ISSN 1198-6727

INCOFISH ECOSYSTEM MODELS: TRANSITING FROM ECOPATH TO ECOSPACE

Fisheries Centre Research Reports
2007 Volume 15 Number 6

ISSN 1198-6727

Fisheries Centre
Research Reports

2007 Volume 15 Number 6

INCOFISH Ecosystem Models: Transiting from Ecopath to Ecospace

Fisheries Centre, University of British Columbia, Canada

INCOFISH Ecosystem Models: Transiting from Ecopath to Ecospace

edited by
Will J.F. Le Quesne, Francisco Arreguín-Sánchez and Sheila J.J. Heymans

Fisheries Centre Research Reports 15 (6)
188 pages © published 2007 by

The Fisheries Centre
University of British Columbia

2202 Main Mall
Vancouver, B.C., Canada, V6T 1Z4

ISSN 1198-6727

Fisheries Centre Research Reports 15 (6)
2007

INCOFISH ECOSYSTEM MODELS: TRANSITING FROM ECOPATH TO ECOSPACE

edited by
Will J.F. Le Quesne, Francisco Arreguín-Sánchez and Sheila J.J. Heymans

CONTENTS

Page

DIRECTOR'S FOREWORD 1

PREFACE 2

TROPHIC MODEL OF THE NORTHERN ADRIATIC SEA, AN EUTROPHIC AND HIGHLY EXPLOITED ECOSYSTEM, *A. Barausse, A. Duci, C. Mazzoldi, Y. Artioli and L. Palmeri* 3
- Abstract 3
- Introduction 3
- Materials and Methods 3
- Results 10
- Discussion........ 11
- Acknowledgements 12
- References 12
- Appendix A 16

UPDATED ECOSYSTEM MODEL FOR THE NORTHERN BENGUELA ECOSYSTEM, NAMIBIA, *S.J.J. Heymans and U.R. Sumaila* 25
- Abstract 25
- Introduction 25
- Materials and Methods 26
- Model Fitting Results 57
- Acknowledgements 63
- References 63
- Appendix A 69

MODELLING THE FOOD WEB IN THE UPWELLING ECOSYSTEM OFF CENTRAL CHILE (33°S–39°S) IN THE YEAR 2000, *S. Neira and H. Arancibia*........ 71
- Abstract 71
- Introduction 71
- Methods........ 72
- References 83

SPATIAL RESOURCES AND FISHERY MANAGEMENT FRAMEWORK IN THE EAST CHINA SEA, *H.Q. Cheng, H. Jiang, H.G. Xu, J. Wu, H. Ding, W. Le Quesne and F. Arreguín-Sánchez* 87
- Abstract 87
- Introduction 87
- Spatial Characteristics of the ECS Ecosystem 88
- Spatial Modelling of Fishery Management Scenarios in the ECS 92
- Acknowledgements 96
- References 96
- Appendix A 98

AN ECOSYSTEM SIMULATION MODEL OF THE NORTHERN GULF OF CALIFORNIA, *D. Lercari, F. Arreguín-Sánchez and W. Le Quesne* 100
- Abstract 100
- Introduction 100
- Description of Model Components: Ecopath 102
- Description of Model Components: Ecosim 105
- Description of Model Components: Ecospace 108
- Conclusions 111
- References 112

MARINE ECOSYSTEM ANALYSES IN THE GULF OF ULLOA, MEXICO: BAC MEETS ECOPATH, *P. del Monte-Luna, F. Arreguín-Sánchez and D. Lluch-Belda* 114
- Abstract 114
- Introduction 114
- Input Data and Ecosystem Characterization 118
- The Ecosim Foundation 119
- The Ecospace Foundation 121
- Results 123
- Discussion 127
- Acknowledgements 129
- References 129
- Appendix A 133

TROPHIC MODEL FOR THE ECOSYSTEM OF LA PAZ BAY, SOUTHERN BAJA CALIFORNIA PENINSULA, MEXICO, *F. Arreguín-Sánchez, P. del Monte-Luna, J.G. Díaz-Uribe, M. Gorostieta, E.A. Chávez and R. Ronzón-Rodríguez* 134
- Abstract 134
- Introduction 134
- Materials and Methods 135
- Results 137
- Discussion 147
- Acknowledgements 150
- References 150
- Appendices 153

SPATIAL MODELLING OF THE SENEGAMBIAN ECOSYSTEM, *B. Samb* 161
- Abstract 161
- Introduction 161
- Ecopath Model Development 161
- Ecospace Model Development 165
- Conclusions 167
- References 168

A BENTHIC ECOSYSTEM MODEL OF THE SINALOA CONTINENTAL SHELF, MEXICO, *L.A. Salcido-Guevara and F. Arreguín-Sánchez* 170
- Abstract 170
- Introduction 170
- Materials and Methods 171
- Model Balancing 176
- Discussion 180
- Acknowledgements 182
- References 182
- Appendix A 187

A Research Report from the Fisheries Centre at UBC

FISHERIES CENTRE RESEARCH REPORTS ARE ABSTRACTED IN THE FAO AQUATIC SCIENCES AND FISHERIES ABSTRACTS (ASFA)
ISSN 1198-6727

DIRECTOR'S FOREWORD

Once again a Fisheries Centre Research Report was produced which features an international cast of authors, and documenting a number of ecosystem models constructed using the Ecopath with Ecosim (EwE) suite of software.

This report, however, also very nicely illustrates the increased sophistication of the users of this software, which parallels the improvements of EwE. Thus, we have here a number of models which emphasize the spatial dimension of EwE, i.e., the use of its Ecospace module. While technically not difficult to use, this module implies familiarity with the spatial dimension of an ecosystem. This is a dimension that all ecosystem modelers should be expected to master, though it may not be apparent to casual users of Ecopath, used for describing food webs, and Ecosim, used to simulate how they may change through time.

This report also illustrates another aspect of ecosystem modeling based on EwE, i.e., that numerous initiatives centered on this modeling approach are emerging outside of UBC's Fisheries Centre. In this case, the initiative was the INCOFISH Project (see www.incofish.org), funded by the European Commission, and which gathered a vast number of international collaborators, only some of whom are associated with the Fisheries Centre. Still, our Villy Christensen interacted with most of the authors of contributions included herein, one of the reasons for their quality.

Finally, I want to congratulate the editors and the authors of the contributions in this report for the enormous amount of contextualized ecological data that they are herewith making available to colleagues, and thus advancing ecosystem modeling everywhere.

Daniel Pauly

Director, Fisheries Centre

PREFACE

The INCOFISH project ("*Integrating multiple demands on coastal zones with emphasis on fisheries and aquatic ecosystems*", European Commission contract 003739) was developed to examine integrated coastal zone management with explicit recognition of ecological, economic and social interactions due to the growing need for ecosystem-based management. A significant component of the overall INCOFISH project is based upon analysis of the ecosystem effects of management with the Ecopath modelling framework.

The INCOFISH project is a global study. Models developed within this project include ecosystems from all five major continents. Specifically, the models include the East China Sea, Gulf of California, Humboldt Current, Northern Benguela, Gulf of Mexico, North Adriatic Sea, West Coast of Baja California, and Senegambian coasts.

The Ecopath modelling framework (www.ecopath.org) includes Ecopath, Ecosim and Ecospace modules. Ecopath develops a static mass balanced network of interactions between components that make up an ecosystem. Ecosim builds upon this to allow time dynamic simulation of ecosystem interactions. Ecosim can incorporate environmental drivers and calibration to independent time series. Ecospace then builds on Ecosim to allow the spatio-temporal analysis of the ecosystem. It includes essential habitats and dispersion for functional groups, and incorporates socio-economic data to attempt to provide realistic simulations of spatial fishery interactions. The temporal (Ecosim) and spatial (Ecospace) components can be used as policy exploration tools.

Critical to the successful use of the Ecopath suite is detailed and accurate parameterization of the Ecopath, Ecosim and Ecospace models for the study region selected. It is essential to document the development procedure to allow critical analysis of any studies subsequently based upon these models.

This report provides detailed descriptions of the Ecopath, Ecosim and Ecospace models developed within the INCOFISH project. Some reports describe new and previously undescribed Ecopath models, while others build on previously described Ecopath models and therefore include mainly Ecosim and/or Ecospace components. We acknowledge the efforts of the authors contributing to this report.

The Editors

TROPHIC MODEL OF THE NORTHERN ADRIATIC SEA, AN EUTROPHIC AND HIGHLY EXPLOITED ECOSYSTEM[1]

Alberto Barausse[a,c], Alessandro Duci[b], Carlotta Mazzoldi[b], Yuri Artioli[a] and Luca Palmeri[a]
[a] - LASA, University of Padova,
via Marzolo 9, 35131, Padova, Italy
[b] - Dept. of Biology, University of Padova,
via U. Bassi 58/B, 35121, Padova, Italy
[c] - Email: alberto.barausse@unipd.it

ABSTRACT

A preliminary Ecopath model of the Northern Adriatic Sea (Italy, Slovenia, Croatia) was developed. The model describes trophic fluxes in a marine ecosystem that is strongly impacted by human actions, being highly fished and characterised by eutrophication due to both anthropogenic and natural causes.

INTRODUCTION

The Northern Adriatic Sea is a shallow, semi-enclosed basin of the Mediterranean Sea and surrounded by Italy, Slovenia and Croatia. It is characterised by strong inter-annual variability in the circulation field connected with meteorological conditions and with huge and fluctuating Po River freshwater input (Russo and Artegiani, 1996; Oddo *et al.*, 2005). The Po River is also responsible for bringing a high load of nutrients into the basin, which, together with the intrinsic shallowness of the Northern Adriatic Sea, causes eutrophication. Temperature shows important seasonal oscillations, while salinity is connected with river runoff (Russo and Artegiani, 1996).

The Northern Adriatic Sea ecosystem is subjected to strong human influence, mainly eutrophication and fisheries, as it is one of the most fished Italian seas. A preliminary model of the Northern Adriatic marine ecosystem trophic network was developed using the Ecopath software package. The data sources and calculations used to parametrize this model are presented in this report.

MATERIALS AND METHODS

Ecopath modelling approach

Ecopath (www.ecopath.org) is a well-known and accepted method for modelling aquatic ecosystems. In an Ecopath model, organisms are arranged together in functional groups (boxes) defined according to some criteria (e.g. taxonomy or common trophic features) and trophic interactions are represented as fluxes from one box to another. Fishing is also accounted for as a flux from the exploited box to the outside of the ecosystem. Ecopath food web models are based on the assumption of steady state and are, consequently, time averaged for a selected period. Hence, an Ecopath static network is an 'instant snapshot' of biomass and energy fluxes flowing in the ecosystem in the modelled time span. A short description of Ecopath follows, but a more comprehensive treatment can be found in Christensen and Walters (2004) and in Christensen *et al.* (2005).

Data input demand for such models is relatively simple, as each functional group only requires information on diet (a diet matrix DC is used, whose elements are the percentage of how much a group

---

[1] Cite as: Barausse, A., Duci, A., Mazzoldi, C., Artioli, Y. and Palmeri, L. 2007. Trophic model of the Northern Adriatic Sea, an eutrophic and highly exploited ecosystem, p. 3–24. *In*: Le Quesne, W.J.F., Arreguín-Sánchez, F. and Heymans, S.J.J. (eds.) INCOFISH ecosystem models: transiting from Ecopath to Ecospace. Fisheries Centre Research Reports 15(6). Fisheries Centre, University of British Columbia [ISSN 1198-6727].

contributes to another's diet), biomass (*B*, e.g. expressed in wet weight, but also in energy currencies), production rate (*P/B*, equal to total mortality $Z=M+F$ (sum of fishing and natural mortality) in steady state assumption), consumption rate (*Q/B*, the quantity of food consumed relative to biomass), catch (*Y*, accounting for discards and unreported catch), percentage of unassimilated consumption (*GS*, excreted and egested food percentage), plus, if any, net emigration flux (*E*) and biomass accumulation (*BA*) for a group in the simulated time period. All inputs should refer to the time period under consideration.

Ecopath is based on two main equations derived from the steady-state assumption. The mass balance of fluxes entering and leaving a generic compartment *i* can be written:

production = predation mortality + catches + other mortality + net emigration + biomass accumulation

or

$$B_i \cdot (P/B)_i - \sum_{i=1}^{n} B_j \cdot (Q/B)_j \cdot DC_{ji} - (P/B)_i \cdot B_i \cdot (1-EE_i) - Y_i - E_i - BA_i = 0 \qquad \textbf{Eq. 1}$$

where *n* is the number of groups in the system, and DC_{ji} represents the percentage that *i* group constitutes in the diet of *j* group. *EE* is called ecotrophic efficiency and is the fraction of the production of a group that is used in the system. Consequently, *(1-EE)·P/B* is the so-called 'other mortality' due to disease or old age.

