST and the depth of the 14 °C isotherm	Mendo et al., (1989), Fig. 2
NO_3 concentration in the thermocline	$nM \cdot m^{-3}$	Relies on correlation of the depth of the 14 °C isotherm and nitrates concentration at 60 m depth	Chavez et al., 1989
NO_3 concentration inshore ($\Leftarrow 60$ km)	$nM \cdot m^{-3}$	Predicted by using a model that includes a relation between depth and nitrate concentration, wind speed and its effect on the water masses moved, and the size of the Rossby radius	Mendo et al., (1989), Fig. 3
Coastal NO_3 flux per unit area	$mmol \cdot m^{-2} \cdot day^{-1}$	Based on Trujillo upwelling index, using constant upwelling depth model. Closely correlated to the predicted new primary production	Mendo et al., (1989), Fig. 5
Oceanic NO_3 flux per unit area	$mmol \cdot m^{-2} \cdot day^{-1}$	Based on Bakun's upwelling index (Bakun and Mendelssohn, 1989)	Mendo et al., (1989), Fig. 4
Coastal NO_3 flux per unit area	$mmol \cdot m^{-2} \cdot day^{-1}$	Based on Trujillo upwelling index, using variable upwelling depth model	Mendo et al., (1989), Fig. 4
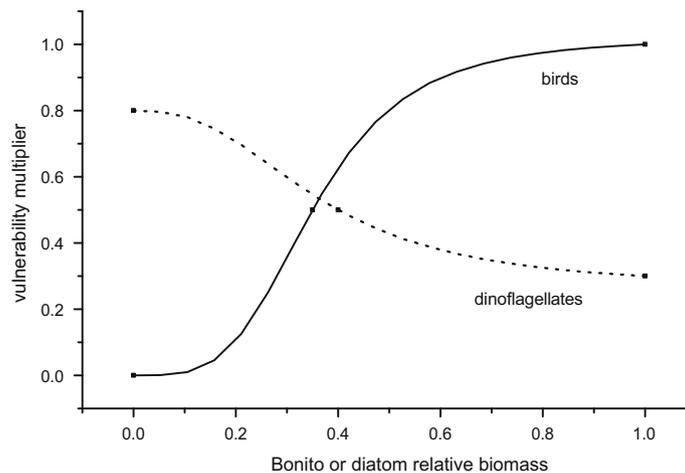
Fig. 2. Shape of the mediation functions used in the model. The solid line shows that, as bonito biomass increases, the vulnerability of prey to birds augments. The dashed line shows that as diatoms' biomass increases, dinoflagellates' access to nutrients decreases.

predicted anchovy biomass and catches occurred, but still not to the levels observed in 1983–1984. Thus, vulnerability was increased to 3 for adult sardine, which resulted in an increase in sardine biomass and a closer fit of predicted and observed anchovy biomass (Fig. 1, scenario 3; SS = 228). The increased sum of squares is due to the decreased fit for birds and bonito biomass.

Anchovies represent 70% of bonito consumption; thus anchovy biomass can be determinant for the trend in bonito biomass. Also, in absence of real time series of sardine and anchovy larvae biomass, the values of vulnerabilities are only dependent on their link with the population dynamics of the adult. Hence, we experimented with several values of vulnerabilities, aiming at obtaining better fits for bonito, sardine and anchovy. We increased the vulnerability of sardine larvae to anchovy (from 2 to 3) and that of anchovy to bonito (from 3 to 4). The resulting trends in biomass and landings came closer to the observed values, with the exception of the bonito which was still overestimated (Fig. 2, scenario 4; SS = 191). Increasing vulnerability of anchovy to bonito again to a value of 10 allowed for a better fit of bonito abundance, but flattened the trend in anchovy biomass (Fig. 3, scenario 5; SS = 171).

Recent results indicate that anchovy feed mainly on large zooplankton rather than diatoms (notably euphausiids, see Espinoza

and Bertrand, 2008), and we next attempted to model this. To balance the model with this new diet, the biomass of large zooplankton, and to a lesser extent, diatoms, had to be increased, while the Q/B for mackerel and horse mackerel were decreased to reduce their intake of zooplankton. It was possible to fit the model to the observed anchovy abundance trends and still obtain the abundance shift from anchovy to sardine starting in the mid-1970s. Under this scenario, however, the anchovy biomass did not reach the levels observed in the late 1960s (Fig. 3, scenario 6; SS = 189).

Of all the scenarios, the best fit was obtained with scenario 4, using a moderate vulnerability of anchovy to bonito, and by increasing the vulnerability of sardine larvae to anchovy. We preferred this solution to that of scenario 5, because it gives more weight to the anchovy time series than to the bonito, which is considered less reliable. The predicted biomass and catch of anchovy and sardine are well predicted by the model (Fig. 4). Predicted catch and biomass of bonito were both overestimated. Observed and predicted biomasses for mackerel and horse mackerel showed little contrast during the study period and although their catches were well predicted by Ecosim, their biomasses were not. The model did not predict the increase in hake biomass that occurred during the 1970s, and thus did not predict the observed peak in
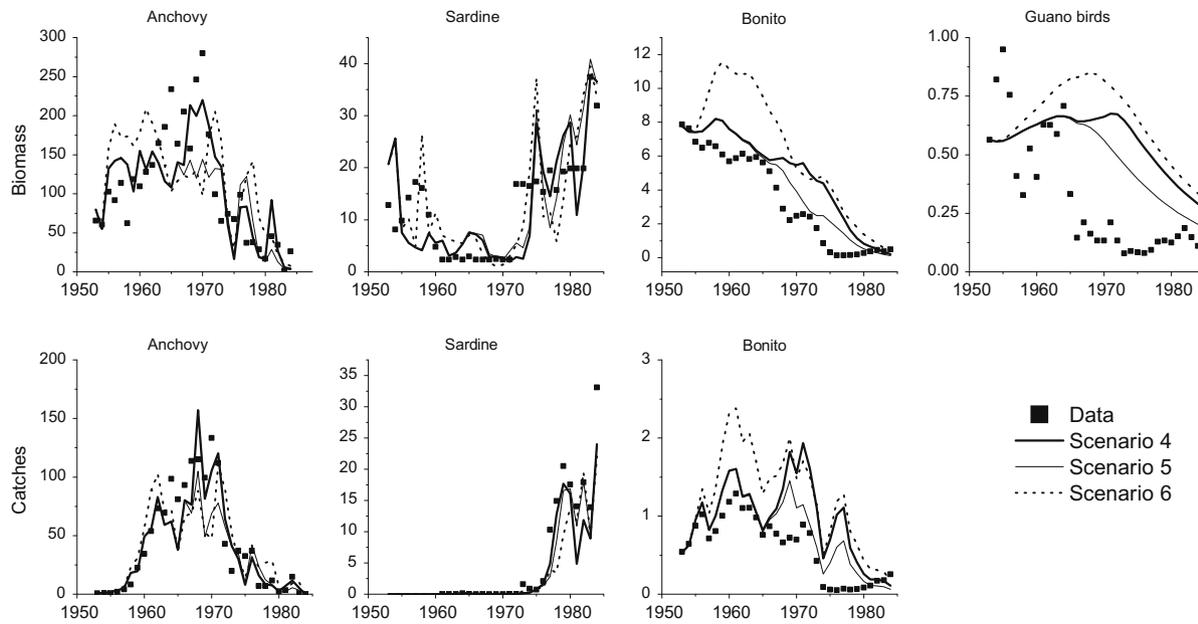
Fig. 3. Comparison of the biomass ($t \cdot km^{-2}$) and catch ($t \cdot km^{-2} \cdot year^{-1}$) time series data (squares) and Ecosim predictions (lines) for four species of the Peruvian upwelling. The thick solid line is the best fit to anchovies and sardines obtained by slightly increasing the vulnerability of anchovy to bonito (scenario 4). The thin line shows the effect of increasing the vulnerability to bonito to a value of 10 (scenario 5). The dotted line shows the effect of assuming that anchovies feeding mainly on large zooplankton (scenario 6). There were no catches of seabirds included in the model.

catches either. Finally, Ecosim did predict the decline in bird populations under this scenario, but starting only in 1972, while the data show a sharp decline between 1964 and 1966 followed by steady low population abundance afterward (Fig. 4).