Repeating the equation for every group of the model, a linear system can be written, with unknowns *B*, *P/B*, *Q/B* and *EE* (since *C*, *GS*, *E*, *BA* are parameters). So, the modeller must specify three out of four of these unknowns in every equation for Ecopath to solve the system and calculate the other unknowns. Usually, *B*, *P/B* and *Q/B* are entered, because *EE* is impossible to calculate experimentally and can only be guessed. However, in case of great uncertainty even on the order of magnitude of one of the three other unknowns for a group, *EE* can reasonably be entered to make the system possible to solve.

Also, an energy balance can be written for every compartment:

consumption = production + respiration + unassimilated food

or

$$R_i = (1-GS_i) \cdot Q_i - P_i \qquad \textbf{Eq. 2}$$

where *R* is respiration. Usually *R* is calculated from this equation, but if respiration values are known it can be also used for calibrating *GS* or other input data in order to achieve the desired *R* value.

It is worth noticing that an Ecopath model cannot be calibrated since accurate *EE* (and often also *R*) values for functional groups are not available. So, the mass and energy balance equations above are very useful in imposing a very simple, but powerful constraint on the input data: the model can be considered 'done' only when it is balanced, and mass and energy conservation are assured. These criteria are met when all *EE* are less than one, and all *R* are positive. If this is not the case, the modeller must check the input data again. Unlike a calibration, mass and energy balance cannot tell you if the model is a realistic description of the ecosystem, but they can assure you that results physically make sense. Moreover, the modeller can perform other checks to test the goodness of results, like checking for realistic values of *P/Q* or *R/B*, using a procedure that somehow resembles a calibration.

Ecopath models are widely applied for a number of purposes, including the assessment of ecosystem trophic structure, its key groups and fishery impact, or the calculation of several indices from theoretical ecology, thermodynamics and information theory, which are very useful in evaluating ecosystem stress level. The Ecopath version used for this model is 5.1, modified with an executable file made available by Villy Christensen (Fisheries Centre, UBC) to participants in the La Paz Ecospace workshop (La Paz, Mexico, March 2007).

Modelled area and period

The Northern Adriatic Sea is represented in Figure 1. The modelled area is mainly a continental shelf with sandy and muddy bottom, spanning from the Gulf of Trieste in the north southwards to the imaginary line joining the Italian city of Ancona to the Croatian island of Pago.

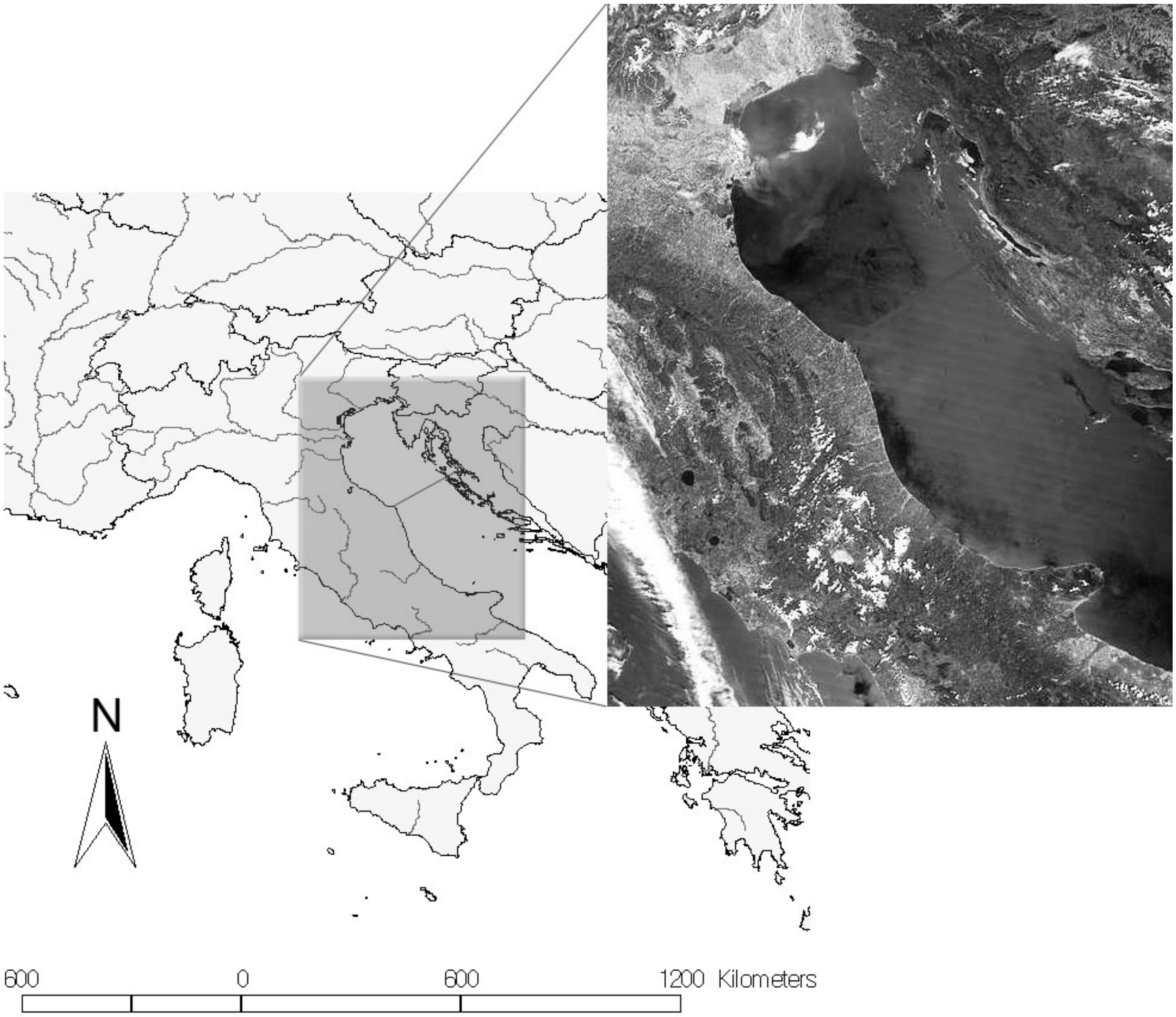


Figure 1. The Adriatic and Northern Adriatic Sea. The line from Italy to Croatia is the southern limit of the modelled area. The Po River plume is clearly visible in the northwest. Satellite image, modified from NASA website (www.nasa.gov).

The Eastern Croatian archipelago has steep and rocky bathymetry, while Italian coasts are gentler and sandy (Russo and Artegiani, 1996). The model does not include coastal lagoons like Venice, nor the Po River delta, since their ecological dynamics are very different from the open sea. They have consequently been considered as a reasonable approximation, external to the model. The surface of the modelled area is about 32,000 km^2 and the mean depth is very shallow (29 m).

The time period for collecting data and averaging is 1996–1998, but since some data had to be taken from outside this range due to limited availability, it would be more correct to speak generally of the 1990s as the reference time span. The mean water temperature for the reference period is 14.5°C and this was calculated from the Medlar/Medatlas II database (MEDAR group, 2002) by dividing the basin into layers of one meter depth and calculating a mean temperature weighted by water volumes.

Description of groups

The model is made of 26 functional groups and 6 fleets (divided according to gear and flag). There are 2 detritus groups, 4 planktonic groups, 1 macroalgae and phanerogam group, 8 invertebrate groups, 10 fish groups and 1 seabird group. Input data before balancing and references for each group can be found in Appendix A, and balanced model data can be found in Table 3. Diet matrix, as modified after balancing, is reported in Table 1. The currency used for biomasses is $t \cdot km^{-2}$ expressed in wet weight ($t_{WW} \cdot km^{-2}$), while the time for rates is $years^{-1}$.

Two detritus groups were chosen: a discard group to account for the role of discard as food in the trophic network, a detritus group to represent dead particulate organic matter in the water column and sediment (excreted and egested matter from all groups, marine snow, etc.). Biomass of detritus groups is a mandatory but not very important input, so detritus biomass was roughly calculated as the difference between particulate organic matter in the water column and the sediment, and phytoplankton and pelagic bacteria biomass. Sediment bacteria were thus not considered and assumed part of detritus. Discard biomass was estimated roughly, as it is not an important parameter. It was assumed that discard production was consumed on average in 10 days, with a linear decay (thus, it was multiplied by 10/365/2 to obtain biomass). Discard production, which is more important in the model (and in the ecosystem), was calculated from rough assumptions and unpublished data (see below). A seabird group was put in the model to account for birds feeding on discard.

Planktonic groups were structured in order to simulate microbial loop, which is known to be a key pathway in energy transfers to higher trophic levels in the Northern Adriatic (Fonda Umani and Beran, 2003). Consequently, one pelagic bacteria group was included in the model. Other groups are zooplankton (micro- and meso-zooplankton, but their diet was corrected to also take into account heterotrophic nanoflagellate predation on bacteria), phytoplankton and a jellyfish group, as the Northern Adriatic has been characterised by outbreaks of several species in the last years, such as *Pelagia noctiluca* and *Aurelia aurita* (Malej, 2001). The jellyfish group biomass is quite unreliable, being based on old surveys for *P. noctiluca*, and so it was given a low value to avoid overestimating its predation, instead of being left out.

Macroalgae and phanerogams were also included in a group, but given the scarce information on the actual bottom surface they cover, a biomass was not given and an *EE* value of 0.100 was chosen, following Christensen *et al.* (2005, p. 56).

Invertebrate groups were chosen following taxonomical criteria and data availability. The filter feeding invertebrate group includes benthic organisms such as poriferans, briozoans, cnidarians, ascidians and sipunculids. Crustacea 1 are macro-crustaceans, such as mantis shrimps and Norway lobsters. Crustacea 2 consist of amphipods, isopods and benthic copepods. Biomass and production for invertebrates were mainly taken from Moodley *et al.* (1998) and Pranovi and Giani (1997), using data taken near the Italian coast and Po River delta, and consequently are not fully representative of the system. Diets were taken from qualitative indications found in literature (e.g. Baccetti *et al.*, 1991) and then corrected with considerations based on personal knowledge and on personal communications by Folco Giomi (Dept. of Biology, University of Padova) and Stefano Cannicci (Dept. of Animal Biology and Genetics "Leo Pardi", University of Firenze).

The first step in constructing fish groups was to list all Northern Adriatic species, based on Riedl (1991) and personal knowledge. Then, fish species were divided into groups obtained through a cluster analysis on diet composition based on the Bray Curtis index, except for flatfish, ray and shark groups, which were defined taxonomically. After the analysis, some species were moved from one group to another, in order to obtain ecologically or commercially significant groups (e.g., fishes were moved following criteria about habitats). Grouping of species is reported in Appendix A.

Diets and other fish data, such as the von Bertalanffy parameter *K*, used for example to calculate production and consumption using empirical equations (see references in Appendix A), were taken from existing literature. When it was not possible to find recent or good data for the Northern Adriatic Sea, literature references for the same species are based on similar ecosystems or (in some few cases) references for similar fish species.

Table 1. Diet matrix of balanced model of the Northern Adriatic.