4. Discussion

The present modelling exercise led to some insights in the Peruvian upwelling ecosystem. The Jarre et al. (1991) model based on 1950s data, constituted the best-snapshot representation of the ecosystem. Nevertheless, the addition of temporal dynamics forced us to reconsider some of the initial parameters of the Jarre et al. (1991) model. For example, the initial biomass of bonito, which appeared acceptable in the Ecopath model, was too low to support the observed catches between 1953 and 1984. In static models, it is impossible to differentiate between a state of large biomass and low production versus a state of low biomass and high production. This can be done by modelling temporal change (now possible with Ecosim), and comparing with observational records (Christensen et al., 2005). As expected, there are still changes that could be made to the Ecopath model to include more recent information of feeding ecology in upwelling ecosystems. For example, the trophic level of anchovy calculated in the model based on a diet mainly composed of diatoms is lower than now believed realistic (van der Lingen et al., 2006; Espinoza and Bertrand, 2008). When a larger proportion of large zooplankton in adult anchovy diet was added (scenario 6), its trophic level increased from 2.22 to 2.67 in Ecopath; a diet completely composed of zooplankton would elevate it further. Diet varies with season, location and prey availability, and sometimes with the analytic technique used. In the model the proportion of prey in the diet of a predator will change through time, depending on changes in prey biomass and the vulnerability of the prey to this predator, and these changes are more important than the initial settings in determining the behaviour of the model (see Guénette et al., 2006 for a detailed discussion on the subject). Obviously, future modelling should add more recent time series (see Taylor et al., 2008 and Tam et al., 2008) and include updated

diets, and indeed, doing so should improve the exploration of the system trophodynamics.

The climate index used as a proxy for nutrient concentration and phytoplankton productivity, explained a large fraction of the observed variations in anchovy biomass. This was expected due to the strong relationship between the upwelling strength and productivity (Faure and Cury, 1998; Binet, 1988; Chesney and Alonso-Noval, 1988; Lluch-Belda et al., 1991). It is interesting that a turbulence index yielded the best results, rather than an upwelling index. An increase in either can be expected to increase the production of large phytoplankton and zooplankton, which favours anchovies (van der Lingen et al., 2006). This may be fortuitous, since the relationship between both turbulence and upwelling with the reproductive success of anchovy and sardine are thought to be dome-shaped – 'optimal windows' (Cury and Roy, 1989; Roy et al., 1992), not accounted for here. Moreover, reproductive success can be impacted by unfavourable values of one or several of the environmental factors such as turbulence, advection, upwelling intensity, all of which become critical at various times of the year (Guisande et al., 2004). Future versions of the model should include a composite index to more realistically model these oceanographic factors. Alternately, several indices might be applied to different parts of the model. For example, turbulence could modify the level of diatom production, but advection could modify the level of larvae mortality brought by inshore concentration or offshore dispersion.

The assumed negative relationship between diatoms and dinoflagellates helped in fitting the model, but considering this mitigation does not imply that we believe in a direct negative relationship between diatoms and dinoflagellates. Rather, this was a way to introduce a driver for dinoflagellates and favour one phytoplankton type over the other. The addition of a relationship of this type was necessary to model the abundance of sardines, and reflects the idea that sardine and anchovies do not directly compete with each other (Bertrand et al., 2004). Structured this way, the model emphasizes the importance of phytoplankton production and feeding conditions. In addition, instead of including only the relationship between diatoms, large zooplankton and
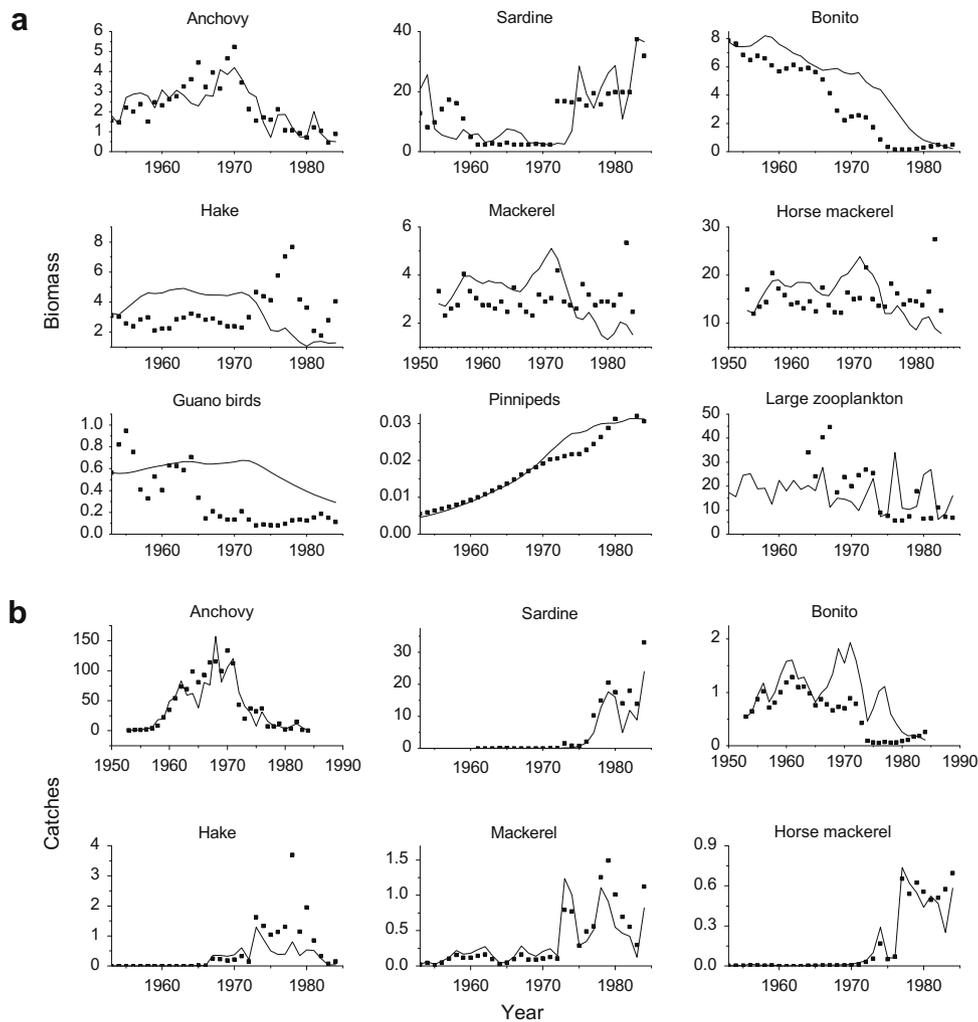
Fig. 4. Comparison of the biomass (t · km^{-2}) and catch (t · km^{-2} · year^{-1}) time series data (squares) and Ecosim predictions (lines), under the best scenario (scenario 4), for all species of the Peruvian upwelling for which we had a time series of biomass.

anchovies, future models should provide mechanisms to link hydrography (calm and warm waters) with nutrients and dinoflagellates, small zooplankton and sardines. This may also involve adding a microbial loop, although such loop is thought to be a minor component of the carbon pathway in upwellings (Moloney et al., 1991).

The division of phytoplankton into two functional groups in the present model is coarse and based, for simplicity's sake, on taxonomic groupings rather than more detailed body size structure (see van der Lingen et al., 2006). Using a model focussed on plankton (and its physiological characteristics) and on carbon and nitrogen flows, Moloney et al. (1991) were able to predict the relative abundance of each size class of phytoplankton in three contrasting systems (oceanic, coastal and upwelling) for 30 days, which emphasizes the importance of size on the rate of nutrients intake and resistance to nitrogen depletion. Such modelling is very useful and described the transfer of energy and nutrients from the upwelling of nutrients to fish (Moloney, 1992) at finer time and space scales. However, the time scale, in such cases, is limited to a few months as opposed to the 30 years considered here.

Part of our model's success is due to the short and direct link between the turbulence index, diatoms, and anchovy on one side, and dinoflagellates, small zooplankton and sardines on the other. However, if anchovy's diet is in fact based more on large zooplankton than diatoms (van der Lingen et al., 2006; Espinoza and Bertrand,

2008), the change in diet can modify the predicted biomass trends. By making such a change in the anchovy diet, scenario 6 was still able to reproduce the main observed trends, but a bit less efficiently. Similarly, the inclusion of a more detailed sized-based zooplankton diet for anchovy and sardine, as suggested in the precedent paragraph (composed of several size-related groups of zooplankton with a small proportion of phytoplankton) (van der Lingen et al., 2006) would likely weaken the link between the turbulence index and fish production unless realistic mechanisms to account for changes in temperature, turbulence and nutrients, and their effects on zooplankton, were added. Ecosim modelling of the Benguela Current, using an anchovy diet based on zooplankton, led to very good results when the vulnerability of zooplankton to anchovy was increased, representing a more top-down dynamics on the plankton (Shannon et al., 2004a). This may be an additional avenue to pursue.