Prey \ Predator	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	24
1 Seabirds																						
2 Sharks		0.00009	0.00002	0.00009		0.000011																
3 Rays		0.0001	0.00001																			
4 European hake		0.00061	0.00015							0.002		0.00051										
5 Zoobenthivorous fish 1	0.05	0.004	0.002	0.017	0.00001	0.002	0.006			0.015	0.0003	0.016	0.003									
6 Zoobenthivorous fish 2	0.05	0.004	0.002	0.018		0.001	0.002			0.015	0.0003	0.007	0.003									
7 Pelagic piscivorous fish	0.01	0.023	0.01	0.097	0.00001	0.023	0.019			0.097	0.002	0.032										
8 Zooplanktivorous fish	0.665	0.178	0.082	0.759	0.0009	0.15	0.574	0.00025		0.765	0.014	0.14										
9 Omnivorous fish	0.01	0.001	0.00048	0.004		0.001	0.002			0.004	0.000099	0.00081										
10 Benthic piscivorous fish	0.01	0.00017	0.00006	0.00031		0.000032				0.00041		0.00017										
11 Flatfishes	0.02	0.006	0.003	0.025		0.004	0.00076			0.024	0.0003	0.01										
12 Cephalopods	0.005	0.204	0.023			0.003	0.008			0.047		0.023										
13 Crustacea 1		0.539	0.508	0.08	0.156	0.642	0.024	0.0004	0.24	0.03	0.02	0.246	0.106									
14 Crustacea 2			0.366		0.123	0.009	0.002	0.004	0.05	0.00054	0.224	0.229	0.04	0.04			0.002					
15 Gastropods					0.017	0.009	0.016	0.00001				0.07	0.078		0.032		1E-04	0.068				
16 Bivalves		0.009	0.00013		0.279	0.008			0.00075		0.181	0.179	0.139		0.032			0.068				
17 Filter feeding inv.		0.023	0.003		0.00013	0.00038			0.00075		0.045				0.032				0.008			
18 Echinoderms					0.087	0.027					0.036		0.021					0.002				
19 Polychaetes			0.00004		0.321	0.107	0.0004	0.002			0.467	0.037	0.106		0.033			0.002	0.03			
20 Jellyfish					0.002	0.000011														0.05		
21 Zooplankton		0.008			0.005	0.004	0.346	0.99	0.008			0.00022		0.047		0.06	0.002	0.099		0.75	0.02	
22 Macroalgae and phan.					0.009			0.003	0.2				0.053		0.033			0.009	0.012			
23 Phytoplankton									0.103				0.021	0.121	0.108	0.22	0.007	0.14	0.12	0.05	0.6	0.15
24 Bacteria														0.193	0.108	0.22	0.491	0.14	0.101		0.19	
25 Discard	0.12										0.000099	0.00001	0.00071	0.0002	0.001			0.00098	0.0004			
26 Detritus						0.01			0.397		0.01	0.01	0.427	0.598	0.621	0.5	0.497	0.472	0.728	0.15	0.19	0.85
Import	0.06																					
Sum	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1

In some extreme cases, especially for diets, data were guessed based on personal knowledge. For all piscivorous fish species, if the preyed fish species were not indicated in the reference for diet, they were chosen based on personal knowledge or assuming that all fishes with mean length smaller than the predator were preyed on in proportion to their own biomass.

Diets of single species were weighted by their absolute consumptions to obtain the group diet, while production and consumption of single species were weighted by their biomasses. Consumption and production were usually taken from empirical equations (sometimes rough), from existing literature (e.g. $P/B=Z=M+F$) or roughly assuming *GE* value (usually in the middle of the range 0.1–0.3). Biomasses for fish species were taken from field surveys and, if this was not possible and if enough data were available, they were computed from $Z=M+F$ with $F=Y/B$ or through the proportion $Y_1/Y_2=B_1/B_2$, where *1* and *2* are species with similar catchability and one of the biomasses and both catches are known. These two methods are indeed very rough and can lead to estimates one order of magnitude wrong. So, if *EE* values computed by Ecopath for fish groups with so-estimated biomasses were low (e.g. for flatfishes during balancing), that was taken as a probable warning that computed biomasses were too high. For these reasons, in some cases it was preferred to assume an *EE* value instead of entering an uncertain biomass. This method can also lead to inaccurate results, especially if production is not accurately estimated, as is probably the case for zoobenthivorous fish groups. The point to keep in mind is that some biomasses are uncertain for fish groups, and this is a weak side of the model.

Catch (Table 2) was taken from cross-estimates derived from unpublished data from the Chioggia fish market (Chioggia is the main fishing harbour in the modelled area), from ISTAT (Italian Institute of Statistics, www.istat.it/agricoltura/datiagri/pesca) database for Veneto, Friuli Venezia Giulia and Emilia Romagna (Italian regions) and from FAO Fisheries Statistics programme–Regional Capture Production database (www.fao.org/fi/statist/statist.asp) for Slovenia and Croatia. Unreported catch was guessed to be 40% of landings, and discard was roughly assumed to be 10% of total catch or roughly estimated from unpublished data (Dept. of Biology, University of Padova). Discard production and impact in the Northern Adriatic must surely be analysed more deeply, and our rough input data are probably underestimated (see Pranovi *et al.*, 2001). Partitioning of Italian catch among different model gears was made according to Osservatorio Socio Economico della Pesca nell'Alto Adriatico database (www.adrifish.org) and only a percentage of about 1/3 of Croatian catch was assumed to be in the Northern Adriatic Sea.

Model balancing

Model balancing was achieved by modifying input data such as to achieve mass ($EE<1$) and energy ($R>0$) conservation. Beside these physical constraints, additional checks were performed on the balanced model. Gross efficiency *GE* ($=P/Q$) values were checked to be physiologically realistic, as they usually are found in the range 0.1 and 0.3 (Christensen *et al.*, 2005, p. 49) and *EE* for groups were checked to have reasonable values ($EE<0.7$ for phytoplankton (Opitz, 1993), relatively low values for not fully preyed or exploited groups, high values for heavily fished and preyed groups). Also, *R/B* values were checked to be physiologically acceptable, e.g. *R/B* ratio for copepods should be 50–100 year^{-1}, as stated in Christensen *et al.* (2005, p. 51), and higher values are to be found for small organisms.

Data that were supposed to hold higher uncertainty were modified first using a 'search and try' procedure until acceptable results were reached. How the input data were collected was taken into consideration when modifying them. For example, data that were known to be uncertain and underestimated were tentatively increased (e.g. cephalopod biomass does not account for Croatian and Slovenian waters) and overestimated data were lowered.

Particularly, biomasses of pelagic fish groups had to be lowered, but this is in accordance with the uncertainty connected with measurement method (acoustic surveys) and with the results of Coll *et al.* (in press). Flatfishes showed very low *EE* and consequently their biomass was lowered (as they are known to be quite exploited, as can be seen also in Coll *et al.*, in press). Some plankton data, which can be unreliable, had to be varied. In particular, zooplankton production was lowered because it appeared quite unexploited and it was known to be overestimated, and the results gave a better *R/B* ratio. Ecotrophic efficiency was entered for cephalopods, since production seemed too low, and also biomass increased, as previously stated. *EE* for macroalgae and phanerogams was raised to 0.2 because otherwise resulting biomass would have been unrealistically high. After some trials, a balanced and coherent model appeared. Final data are reported in Tables 1 and 3.

Table 2. Landings and discards by fleet (t·km^{-2}·year^{-1}). There are 5 Italian fleets and a Slovenian-Croatian fleet. Italian fleets are hydraulic dredge, mid-water trawling (volante), bottom trawling (coccia), beam trawling (rapido), other fisheries. (Phytoplankton, bacteria, discards and detritus are here omitted.)

Landings (t·km^{-2}·year^{-1})

Group Name	CRO-SLO fleet	Hydraulic dredge	Other fisheries	Beam trawling (rapido)	Bottom trawling (coccia)	Mid-water trawling (volante)	Total
Sea-birds							0
Sharks	0.000758		0.0028	0.000017	0.000417	0.000214	0.004
Rays	0.000517		0.00095	0.000436	0.000653	0.000135	0.003
European hake	0.0124		0.000097		0.0373	0.00108	0.051
Zoobenthivorous fish 1	0.0184		0.0213	0.00639	0.0423	0.000994	0.089
Zoobenthivorous fish 2	0.00207		0.0107	0.00428	0.038	0.000535	0.056
Pelagic piscivorous fish	0.0143		0.00978		0.0282	0.0392	0.091
Zooplanktivorous fish	0.38		0.00956		0.0701	1.513	1.973
Omnivorous fish	0.0021		0.0395		0.00719	0.0252	0.074
Benthic piscivorous fish	0.00147		0.00032	0.000222	0.0026	0.000032	0.005
Flatfishes	0.00323		0.0032	0.0416	0.0192		0.067
Cephalopods	0.0135	0.000499	0.0889	0.0166	0.0582	0.00199	0.18
Crustacea 1	0.00482		0.0197	0.0233	0.103	0.00107	0.152
Crustacea 2							0
Gastropods	0.000198	0.00686	0.123	0.00686			0.137
Bivalves	0.000508	0.0581		0.0895	0.0224		0.171
Filter feeding invertebrates	0.0000833						0
Echinoderms		0.0000252		0.000039	0.000010		0
Polychaetes							0
Jellyfish							0
Zooplankton							0
Macroalgae and phanerogams							0
Sum	0.454	0.065	0.33	0.189	0.43	1.583	3.051

Discards (t·km^{-2}·year^{-1})

Group Name	CRO-SLO fleet	Hydraulic dredge	Other fisheries	Beam trawling (rapido)	Bottom trawling (coccia)	Mid-water trawling (volante)	Total
Sea-birds							0
Sharks	0.0000758	0.0000172	0.000052	0.000086	0.000137	0.000052	0
Rays	0.0000517	0.0000109	0.000033	0.000055	0.000087	0.000033	0
European hake	0.00124		0.00115		0.00077	0.00192	0.005
Zoobenthivorous fish 1	0.00184	0.000355	0.00248	0.00142	0.00248	0.000355	0.009
Zoobenthivorous fish 2	0.000207	0.000268	0.00187	0.00107	0.00187	0.000268	0.006
Pelagic piscivorous fish	0.00143		0.00231		0.00154	0.00386	0.009
Zooplanktivorous fish	0.038		0.0478		0.0319	0.0797	0.197
Omnivorous fish	0.00021		0.00288	0.000719	0.00216	0.00144	0.007
Benthic piscivorous fish	0.000147		0.000063	0.000095	0.000127	0.000032	0
Flatfishes	0.000323	0.00192	0.00064	0.00192	0.00192		0.007
Cephalopods	0.00135	0.0000499	0.00889	0.00166	0.00582	0.000199	0.018
Crustacea 1	0.000482	0.00147	0.00294	0.00734	0.00294		0.015
Crustacea 2							0
Gastropods	0.0000198	0.00457		0.00457	0.00457		0.014
Bivalves	0.0000508	0.00567		0.00567	0.00567		0.017
Filter feeding invertebrates	0.0000391	0.00872		0.0134	0.00335		0.026
Echinoderms	0.0000391	0.00581		0.00896	0.00224		0.017
Polychaetes	0.0000969	0.0127	0.00127	0.0102	0.00127		0.026
Jellyfish							0
Zooplankton							0
Macroalgae and phanerogams	0.0000313	0.017	0.0017	0.0136	0.0017		0.034
Sum	0.046	0.059	0.074	0.071	0.071	0.088	0.409

RESULTS

Trophic levels (Table 3) are in good agreement with literature (Stergiou and Karpouzi, 2002) and the highest values are found for European hake and benthic piscivorous fishes. Omnivory index (see Christensen *et al.*, 2005) is particularly high for macrocrustaceans (Crustacea 1), which are one of the key groups in the system, as can be seen from the mixed trophic impact analysis (Ulanowicz and Puccia, 1990; see Figure 2), because of their high biomass and consumption and their wide predation spectra.

The mixed trophic impact shows also that other key groups are detritus, zooplankton, phytoplankton and zooplanktivorous fish, and that the remaining fish groups have little or no impact on the network. Consequently, the ecosystem appears to have a bottom-up or more probably a wasp-waist controlled structure, possibly due to natural and anthropogenic eutrophication and the exploitation of higher trophic levels.

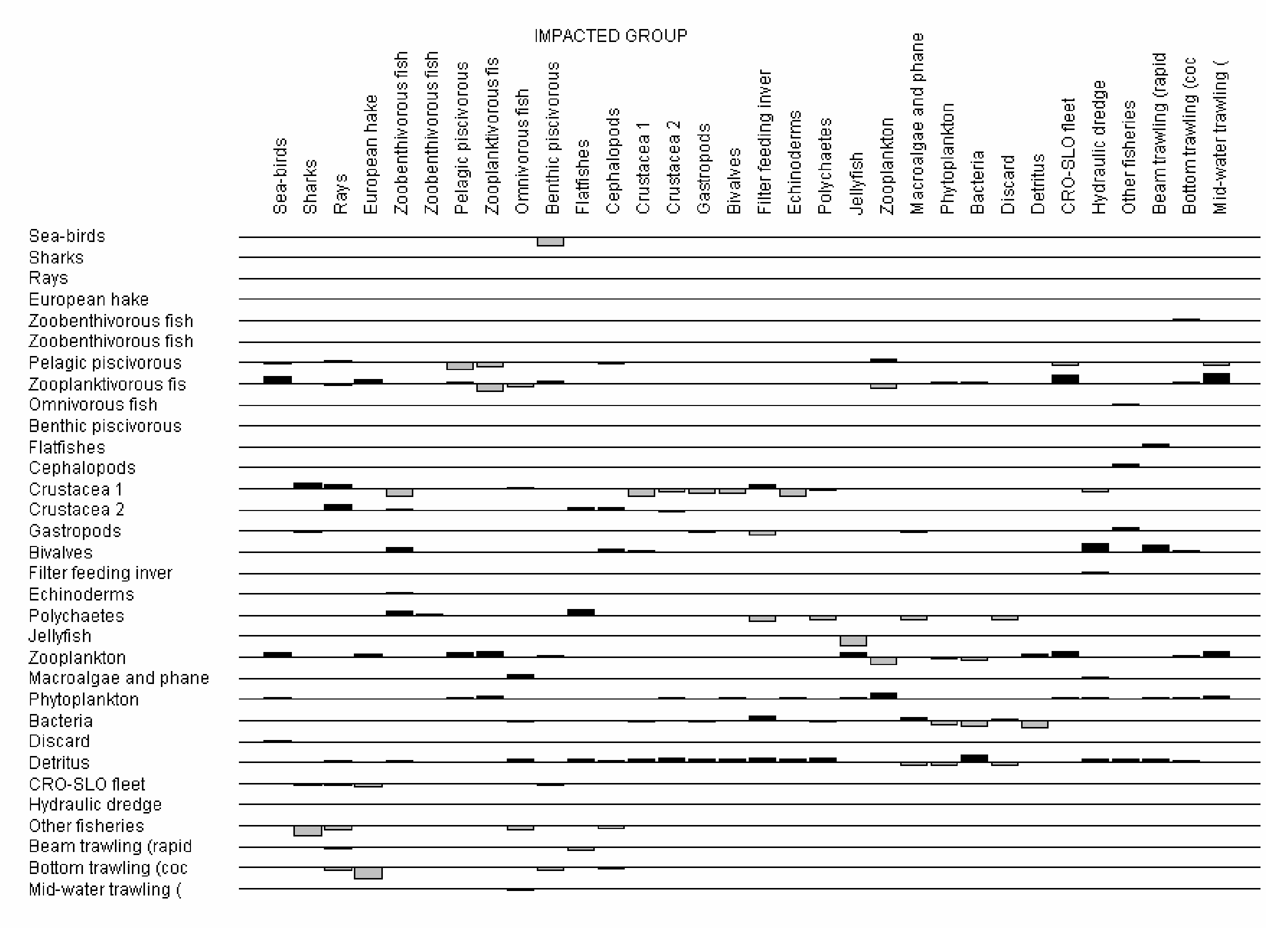


Figure 2. Mixed trophic impact evaluation. Fish groups have little impact on the ecosystem, which seems to be wasp-waist controlled.

The fishing fleets appear to have relatively little impact on the ecosystem, as it was found in Zucchetta *et al.* (2003), which argued that the Northern Adriatic Sea is in a 'fished state'. This means that the system was intensely fished for so long that now it is in a depressed state, and it will not react to a reduction of fishing effort. This might be the case, but the real reason is probably the too high degree of aggregation in this model, which can overshadow and 'buffer' the intense fishing on the few commercial species.

Simple system statistics calculated by Ecopath are reported in Table 4 for the balanced model. Explanations of the calculated indexes can be found in Christensen *et al.* (2005). Noticeably, thermodynamics indexes like total primary production–total respiration ratio are strongly influenced by bacteria presence, and so are not useful in evaluating ecosystem condition; in any case, the network shows some signs of exploitation. The structure is linear (low system omnivory index) with little recycling (low

Table 3. Balanced model data and some calculated indexes. Data in italics were calculated by Ecopath (not entered).

Group name	Trophic level	Biomass ($t·km^{-2}$)	Prod./ biom. ($year^{-1}$)	Cons./ biom. ($year^{-1}$)	Ecotrophic efficiency	Production / consumption	Net efficiency index	Omnivory index
Seabirds	3.97	0.0088	4.61	69.34	*0*	0.066	0.076	0.598
Sharks	3.99	0.0262	0.289	2.877	*0.619*	0.1	0.118	0.177
Rays	3.62	0.0127	0.612	3.058	*0.382*	0.2	0.235	0.11
European hake	4.24	0.05	1.157	4.4	*0.979*	0.263	0.309	0.069
Zoobenthivorous fish 1	3.31	*0.759*	0.776	5.137	0.95	0.151	0.216	0.049
Zoobenthivorous fish 2	3.7	*0.731*	0.648	3.96	0.95	0.164	0.234	0.144
Pelagic piscivorous fish	3.85	2.5	0.899	6.2	*0.235*	0.145	0.171	0.248
Zooplanktivorous fish	3.21	14	0.89	8.776	*0.988*	0.101	0.119	0.005
Omnivorous fish	2.48	0.08	1.6	13.193	*0.965*	0.121	0.187	0.546
Benthic piscivorous fish	4.29	0.023	0.521	3.295	*0.966*	0.158	0.186	0.059
Flatfishes	3.25	0.150	0.888	4.439	*0.949*	0.2	0.286	0.049
Cephalopods	3.62	0.1	*3.936*	9	0.95	0.437	0.533	0.227
Crustacea 1	2.68	5.47	2.894	17.785	*0.88*	0.163	0.325	0.491
Crustacea 2	2.3	0.95	8.4	51.181	*0.929*	0.164	0.226	0.24
Gastropods	2.28	*7.405*	1.699	9.51	0.95	0.179	0.447	0.253
Bivalves	2.29	25.599	1.415	6.35	*0.521*	0.223	0.637	0.223
Filter feeding inv.	2.5	7.652	0.761	3.804	*0.924*	0.2	0.364	0.251
Echinoderms	2.44	8.847	0.803	2.514	*0.362*	0.319	0.581	0.323
Polychaetes	2.15	26.989	1.644	14.27	*0.595*	0.115	0.256	0.137
Jellyfish	3.01	1.02	8.43	25.3	*0.151*	0.333	0.417	0.285
Zooplankton	2.21	3.279	55	160	*0.95*	0.344	0.454	0.174
Macroalgae and phan.	1	*38.198*	1.699	-	0.2	-	-	0
Phytoplankton	1	12.76	169.28	-	*0.38*	-	-	0
Bacteria	2	4.014	127.241	670	*0.409*	0.19	0.237	0
Discard	1	0.006	-	-	*0.974*	-	-	0
Detritus	1	361.93	-	-	*0.999*	-	-	0.354

predatory cycling index), which implies a 'developmental' stage *sensu* Odum (1969). Gross efficiency of fishery is relatively high, even if the system is eutrophicated. The mean trophic level is low and comparable to existing literature values (Coll *et al.*, in press), and is reflective of the fact that the main landings in the area are small pelagics and invertebrates.

Total primary production–total biomass ratio is high and shows that the ecosystem is immature and strongly productive, because of eutrophication, even if energy fluxes are mainly (65%) based on detritus, which is usually seen as a sign of maturity. However, the causes are probably to be found in the shallowness of the basin and in the variable hydrodynamic regime, which increase sediment-water column interactions. Energy transfer efficiency *TE* between trophic levels is 12.6% on average (calculated as geometric mean of trophic levels from II to IV), and the primary producer–based transfer is more efficient (*TE*=13%) than the detritus-based one (*TE*=12.5%).

DISCUSSION

The Northern Adriatic Sea appears to be a quite immature ecosystem. However, it is not clear in which degree its stressed structure is due to anthropogenic causes (eutrophication, fishing) or to its natural characteristics (shallowness, low residence time, Po River input). Consequently it is difficult to quantify ecosystem health. This model provides some interesting insights on trophic structure, key functional groups and energy flows in the system, but it would probably benefit from a lower degree of aggregation and from more precise fish biomass values. Time simulation could be surely useful in order to test hypotheses on ecosystem control and on the importance of fisheries.

Table 4. System statistics for the tropic model of the Northern Adriatic Sea.

Attribute	Value	Units
Sum of all consumption	4203.986	$t \cdot km^{-2} \cdot year^{-1}$
Sum of all exports	6.561	$t \cdot km^{-2} \cdot year^{-1}$
Sum of all respiratory flows	2218.795	$t \cdot km^{-2} \cdot year^{-1}$
Sum of all flows into detritus	2894.021	$t \cdot km^{-2} \cdot year^{-1}$
Total system throughput	9324	$t \cdot km^{-2} \cdot year^{-1}$
Sum of all production	3070	$t \cdot km^{-2} \cdot year^{-1}$
Mean trophic level of the catch	3.11	
Gross efficiency of fishery (catch/net p.p.)	0.001555	
Calculated total net primary production	2224.912	$t \cdot km^{-2} \cdot year^{-1}$
Total primary production/total respiration	1.003	
Net system production	6.117	$t \cdot km^{-2} \cdot year^{-1}$
Total primary production/total biomass	13.852	$year^{-1}$
Total biomass/total throughput	0.017	year
Total biomass (excluding detritus)	160.623	$t \cdot km^{-2}$
Total catches	3.46	$t \cdot km^{-2} \cdot year^{-1}$
Connectance Index	0.372	
System Omnivory Index	0.209	
Throughput cycled (excluding detritus)	38.62	$t \cdot km^{-2} \cdot year^{-1}$
Predatory cycling index	1.09	% of throughput w/o detritus
Throughput cycled (including detritus)	2138.66	$t \cdot km^{-2} \cdot year^{-1}$
Finn's cycling index	22.94	% of total throughput
Finn's mean path length	4.19	
Finn's straight-through path length	1.573	without detritus
Finn's straight-through path length	3.229	with detritus

ACKNOWLEDGEMENTS

This work was developed under the EU-sponsored INCOFISH project (contract INCO-003739). We thank Prof. Corrado Piccinetti (BES, University of Bologna) for cephalopod MEDITS data, and Folco Giomi (Dept. of Biology, University of Padova) and Stefano Cannicci (Dept. of Animal Biology and Genetics "Leo Pardi", University of Firenze) for their advice.

REFERENCES

Abdel Aziz, S.H. 1992. The use of vertebral rings of the brown ray *Raja miraletus* (Linnaeus, 1758) off Egyptian mediterranean coast for estimation of age and growth. Cybium, 16 (2): 121-132.

Arreguín-Sánchez, F., Seijo, J.C. and Valero-Pacheco, E. 1993. An application of ECOPATH II to the north continental shelf ecosystem of Yucatan, Mexico. p. 269-278. In V. Christensen and D. Pauly (eds.) Trophic models of aquatic ecosystems. ICLARM Conf. Proc. 26, 390 pp.

Artuz, M.L. 2005. The diet and food consumption of whiting *Merlangius merlangus merlangus* (Linné) 1758 in the Sea of Marmara. Hidrobiologica, 1.

Azevedo, J.M.N. and Simas, A.M.V. 2000. Age and growth, reproduction and diet of a sublittoral population of therock goby *Gobius paganellus* (Teleostei, Gobiidae). Hydrobiologia, 440: 129–135.

Azzali, M., De Felice, A., Luna, M., Cosimi, G. and Parmigiani, F. 2002. The state of the Adriatic Sea centered on the small pelagics fish populations. Marine Ecology, 23, Supplement 1: 78-91.

Baccetti, B., Baldaccini, N.E., Bedini, C., Brandymar, P., Capanna, E., Chieffi, G., Coboldi, M., Ferraguti, M., Ghirardelli, E., Ghiretti, F., Giusti, F., Gigolo, A., Mainardi, D., Minelli, A., Papi, F., Parriniello, N., Ricci, N., Ruffo, S., Sarà, M., Scali, V. and Zullini, A. 1991. Zoologia 2 – Trattato italiano, Editoriale Grasso, Bologna.

Bartulovic, V., Glamuzina, B., Conides, A., Dulcic, J., Lucic, D., Njire, J. and Kozul, V. 2004. Age, growth, mortality and sex ratio of sand smelt, *Atherina boyeri* Risso, 1810 (Pisces: Atherinidae) in the estuary of the Mala Neretva River (middle-eastern Adriatic, Croatia). Journal of Applied Ichthyology, 20: 427-430.

Benovic, A. 2000. Zooplankton biomass and fish production in the Adriatic. CIESM workshop series, Kerkyra (Greece), 26th august-30th July 2000.

Brey, T. 1999. Growth performance and mortality in aquatic macrobenthic invertebrates. Advances in Marine Biology, 35: 153-223.

Brey, T. 2001. Population dynamics in benthic invertebrates. A virtual handbook. Version 01.2. http://www.awi-bremerhaven.de/Benthic/Ecosystem/FoodWeb/Handbook/main.html. Alfred Wegener Institute for Polar and Marine Research, Germany.