The biomass of horse mackerel and mackerel did not show any major trends. This is mainly because their oceanic distribution only partly overlaps with that of the more coastal anchovy. The distributions of horse mackerel, and mackerel also probably, are related to the amount of prey and dissolved oxygen more than to water temperature (Bertrand et al., 2006), and they are usually found more offshore than anchovies except in El Niño years when they move inshore (Muck and Sanchez, 1987). The model scenarios also did not predict hake biomass correctly, which may be due to its

variable latitudinal distribution, and hence variable presence in the model study area. Hake distribution is also strongly influenced by oxygen availability in subsurface waters (Muck, 1989a), a feature not included in this model as implemented.

The positive influence of tuna on bird feeding on anchovy was based on field work (Au et al., 1999), but no quantitative functional relationship has been described. Using what appeared to be a reasonable relationship (Fig. 3), the model predicted a decline in seabirds; this was not nearly as steep as observed, suggesting that our tuna/bird relationship needs improvement or that additional mechanisms explain the decline in seabirds. For example, changes in thermocline and oxycline depth could have the effect driving small pelagics to the surface as well. However, these factors, when included in the model, could help explain the observed decline in seabirds abundance.

Although we focussed on the pelagic community, demersal groups were included in the model in an attempt to suggest a more global view of the ecosystem. Due to the lack of data on these groups, however, they add little value at this point. Demersal groups may eventually be required if the more coastal demersal fisheries are included. The artisanal fisheries operating 'Viking'-type boats are now exploiting both demersal fish and juvenile anchovies (P. Majluf, Universidad Peruana Cayetano Heredia, Lima Peru, personal communication), and as their size and number has increased appreciably since 1998, their impact on the stock may have become strong enough to be included in models otherwise focussing on the pelagic part of the system.

The modelling has also shown the importance of predation of anchovy and sardine on each other's larvae to explain biomass trends. Indeed, the best-fitting model required an increase in vulnerability for the larvae to the adult of the other species, which suggests that the there is little density-dependence at play in the interaction of these species' feeding on the other species' larvae. If one of these species increases, they can eat nearly proportionally more of the other species larvae when vulnerabilities are high. Similarly, empirical work has shown that the contribution of dietary carbon from larvae can be quite important, e.g. carbon from anchovy (E. encrasicolus) eggs contributed 15% in the Benguela sardines (Alheit and Niquen, 2004). In the present model, only predation from mackerel and horse mackerel on adult anchovy and sardine has been included, while predation on eggs and larvae (Alheit and Niquen, 2004) has been ignored. Egg cannibalism could also add density-dependent mortality in a future model.

Thus, based on a snapshot of the Peruvian upwelling ecosystem of the early 1950s created in the late 1980s, and time series that spanned during this period, it was possible to recreate the major fluctuations in anchovy and sardine. To do so, however, it was necessary to modify our underlying Ecopath (static) model and, more importantly, it was also necessary to include additional (hypothetical) relationships suggested by empirical studies in other ecosystems. A similar modelling exercise for the Southern Benguela for the period 1997–2002 (Shannon et al., 2004b) was also successful at explaining biomass of trends for sardine and, to a lesser degree anchovy biomasses, using an upwelling index, fishing and changes in vulnerabilities. In this case, environmental variation was the most important factor as well.

Models built with Ecopath with Ecosim are aimed at understanding the dynamics of the upper levels of the food chain, mainly fish, and the impact of fisheries on the ecosystem (Christensen and Walters, 2004; Guénette et al., 2007). Although detailed modelling of the planktonic phase has not been deemed necessary in several models, we have here shown the importance of including processes regulating primary production due to their strong effects on anchovy and sardine populations.

We gave strong emphasis to fitting older time series, although recent, albeit shorter, series are available. All over the world, it is common to see analysis and modelling of relatively short time series which may suffer from the "shifting baseline syndrome" (Pauly, 1995). Here we emphasize long-term time series spanning numerous contrasting events that help identify mechanisms. Recent time series may lack such changes and consequently be too easy to fit a model to. The best situation would be for models to accommodate all the time series available for a given system, i.e., the old, contrast-rich series, and the more precisely estimated new ones. Only when we have models that can accommodate the whole period for which we have data will we be able to use them in a constructive way for fisheries management. To support such work, we have made all data used here, and the books in which they are documented, freely available from the website of the *Sea around Us* Project (http://www.seaaroundus.org).

Acknowledgements

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