Cabrini, M., Andri, M., Cok, S., Pecchiar, I. and Fonda Umani, S. 2002. Carbon partitioning among the first trophic levels in the North Western Adriatic basin. Chemistry and Ecology 18(1-2): 95-105.

Christensen, V. and Walters, C. 2004. Ecopath with Ecosim: methods, capabilities and limitations. Ecological Modelling, 172(2-4): 109-139.

Christensen, V., Walters, C.J. and Pauly, D. 2005. Ecopath with Ecosim: a user's guide. Fisheries Centre, University of British Columbia, Vancouver. November 2005 edition, 154 pp. (available online at www.ecopath.org).

Cingolani, N., Santojanni, A., Arneri, E., Berlardinelli, A., Colella, S., Donato, F., Giannetti, G., Sinovcic, G. and Zorica, B. 2004a. Sardine (*Sardina pilchardus*, Walb.) stock assessment in the Adriatic Sea: 1975-2003. Paper presented at the GFCM-SAC Working Group on Small Pelagic Species, GCP/RER/010/ITA/OP-13.

Cingolani, N., Santojanni, A., Arneri, E., Berlardinelli, A., Colella, S., Donato, F., Giannetti, G., Sinovcic, G. and Zorica, B. 2004b. Anchovy (*Engraulis encrasicolus*, L.) stock assessment in the Adriatic Sea: 1975-2003. Paper presented at the GFCM-SAC Working Group on Small Pelagic Species, GCP/RER/010/ITA/OP-14.

Coelho, M., Domingues, P., Balguerias, E., Femandez, M. and Andrade, J.P. 1997. A comparative study of the diet of *Loligo vulgaris* (Lamarck, 1799) (Mollusca: Cephalopoda) from the south coast of Portugal and the Saharan Bank (Central-East Atlantic). Fisheries Research, 29: 245-255.

Coll, M., Santojanni, A., Palomera, I., Tudela, S. and Arneri, E. In press. An ecological model of the Northern and Central Adriatic Sea: analysis of ecosystem structure and fishing impacts.

Cortés, E. 1999. Standardized diet compositions and trophic levels of sharks. ICES Journal of Marine Science, 56: 707-717.

Curtis, J.M.R. and Vincent, A.C.J. 2006. Life history of an unusual marine fish: survival, growth and movement patterns of *Hippocampus guttulatus* (Cuvier 1829). Journal of Fish Biology, 68: 707–733.

Danovaro, R. 2003. Interazioni DOM/POM nei processi di formazione dei macroaggregati mucillaginosi in Adriatico Settentrionale: ruolo dei virus e dei batteri. Istituto per la ricerca scientifica e tecnologica applicata al mare, Programma di monitoraggio e studio sui "Processi di formazione delle Mucillaggini nell'Adriatico e nel Tirreno" – MAT, Rapporto finale giugno 1999-maggio 2003. Giugno 2003. CD-ROM.

Danovaro, R., Manini, E. and Fabiano, M. 2001. Exoenzymatic activity and organic matter composition in sediments of the Northern Adriatic sea: response to a river plume. Microbial Ecology, 44: 235-251.

Degobbis, D., Vojvodic, V., Ahel, M., Tepic, N., Cosovic, B., Muhin, N., Zovko, Z., Zangrando, V., Giani, M. and Savelli, F. 2003. Ruolo del carbonio organico, carboidrati e azoto particellato negli eventi di mucillagini lungo il transetto A nel periodo 1999-2002. Istituto per la ricerca scientifica e tecnologica applicata al mare, Programma di monitoraggio e studio sui "Processi di formazione delle Mucillaggini nell'Adriatico e nel Tirreno" – MAT, Rapporto finale giugno 1999-maggio 2003. Giugno 2003. CD-ROM.

Duarte, C.M. and Chiscano, C.L. 1999. Seagrass biomass and production: a reassessment. Aquatic Botany, 65: 159-174.

Dulcic, J. and Glamuzina, B. 2006. Length–weight relationships for selected fish species from three eastern Adriatic estuarine systems (Croatia). Journal of Applied Ichthyology, 22: 254– 256.

Dulcic, J. and Kraljevic, M. 1995. Age, growth and mortality of damselfish (*Chromis chromis* L.) in the eastern middle Adriatic. Fisheries Research, 22: 255-264.

Dulcic, J. and Kraljevic, M. 1997. Corrigendum to "Weight-length relationships for 40 fish species in the eastern Adriatic (Croatian waters)" [Fisheries Research 28 (1996) 243- 25 l]. Fisheries Research, 30: 169-171.

Dulcic, J., Kraljevic, M., Grbec, B. and Cetinic, P. 2000. Age, growth and mortality of blotched picarel *Spicara maena* L. (Pisces: Centracanthidae) in the eastern central Adriatic. Fisheries Research, 48: 69-78.

Dulcic, J., Pallaoro, A., Cetinici, P., Kraljevic, M., Soldo, A. and Jardas, I. 2003. Age, growth and mortality of picarel, *Spicara smaris* L. (Pisces: Centracanthidae), from the eastern Adriatic (Croatian coast). Journal of Applied Ichthyology, 19 (1).

FAO Adriamed–Loligo vulgaris, 2006. Visited November 2006: www.faoadriamed.org/html/Species/LoligoVulgaris.html.

FAO Adriamed-Lophius budegassa*,* 2006. Visited November 2006: www.faoadriamed.org/html/Species/ LophiusBudegassa.html.

FAO Adriamed-Lophius piscatorius*,* 2006. Visited November 2006: www.faoadriamed.org/html/Species/ LophiusPiscatorius.html.

FAO Adriamed-Merlangius merlangus*,* 2006. Visited November 2006: www.faoadriamed.org/html/Species/Merlangius Merlangus.html.

FAO Adriamed-Merluccius merluccius*,* 2006. Visited November 2006: www.faoadriamed.org/html/Species/Merluccius Merluccius.html.

FAO Adriamed-Mullus barbatus*,* 2006. Visited November 2006: www.faoadriamed.org/html/Species/MullusBarbatus.html.

FAO Adriamed-Pagellus erythrinus*,* 2006. Visited November 2006: www.faoadriamed.org/html/Species/ PagellusErythrinus.html.

FAO Adriamed-Sepia officinalis*,* 2006. Visited November 2006: www.faoadriamed.org/html/Species/SepiaOfficinalis.html.

FAO Adriamed-Solea vulgaris*,* 2006. Visited November 2006: www.faoadriamed.org/html/Species/SoleaVulgaris.html.

Filiz, H. and Bilge, G. 2004. Length–weight relationships of 24 fish species from the North Aegean Sea, Turkey. Journal of Applied Ichthyology, 20: 431–432.

Filiz, H. and Mater, S. 2002. A Preliminary Study on Length-Weight Relationships for Seven Elasmobranch Species from North Aegean Sea, Turkey. E.U. Journal of Fisheries and Aquatic sciences, 19 (3-4): 401-409.

Fonda Umani, S. and Beran, A. 2003. Seasonal variations in the dynamics of microbial plankton communities: first estimates from experiments in the Gulf of Trieste, Northern Adriatic Sea. Marine Ecology Progress Series, 247: 1-16.

Fonda Umani, S., De Olazabal, A., Parlato, S., and Boglich Perasti, B. 2003. Evoluzione del popolamento mesozooplanctonico lungo i transetti B e C. Istituto per la ricerca scientifica e tecnologica applicata al mare, Programma di monitoraggio e studio sui "Processi di formazione delle Mucillaggini nell'Adriatico e nel Tirreno" – MAT, rapporto finale giugno 1999-maggio 2003. Giugno 2003. CD-ROM.

Fonda Umani, S., Tirelli, V., Beran, A. and Guardiani, B. 2005. Relationships between microzooplankton and mesozooplankton: competition versus predation on natural assemblages of the Gulf of Trieste (northern Adriatic Sea). Journal of Plankton Research, 27 (10): 973-986.

Froese, R. and Pauly, D., Editors. 2007. FishBase. World Wide Web electronic publication. www.fishbase.org, version (05/2007). Visited from June 2006 to May 2007.

Giani, M., Baldan, C., Savelli, F., Zangrando, V., Mecozzi, M. and Amici, M. 2003. Distribuzione e variazioni temporali della sostanza organica disciolta e particellata nell'Adriatico sulle sezioni Senigalli-isola di Sansego e Cesenatico-Capo Promontore. Istituto per la ricerca scientifica e tecnologica applicata al mare, Programma di monitoraggio e studio sui "Processi di formazione delle Mucillaggini nell'Adriatico e nel Tirreno" – MAT, rapporto finale giugno 1999-maggio 2003. Giugno 2003. CD-ROM.

Guenette, S., Morato, T. 1997. The Azores Archipelago. *In:* Fisheries impacts on North Atlantic ecosystems: models and analyses. S. Guénette, Christensen, V. and Pauly, D. (eds.). Fisheries Centre Research Reports 9 (4).

Guidetti, P., Lorenti, M., Buia, M.C. and Mazzella, L. 2002. Temporal Dynamics and Biomass Partitioning in the Three Adriatic Seagrass Species: *Posidonia oceanica, Cymodocea nodosa, Zostera marina.* Marine Ecology, 23 (1): 51-67.

Ismen, A. 2003. Age, growth, reproduction and food of common stingray (*Dasyatis pastinaca* L., 1758) in Iskenderun Bay, the eastern Mediterranean. Fisheries Research, 60: 169–176.

Jukic-Peladic, S., Vrgoc, N., Krtulovic-Sifner, S., Piccinetti, C., Piccinetti-Manfrin, G., Marano, G. and Ungaro, N. 2001. Long-term changes in demersal resources of the Adriatic Sea: comparison between trawl surveys carried out in 1948 and 1998, Fisheries Research, 53: 95-104.

Kallianiotis, A., Torre, M. and Argyri, A. 2005. Age, growth, mortality, reproduction and feeding habits of the striped seabream, *Lithognathus mormyrus* (Pisces: Sparidae), in the coastal waters of the Thracian Sea, Greece. Scientia Marina, 69 (3): 391-404.

Khailov, K.M. and Burlakova, Z.P. 1969. Release of Dissolved Organic Matter by Marine Seaweeds and Distribution of Their Total Organic Production to Inshore Communities. Limnology and Oceanography, 14 (4): 521-527.

Kozul, V., Skaramuca, B., Kraljevic, M., Dulcic, J. and Glamuzina, B. 2001. Age, growth and mortality of the Mediterranean amberjack *Seriola dumerili* (Risso 1810) from the south-eastern Adriatic Sea. Journal of Applied Ichthyology, 17: 134-141.

Kraljevic, M., Dulcic, J., Cetinic, P. and Pallaoro, A. 1996. Age, growth and mortality of the striped sea bream, *Lithognathus mormyrus* L., in the Northern Adriatic. Fisheries Research, 28: 361-370.

La Ferla, R., Azzaro, M., Zaccone, R. and Caruso, G. 2002. Microbial respiratory and ectoenzymatic activities in the Northern Adriatic sea (Mediterranean sea). Chemistry and Ecology, 18(1-2): 75-84.

Labropoulou, M., Tserpes, G. and Tsimenides, N. 1998. Age, Growth and Feeding Habits of the Brown Comber *Serranus hepatus* (Linnaeus, 1758) on the Cretan Shelf. Estuarine, Coastal and Shelf Science, 46: 723-732.

Link, J.S., Griswold, C.A., Methratta, E.T. and Gunanrd, J. (eds). 2006. Documentation for the Energy Modeling and Analysis eXercise (EMAX), Northeast Fisheries Science Centre Reference Document 06-15, August 2006.

Lipej, L., Bonaca, M.O. and Sisko, M. 2003. Coastal Fish Diversity in Three Marine Protected Areas and One Unprotected Area in the Gulf of Trieste (Northern Adriatic). Marine Ecology, 24 (4): 259–273.

Malej, A. 1989. Behaviour and trophic ecology of the jellyfish *Pelagia noctiluca* (Forsskål, 1775). Journal of Experimental Marine Biology and Ecology, 126: 259-270.

Malej, A. 2001. Are irregular plankton phenomena getting more frequent in the northern Adriatic Sea?. Gelatinous zooplankton outbreaks, theory and practice, CIESM workshop series, Naples (Italy), 29th august-1st september 2001.

Malej, A. and Malej, A. Jr. 2004. Invasion of the jellyfish *Pelagia noctiluca* in the Northern Adriatic: a non-success story. H. Dumont *et al.* (eds.) Aquatic invasion in the Black, Caspian and Mediterranean Seas: 273-285.

MEDAR group, 2002. MEDATLATS/2002 database. Mediterranean and Black Sea database of temperature, salinity and bio-chemical parameters. Climatological Atlas. 4 CD-ROM, IFREMER edition.

Moodley, L., Heip, C.H.R. and Middelburg, J.J. 1998. Benthic activity in sediments of the northwestern Adriatic Sea: sediment oxygen consumptiom, macro- and meiofauna dynamics. Journal of Sea Research, 40: 263-280.

Munda, I.M. 1990. Resources and possibilities for exploitation of North Adriatic seaweeds. Hydrobiologia, 204-205: 309-315.

Munda, I.M. 1993. Change and degradation of seaweeds stands in the Northern Adriatic seaweeds. Hydrobiologia, 260-261: 239-253.

Oddo, P., Pinardi, N. and Zavatarelli, M. 2005. A numerical study of interannual variability of the Adriatic Sea (2000-2002). Science of the Total Environment, 353: 39-56.

Odum, E.P. 1969. The strategy of ecosystem development. Science, 164: 262-270.

Opitz, S. 1993. A quantitative model of the trophic interactions in a Caribbean coral reef ecosystem. p. 259-267. In V. Christensen and D. Pauly (eds.) Trophic models of aquatic ecosystems. ICLARM Conf. Proc. 26, 390 pp.

Opitz, S. 1996. Trophic Interactions in Caribbean Coral Reef. ICLARM Tech. Rep. 43, ICLARM, Makati City, Philippines, 341 pp.

Osservatorio Socio Economico della Pesca nell'Alto Adriatico database (www.adrifish.org, La pesca e l'aquacultura nel Veneto, La pesca e l'aquacultura in Emilia Romagna, La pesca e l'aquacultura in Friuli Venezia Giulia).

Pallaoro, A., Cetinic, P., Dulcic, J., Jardas, I. and Kraljevic, M. 1998. Biological parameters of the saddled bream *Oblada melanura* in the eastern Adriatic. Fisheries Research, 38: 199-205.

Pallaoro, A. and Jardas, I. 2003. Some biological parameters of the peacock wrasse *Symphodus (Crenilabrus) tinca* (L. 1758) (Pisces: Labridae) from the middle eastern Adriatic (Croatian coast). Scientia Marina, 67 (1): 33-41.

Pinnegar, J.K. and Polunin, N.V.C. 2004. Predicting indirect effects of fishing in Mediterranean rocky littoral communities using a dynamic simulation model. Ecological Modelling, 172: 249-267.

Pranovi, F. and Giani, M. 1997. Popolazioni macrobentoniche in alcuni siti dell'Adriatico settentrionale: composizioni e biomasse. Pesca e ambiente nella laguna di Venezia e nell'alto Adriatico, "Il Leggio" Libreria Editrice, Sottomarina – Chioggia (VE).

Pranovi, F., Raicevich, S., Franceschini, G., Torricelli, P. and Giovanardi, O. 2001. Discard analysis and damage to non-target species in the "rapido" trawl fishery. Marine Biology, 139: 863-875.

Ragonese, S., Fiorentino, F., Garofalo, G., Gristina, M., Levi, D., Gancitano, S., Giusto, G.B., Rizzo, P., Sinacori, G., n.d. Distribution, abundance and biological features of picarel (Spicara flexuosa), Mediterranean (Trachurus mediterraneus) and Atlantic (T. trachurus) horse mackerel based on experimental bottom-trawl data (MEDITS, 1994–2002) in the Strait of Sicily. MedSudMed Technical Documents, 5.

Riedl, R. 1991. Flora e fauna del mediterraneo, Franco Muzzio & c. Editore, Padova.

Rodriguez-Cabello, C. and Sanchez, F. 2005. Mortality estimates of *Scyliorhinus canicula* in the Cantabrian sea using tag-recapture data. Journal of Fish Biololgy, 66 (4) pp. 1116-1126.

Russo, A. and Artegiani, A. 1996. Adriatic sea hydrography. Scientia Marina, 60(2): 33-43.

Santic, M., Jardas, I. and Pallaoro, A. 2002. Age, growth and mortality rate of horse mackerel, *Trachurus trachurus* (L.), living in the eastern central Adriatic. Periodicum Biologorum, 104 (2): 165-173.

Sartor, P., Sbrana, M., Ungaro, N., Marano, A.C., Piccinetti, C. and Manfrin, G. 2002. Distribution and abundance of *Citharus linguatula* (Linnaeus, 1758), *Lepidorhombus boscii* (Risso, 1810) and *Solea vulgaris*, Quensel, 1806 (Osteichthyes, Pleuronectiformes) in the Mediterranean sea. Scientia Marina, 66 (2): 83-102.

SIBM, 2006. Standardizzazione delle metodiche di determinazione specifica e valutazione degli stocks delle razze Società italiana di Biologia Marina, Comitato Necton e Pesca, GRUppo Nazionale Risorse Demersali.

Sinovcic, G. 2001. Small pelagic fish from the Croatian fishing grounds. In Mannini, P., Massa, F. and Milone, N. (eds), Priority topics related to small pelagics fishery resources of the Adriatic Sea, GCP/RER/010/ITA/TD-03, FAO-AdriaMed.

Sinovcic, G., Franicevic, M., Zorica, B. and Cikes, V. 2004. Length–weight and length–length relationships for 10 pelagic fish species from the Adriatic Sea (Croatia). Journal of Applied Ichthyology, 20: 156–158.

Spedicato, M.T., Greco, S., Sophronidis, K., Lembo, G., Giordano, D. and Argyri, A. 2002. Geographical distribution, abundance and some population characteristics of the species of the genus *Pagellus* (Osteichthyes: Perciformes) in different areas of the Mediterranean. Scientia Marina, 66 (2).

Stergiou, K.I. and Karpouzi, V.S. 2002. Feeding habits and trophic levels of Mediterranean fish. Reviews in Fish Biology and Fisheries, 11: 217–254.

Ulanowicz, R.E. and Puccia, C.J. 1990. Mixed trophic impacts in Ecosystems. Coenoses, 5: 7-16.

Vannucci, S. 2005. Ecologia di alcune specie di Rajidae nel Mar Ligure meridionale con particolare riferimento all'alimentazione', Thesis, Università degli Studi di Pisa. Visited October 2006: http://etd.adm.unipi.it/theses/available/etd-06292005-122910/unrestricted/Tesi_Simona_Vannucci.pdf.

Villamil, M.M., Lorenzo, J.M., Pajuelo, J.G., Ramos, A. and Coca, J. 2002. Aspects of the life history of the salema, *Sarpa salpa* (Pisces, Sparidae), off the Canarian Archipelago (central-east Atlantic). Environmental Biology of Fishes, 63: 183-192.

Vrgoc, N., Krstulovic Sifner, S., Dadic, V. and Jukic-Peladic, S. 2006. Demographic structure and distribution of John Dory, *Zeus faber* L. 1758, in the Adriatic Sea. Journal of Applied Ichthyology, 22: 205–208.

Zorica, B., Sinovcic, G., Pallaoro, A. and Cikes Kec, V. 2006. Reproductive biology and length–weight relationship of painted comber, *Serranus scriba* (Linnaeus, 1758), in the Trogir Bay area (middle-eastern Adriatic). Journal of Applied Ichthyology, 22: 260–263.

Zucchetta, M., Libralato, S., Granzotto, A., Pranovi, F., Raicevich S. and Torricelli, P. 2003. Modelling Approach for the Evaluation of the Efficacy of MPA in the Northern Adriatic Sea. Proceedings of the sixth international conference on the Mediterranean coastal environment. MEDCOAST 03. Erdal Özhan (Editor), 7th-11th October 2003, Ravenna, Italy.

Appendix A. Input data for Northern Adriatic Sea Ecopath model (before balancing).

Detritus	Value	References	Conversion factors	Notes
B	361.930 t·km^{-2}	Danovaro *et al.* (2001); Degobbis *et al.* (2003); Giani *et al.* (2003)	10 gWW/gC (Opitz, 1996)	Calculated as the difference between particulate organic matter (in water and 1 cm sediment) and biomass of phytoplankton and pelagic bacteria
Discard	Value	Source	Conversion factors	Notes
B	0.0056 t·km^{-2}			Consumed in 10 days, linear decaying
Bacteria	Value	Source	Conversion factors	Notes
B	4.014 t·km^{-2}	La Ferla *et al.* (2002); Danovaro (2003)	10 gWW/gC (Link *et al.*, 2006)	
P/B	127.241 year^{-1}	La Ferla *et al.* (2002); Danovaro (2003)		
Q/B	760.018 year^{-1}	La Ferla *et al.* (2002); Danovaro (2003)		Computed from equation 2 using *P/B* and R/B from La Ferla *et al.* (2003), and *GS* from Link *et al.* (2006), and then re-calculated as (P/B)/(GE) from input *P/B* and *GE* from La Ferla *et al.* (2003)
GS	0.200	Link *et al.* (2006)		
DC	Table 1	Link *et al.* (2006)		
Phytoplankton	Value	References	Conversion factors	Notes
B	12.760 t·km^{-2}	MEDAR group (2002)	10 gWW/gC, 400 gWW/gChl-a (Link *et al.*, 2006)	Averaged over 1990s
P/B	169.280 year^{-1}	MEDAR group (2002)		Averaged over 1990s
Macroalgae and phanerogams	Value	References	Conversion factors	Notes
EE	0.100 t·km^{-2}	Christensen *et al.* (2005)		No reliable biomass estimates
P/B	1.699 year^{-1}	Khailov and Burlakova (1969); Guidetti *et al.* (2002); Duarte and Chiscano (1999); Munda (1990); Munda (1993)	7.7 gWW/gDW for *Posidonia oceanica* (Arreguín-Sánchez *et al.*, 1993); 4.4 gWW/gDW for *Zostera marina*, 5 gWW/gDW for *Cymodocea nodosa* (Brey, 2001)	Considered biomass above ground. Phanerogams: *Z. marina*, *P. oceanica*, *C. nodosa*. *P/B* s of macroalgae and phanerogams weighted on biomasses and assuming a covered bottom surface ratio of about 1.87, following bathymetric considerations on vegetated bottom
Zooplankton	Value	Source	Conversion factors	Notes
B	3.279 t·km^{-2}	Cabrini *et al.* (2002); Fonda Umani *et al.* (2003)	Mesozooplankton: 5.6 gWW/gDW; 2,222 gDW/gC (Brey, 2001); Microzooplankton: 5.556 gWW/gDW; 2.174 gDW/gC (Link *et al.*, 2006)	Computed as sum of microzooplankton (1996-1998) and mesozooplantkon (in 1999-2000)
P/B	90.557 year^{-1}	Benovic (2000); Pinnegar and Polunin (2004)		Computed as mean weighted on biomasses of microzooplankton and mesozooplankton *P/B*s

Q/B	197.759 year^{-1}			Computed choosing GE=0.5 for microzooplankton and GE=0.3 for mesozooplankton (Pinnegar and Polunin, 2004).
GS	0.243	Link *et al.* (2006)		Computed as mean weighted on biomasses of microzooplankton and mesozooplankton *GS*'s
DC	Table 1	Fonda Umani and Beran (2003); Fonda Umani *et al.* (2005); Link *et al.* (2006)		Detritus percentage in diet taken from Link *et al.* (2006). Value similar to the one in Coll *et al.* (in press)
Jellyfish	Value	Source	Conversion factors	Notes
B	1.020 t·km^{-2}	Malej and Malej (2004)		1984 (a low value was taken, since *P. noctiluca* in 1990s is lower than 1980s)
P/B	8.430 year^{-1}	Malej (1989)	0.0049 gC/gWW (Malej, 1989)	
Q/B	25.300 year^{-1}	Malej (1989)		
GS	0.200	Malej (1989)		
DC	Table 1	Coll *et al.* (in press)		
Polychaetes	Value	Source	Conversion factors	Notes
B	26.989 t·km^{-2}	Moodley *et al.* (1998)		
P/B	1.644 year^{-1}	Moodley *et al.* (1998)		
Q/B	14.270 year^{-1}	Arreguín-Sánchez *et al.* (1993); Pinnegar and Polunin (2004)	15.2124 gWW/gC (Brey, 2001)	Average of values corrected to account for temperature difference, with empirical equation from Opitz (1996)
GS	0.550	Coll *et al.* (in press); Link *et al.* (2006)		Mean value
DC	Table 1	Baccetti *et al.* (1991)		
Echinoderms	Value	Source	Conversion factors	Notes
B	8.847 t·km^{-2}	Moodley *et al.* (1998)		
P/B	0.803 year^{-1}	Moodley *et al.* (1998)		
Q/B	2.514 year^{-1}	Pinnegar and Polunin (2004)	26.7 gWW/gC (Brey, 2001)	Value corrected to account for temperature difference, with empirical equation from Opitz (1996)
GS	0.450	Coll *et al.* (in press); Link *et al.* (2006)		
DC	Table 1	Baccetti *et al.* (1991)		
Filter feeding invertebrates	Value	Source	Conversion factors	Notes
B	7.652 t·km^{-2}	Moodley *et al.* (1998)	0.043 gC/gWW (Moodley *et al.*, 1998)	Calculated as 'rest'
P/B	0.761 year^{-1}	Moodley *et al.* (1998)		

Q/B	3.804 year^{-1}			Assuming *GE*=0.2
GS	0.450	Coll *et al.* (in press); Link *et al.* (2006)		
DC	Table 1	Baccetti *et al.* (1991)		
Bivalves	Value	Source	Conversion factors	Notes
B	25.599 t·km^{-2}	Pranovi and Giani (1997)		Weighted station depths according to Northern Adriatic bathymetry
P/B	1.415 year^{-1}	Moodley *et al.* (1998)		Based on *Corbula gibba*
Q/B	6.350 year^{-1}	Opitz (1996)	0.435 gWW/gWW+shell (Brey 2001)	Value corrected to account for temperature difference, with empirical equation from Opitz (1996)
GS	0.650	Coll *et al.* (in press); Link *et al.* (2006)		
DC	Table 1	Baccetti *et al.* (1991)		
Gastropods	Value	Source	Conversion factors	Notes
EE	0.950	Christensen *et al.* (2005)		No reliable biomass estimates
P/B	1.699 year^{-1}	Opitz (1996); Pinnegar and Polunin (2004)		Assuming *GE*=0.178, as in the references
Q/B	9.510 year^{-1}	Pinnegar and Polunin (2004)		Value corrected to account for temperature difference, with empirical equation from Opitz (1996)
GS	0.600	Link *et al.* (2006)		
DC	Table 1	Baccetti *et al.* (1991)		
Crustacea 1	Value	Source	Conversion factors	Notes
B	5.384 t·km^{-2}	Pranovi and Giani (1997)		Computed as difference of crustacean biomass (in reference) and Crustacea 2 biomass (in model). In reference, station depths were weighted according to Northern Adriatic bathymetry.
P/B	2.894 year^{-1}	Moodley *et al.* (1998)	10.215 gWW/gC (Brey, 2001)	Computed subtracting Crustacea 2 production (from model) to total crustacean production in reference
Q/B	17.785 year^{-1}	Pinnegar and Polunin (2004)		Value corrected to account for temperature difference, with empirical equation from Opitz (1996)
GS	0.500	Link *et al.* (2006)		
DC	Table 1	Baccetti *et al.* (1991)		
Crustacea 2	Value	Source	Conversion factors	Notes
B	1.010 t·km^{-2}	Coll *et al.* (in press)		
P/B	7.908 year^{-1}			Assumed *GE*=0.154 as in Coll *et al.* (in press)

Q/B	51.181 year^{-1}	Coll *et al.* (in press)		Value corrected to account for temperature difference, with empirical equation from Opitz (1996)
GS	0.275	Coll *et al.* (in press)		
DC	Table 1			

Cephalopods	Value	Source	Conversion factors	Notes
B	0.030 t·km^{-2}	Unpublished MEDITS trawl surveys data (1996-1998) from prof. C. Piccinetti (BES, University of Bologna)		
P/B	2.100 year^{-1}	FAO Adriamed - *Loligo vulgaris* (2006); FAO Adriamed - *Sepia Officinalis* (2006); Riedl (1991)	0.2 gDW/gWW; 22.03 kJ/gDW (Brey, 2001)	Weighted mean for production of *Loligo vulgaris* (*Z=M+F*, *M* from eq. B2 in Brey, 1999), *Eledone moschata* and *Sepia officinalis* *(*empirical equation from Hoenig (1983, cit. in Christensen *et al.*, 2005, p. 39)
Q/B	8.470 year^{-1}	Guenette and Morato (1997)		Value for *Loligo forbesi* corrected to account for temperature difference, with empirical equation from Opitz (1996)
GS	0.180	Coll *et al.* (in press); Link *et al.* (2006)		
DC	Table 1	Baccetti *et al.* (1991); Coehlo *et al.* (1997); FAO Adriamed - *Sepia officinalis* (2006); Riedl (1991)		

Flatfishes	Value	Source	Notes
B	0.404 t·km^{-2}	Froese and Pauly (2007); Sartor *et al.* (2002)	Species: *Psetta maxima, Platichthys flesus, Lepidorhombus boschi, Microchirus variegatus, Pegusa impar, Synapturichthys kleinii kleini, Solea solea, Lepidorhombus whiffiagonis, Citharus linguatula.* MEDITS trawl surveys. Proportion between catches and biomasses; *Z=M+Y/B* (see Description of groups)
P/B	0.888 year^{-1}	Coll *et al.* (in press)	Assumed *GE*=0.2
Q/B	4.439 year^{-1}	Dulcic and Glamuzina (2006); Fao Adriamed - *Solea Vulgaris* (2006); Froese and Pauly (2007)	Empirical eq. 17 in Christensen *et al.* (2005)
GS	0.300	Coll *et al.* (in press); Link *et al.* (2006)	
DC	Table 1	Froese and Pauly (2007)	

Benthic piscivorous fishes	Value	Source	Notes
B	0.021 t·km^{-2}	FAO Adriamed - Lophius Piscatorius (2006); FAO Adriamed - Lophius Budegassa (2006); Froese and Pauly (2007); Jukic-Peladic *et al.* (2001); Vrgoc *et al.* (2006)	Species: *Belone belone, Lichia amia, Seriola dumerilii, Trachinotus ovatus, Conger conger, Lophius piscatorius, Sarda sarda, Scorpaena scrofa, Serranus cabrilla, Dentex dentex, Trachinus draco, Trachinus Aranaeus, Uranoscopus scaber, Zeus faber, Lophius Budegassa.* MEDITS trawl surveys. Proportion between catches and biomasses; Z=M+Y/B (see description of groups)
P/B	0.521 year^{-1}	FAO Adriamed - Lophius Piscatorius (2006); FAO Adriamed - Lophius Budegassa (2006); Froese and Pauly (2007); Kozul *et al.* (2001); Sinovcic *et al.* (2004); Vrgoc *et al.* (2006)	*Z=M+F*; *M* from eq. B3 in Brey (1999). Assumed *GE*=0.2 for *C. conger, S. sarda, S. scrofa, D. dentex*; Inverted empirical eq. 19 in Christensen *et al.* (2005)
Q/B	3.295 year^{-1}		Empirical eq. 17 and 19 in Christensen *et al.* (2005)
GS	0.150	Coll *et al.* (in press); Link *et al.* (2006)	
DC	Table 1	Froese and Pauly (2007), Stergiou and Karpouzi (2002)	

Omnivorous fishes	Value	Source	Notes
B	0.0736 t·km^{-2}	Froese and Pauly (2007); Lipej *et al.* (2003)	Species: *Aidablennius sphynx, Coryphoblennius galerita, Lipophrys canevae, Parablennius zvonimiri, Parablennius sanguinolentus, Sarpa salpa, Parablennius gattorugine, Parablennius incognitus, Parablennius rouxi, Parablennius tentacularis, Salaria pavo, Chelon labrosus, Liza aurata, Liza ramado, Liza sapiens, Mugil cephalus, Tripterygion delaisi, Tripterygion melanurus, Tripterygion tripteronotus, Lipophrys dalmatinus.* Proportion between catches and biomasses; Z=M+Y/B (see Description of groups). Visual census data (using mean species weight and assuming habitat area in Eastern Adriatic from 0 to 100 m distance from coast = 437 km^2)
P/B	1.571 year^{-1}	Dulcic and Kraljevic (1997); Froese and Pauly (2007)	Assumed *GE*=0.2 for *L. aurata, L. ramada, L. saliens, M. cephalus, S. salpa*; Inverted empirical eq. 19 in Christensen *et al.* (2005)
Q/B	13.193 year^{-1}	Dulcic and Kraljevic (1997); Froese and Pauly (2007); Villamil *et al.* (2002)	Empirical eq. 17 in Christensen *et al.* (2005)

GS	0.350	Coll *et al.* (in press); Link *et al.* (2006)	
DC	Table 1	Froese and Pauly (2007)	
Zooplantivorous fishes	Value	Source	Notes
B	15.922 t·km^{-2}	Azzali *et al.* (2002); Cingolani *et al.* (2004a); Cingolani *et al.* (2004b); Froese and Pauly (2007); Lipej *et al.* (2003)	Species: *Atherina boyeri, Spicara maena, Spicara smaris, Sardina pilchardus, Sardinella aurita, Sprattus sprattus, Engraulis enchrasiculos, Trisopterus minutus, Chromis chromis, Oblada melanura, Spondyliosoma cantharus, Chelidonichthys lucernus*. Acoustic surveys, Proportion between catches and biomasses; Z=M+Y/B (see Description of groups). Visual census data (using mean species weight and assuming habitat area in Eastern Adriatic from 0 to 100 m distance from coast = 437 km^2)
P/B	0.850 year^{-1}	Bartulovic *et al.* (2004); Cingolani *et al.* (2004a); Cingolani *et al.* (2004b); Dulcic and Kraljevic (1995); Dulcic *et al.* (2000); Dulcic *et al.* (2003); Froese and Pauly (2007); Pallaoro *et al.* (1998); Sinovcic (2001); Sinovcic *et al.* (2004)	*Z=M+F* or from literature; *M* from eq. B3 in Brey (1999) and from literature. Inverted empirical eq. 19 in Christensen *et al.* (2005); assumed *GE*=0.12 for *S. aurita* and *T. minutus*, and *GE*=0.2 for *C. lucernus*
Q/B	8.776 year^{-1}		Empirical eq. 17 and 19 in Christensen *et al.* (2005)
GS	0.150	Coll *et al.* (in press); Link *et al.* (2006)	
DC	Table 1	Froese and Pauly (2007), Stergiou and Karpouzi (2002)	
Pelagic piscivorous fishes	Value	Source	Notes
B	3.311 t·km^{-2}	Azzali *et al.* (2002); Froese and Pauly (2007); Jukic-Peladic *et al.* (2001); Ragonese *et al.* (n.d.)	Species: *Trachurus mediterraneus, Trachurus trachurus, Alosa fallax, Micromesistius poutassou, Scomber scombrus, Scomber japonicus.* Acoustic surveys, MEDITS trawl surveys; Proportion between catches and biomasses; *Z=M+Y/B* (see description of groups).
P/B	0.899 year^{-1}	Froese and Pauly (2007); Ragonese *et al.* (n.d.); Santic *et al.* (2002); Sinovcic *et al.* (2004)	*Z=M+F* or from literature; *M* from eq. B3 in Brey (1999) and from literature. Inverted empirical eq. 19 in Christensen *et al.* (2005); assumed *GE*=0.2 for *A. fallax* and *S. scombrus*, and *GE*=0.1 for *M. poutassou*
Q/B	6.379 year^{-1}		Empirical eq. 17 and 19 in Christensen *et al.* (2005)
GS	0.150	Coll *et al.* (in press); Link *et al.* (2006)	

DC	Table 1	Froese and Pauly (2007)	

Zoobenthivorous fishes 1	Value	Source	Notes
EE	0.950	Christensen *et al.* (2005)	Species: *Callionymus lyra, Callionymus phaeton, Callionymus risso, Deltentosteus quadrimaculatus, Gobius bucchichi, Gobius cobitis, Gobius cruentatus, Gobius paganellus, Pomatoschistus marmoratus, Pomatoschistus minutus, Pomatoschistus norvegicus, Labrus merula, Symphodus cinereus, Symphodus melops, Symphodus ocellatus, Symphodus roissali, Symphodus rostratus, Symphodus tinca, Mullus barbatus, Mullus surmuletus, Boops boops, Diplodus annularis, Diplodus puntazzo, Diplodus sargus, Diplodus vulgaris, Lithognathus mormyrus, Sparus aurata, Hippocampus guttulatus.* Not enough reliable biomass estimates
P/B	0.776 year^{-1}	Azevedo and Simas (2000); Curtis and Vincent (2006); Dulcic and Glamuzina (2006); FAO Adriamed - Mullus Barbatus (2006); Froese and Pauly (2007); Kallianiotis *et al.* (2005); Kraljevic *et al.* (1996); Pallaoro and Jardas (2003); Stergiou and Karpouzi (2002)	$Z=M+F$; M from eq. B3 in Brey (1999). Inverted empirical eq. 19 in Christensen *et al.* (2005); Assumed GE=0.1 for *G. cobitis*, and GE=0.2 for *G. paganellus, D. annularis* and *S. aurata.*
Q/B	5.137 year^{-1}		Empirical eq. 17 and 19 in Christensen *et al.* (2005)
GS	0.300	Coll *et al.* (in press); Link *et al.* (2006)	
DC	Table 1	Azevedo and Simas (2000); Froese and Pauly (2007); Kallianiotis *et al.* (2005); Stergiou and Karpouzi (2002)	

Zoobenthivorous fishes 2	Value	Source	Notes
EE	0.950	Christensen *et al.* (2005)	Species: *Gaidropsarus mediterraneus, Gobius niger, Dicentrarchus labrax, Sciaena umbra, Umbrina cirrosa, Scorpaena notata, Scorpaena porcus, Serranus hepatus, Serranus scriba, Pagellus erythrinus, Pagellus acarne, Syngnathus acus, Trigla lyra, Trigloporus lastoviza, Merlangius merlangus.* Not enough reliable biomass estimates
P/B	0.648 year^{-1}	FAO Adriamed - Pagellus Erythrinus (2006); FAO Adriamed - Merlangius	$Z=M+F$; M from eq. B3 in Brey (1999). Inverted empirical eq. 19 in Christensen *et al.* (2005); Assumed GE=0.3 for *G. niger* and *P. acarne*, and GE=0.2 for *D. labrax* and *S. umbra.*

Q/B	3.954 year^{-1}	Merlangus (2006); Froese and Pauly (2007); Jukic-Peladic *et al.* (2001); Labropoulou *et al.* (1998); Spedicato *et al.* (2002); Zorica *et al.* (2006)	Empirical eq. 17 and 19 in Christensen *et al.* (2005)
GS	0.300	Coll *et al.* (in press); Link *et al.* (2006)	
DC	Table 1	Artuz (2005); Froese and Pauly (2007); Stergiou and Karpouzi (2002)	

European hake	Value	Source	Notes
B	0.0475 t·km^{-2}	FAO Adriamed - Merluccius Merluccius (2006)	Species: *Merluccius merluccius*. MEDITS trawl surveys
P/B	1.157 year^{-1}	FAO Adriamed - Merluccius Merluccius (2006)	$Z=M+F$; M from eq. B3 in Brey (1999). $F=Y/B$
Q/B	4.241 year^{-1}	FAO Adriamed - Merluccius Merluccius (2006)	Empirical eq. 19 in Christensen *et al.* (2005)
GS	0.150	Coll *et al.* (in press); Link *et al.* (2006)	
DC	Table 1	Stergiou and Karpouzi (2002)	

Rays	Value	Source	Notes
B	0.0127 t·km^{-2}	Jukic-Peladic *et al.* (2001)	Species: *Torpedo torpedo, Torpedo mormorata, Dasyatis centroura, Dasyatis pastinaca, Myliobatis aquila, Raja asterias, Raja clavata, Raja miraletus, Raja montagui.* MEDITS trawl surveys.
P/B	0.612 year^{-1}		Assumed GE=0.2 (also, close to value from Coll *et al.*, in press)
Q/B	3.058 year^{-1}	Abdel Aziz (1992); Filiz and Bilge (2004); Froese and Pauly (2007); Ismen (2003); SIBM (2006)	Empirical eq. 17 in Christensen *et al.* (2005)
GS	0.150	Coll *et al.* (in press); Link *et al.* (2006)	
DC	Table 1	Froese and Pauly (2007); Ismen (2003); Stergiou and Karpouzi (2002); Vannucci (2005)	

Sharks	Value	Source	Notes
B	0.0262 t·km^{-2}	Jukic-Peladic *et al.* (2001)	Species: *Mustelus mustelus, Scyliorhinus stellaris, Squalus blainvillei, Squalus acanthias, Mustelus asterias, Scyliorhinus canicula.* MEDITS trawl surveys.
P/B	0.264 year^{-1}	Filiz and Mater (2002); Froese and Pauly (2007), Jukic-Peladic *et al.* (2001); Opitz (1996)	*Z=M+F; M* from eq. B3 in Brey (1999). Inverted empirical eq. 19 in Christensen *et al.* (2005). *M* divided by 2, because it is probably overestimated (Rodriguez-Cabello and Sanchez, 2005)
Q/B	2.877 year^{-1}		Empirical eq. 17 and 19 in Christensen *et al.* (2005)
GS	0.150	Coll *et al.* (in press); Link *et al.* (2006)	
DC	Table 1	Cortés (1999); Froese and Pauly (2007)	

Seabirds	Value	Source	Notes
B	0.0088 t·km^{-2}	Matteo Griggio (Dept. Of Biology, University of Padova) and Lorenzo Serra (Ist. Naz. Fauna Selvatica) Pers. Comm.	*Larus michaellis, Larus melanocephalus, Larus ridibundus, Larus canus, Puffinus yelkuoan, Calonectris diomedea, Phalacrocorax carbo, Phalacrocorax aristotelis, Podiceps nigricollis, Podiceps cristatus.*
P/B	4.610 year^{-1}	Coll *et al.* (in press)	
Q/B	69.340 year^{-1}	Coll *et al.* (in press)	
GS	0.125	Coll *et al.* (in press)	
DC	Table 1	Coll *et al.* (in press)	

UPDATED ECOSYSTEM MODEL FOR THE NORTHERN BENGUELA ECOSYSTEM, NAMIBIA[1]

Sheila J.J. Heymans
Scottish Association for Marine Science, Dunbeg, Oban PA37 1QA, Scotland;
Email: Sheila.Heymans@sams.ac.uk

U. Rashid Sumaila
Fisheries Centre, 2202 Main Mall, Vancouver, BC, V6T1Z4, Canada;
Email: r.sumaila@fisheries.ubc.ca

ABSTRACT

An ecosystem model of the northern Benguela ecosystem from the coast to the 500 m depth contour (between 15°S and 29°S) was constructed for 1956. This model consists of 31 living compartments and detritus. It includes all the commercially important fish and marine mammal species in the ecosystem. The model was driven by effort time series for the 10 different fleets operating currently in the ecosystem, namely the purse seine, midwater trawlers and demersal fleets (all fishing from 1956 to 2003); the longline tuna fleet fishing from 1961 to 2003; the deep water crab fleet (1973–2003); the lobster fleet (1956–2003); commercial and recreational line fishery (1956–2003); seal hunt (1956–2003) and the seaweed collection fishery (1980–2003). The model was fitted by changing the vulnerabilities of predators to their prey and by estimating an environmental anomaly that was significantly correlated with sea surface temperature (negative correlation) and wind stress (positive correlation). The temporal model reproduced the general anchovy decline but was not able to reproduce the large increase in sardine in 1960 that was estimated by Virtual Population Analysis (VPA). The good fit of the hake and monkfish biomass in the model to the data was related to the high catches in the system, and their catches were reproduced very well, as were the catches of other demersal fish species and crabs. For predators such as seals, sharks and snoek the model reproduced the catch series well even when no good biomass estimates were available. The spatial model reproduced the known distribution of benthic species such as crabs and lobster as well as more mobile species such as seals, snoek, hake and others.

INTRODUCTION

Ecosystem models of the northern Benguela include those constructed by Heymans (1997), Shannon and Jarre-Teichmann (1999), Heymans and Baird (2000) and Roux and Shannon (2004) and span the time period from 1970 to 1999. Heymans (2004) examined the effects of internal (bottom up) and external (top down) control by means of ecosystem modelling from the 1970s onwards. Similarly, Cury and Shannon (2004) documented top-down control (fishing) and bottom-up control that initiated and sustained regime shifts or species replacements via environmental forcing. The aim of this model developement is to look at the northern Benguela over a longer time span and to model the system from 1956 onwards. A secondary aim is to look at the spatial patterns within the ecosystem.

By 1956 the main fisheries were either underway or just beginning. This report therefore describes an Ecopath model for 1956 where possible or for the 1950s in general, all the time series data available since then to reproduce these trends in Ecosim, and the spatial information available to construct an Ecospace model of the ecosystem.

---

[1] Cite as: Heymans, S.J.J. and Sumaila, U.R. 2007. Updated ecosystem model for the northern Benguela ecosystem, Namibia, p. 25–70. *In*: Le Quesne, W.J.F., Arreguín-Sánchez, F. and Heymans, S.J.J. (eds.) INCOFISH ecosystem models: transiting from Ecopath to Ecospace. Fisheries Centre Research Reports 15(6). Fisheries Centre, University of British Columbia [ISSN 1198-6727].

MATERIALS AND METHODS

Spatially the ecosystem model of the northern Benguela ecosystem extends between 15°S and 29°S from the coast to the 500 m depth contour, a total area of approximately 179,000 km^2. The model consists of 31 living compartments and detritus. The living compartments include 2 marine mammal groups, seabirds, 18 fish groups, 8 invertebrate groups and 2 primary producers. It includes all the commercially important fish, of which 6 species were divided between adults and juveniles, namely anchovy (*Engraulis japonicus*), sardine (*Sardinops ocellatus*), gobies (*Suffoglobius bibarbatus*), horse mackerel (*Trachurus trachurus capensis*), hake (*Merluccius* spp.) and jellyfish (mainly *Chrysoara hyoscella* and *Aequorea aequorea*). The main fisheries in the system are also defined, with economic and social information added for policy exploration.

Fishery

Best (2006) gives data on the French whaling fleet of the late 1700s, showing that French whalers fished in Walvis Bay and Tiger Bay (northern Namibia) from 1787 to 1793 at least. The English started whaling off the coast of Namibia in the nineteenth century and exploited guano from the offshore islands; by the latter part of the nineteenth century guano mining, sealing and fishing establishments at Sandwich Harbour were major commercial enterprises on the Namibian coast (Kinahan, 1991). Whaling off Namibia usually occurred from May to August (Best, 2006).

The first land-based commercial fishery in Namibia was established at Sandwich Harbour in 1851 where fish were caught with hook and line from rowboats, salted and sun dried, then shipped to South Africa, from where they were exported to Mauritius (Kinahan, 1991). The fishery caught silver kob (*Argyrosomus* spp.), steenbras (*Lithognathus aureti*), sea barbel (*Galeichthys feliceps*), hake and snoek (*Thyrsites atun*), and also exported fish oil that consisted of shark liver oil (Elasmobranchii), whale (various species) and seal blubber (Cape fur seal, *Arctcephalus pusillus pusillus*) (Kinahan, 1991). The natural closing of Sandwich Harbour in 1891 ended the fishery, and no commercial fishing took place for the next 73 years (Holtzhausen *et al.*, 2001).

According to Sparks (1984), most fishing before World War II was small scale and seasonal, and the industry only expanded after the war. Canning activities and fish oil production began in the 1950s and were based in Walvis Bay (Sparks, 1984). The South African fishers were being restricted in their own country and began moving into Namibian waters, and by the 1960s the catches had expanded rapidly (Sparks, 1984).

By the mid-1960s as many as 100 foreign vessels, under 15 or more national flags including the USSR, Poland and Spain, were fishing off Namibia (Fuller and Prommer, 2000). The Ukrainian fleet started fishing in the northern Benguela in 1963 and initially targeted sardine and Cape horse mackerel, but in 1968 hake became one of the principal target species (Romanov, 2001). The fleet switched between horse mackerel and hake depending on fishing success, but the fishery for sardine was stopped early (Romanov, 2001). In the mid-1980s hake biomass declined and regulatory measures for hake were introduced; the Ukrainian fleet shifted to chub mackerel (*Scomber japonicus*) (Romanov, 2001).

Ten fisheries were defined in the model to represent the dynamics of the fishery operations in the region from 1956 to 2003, namely:

1. Purse seine fishery

The pelagic purse seine fishery targeted sardine since before 1947 (Hampton, 2003) and anchovy since 1964. Lees (1969) found that in 1952 there were over 100 purse seine boats and 6 factories operational in Walvis Bay. Similarly, in 1953 there were 6 factories in Walvis Bay and Lüderitz and 100 small purse-seiners were catching 262,000 tonnes of sardine (Hampton, 2003), which were exported in 509,234 cartons of canned sardines (Lees, 1969). The factories had a quota of 90,000 tonnes each (Lees, 1969). By 1955 there were 217 boats, and in 1956 around 1.8 million cartons of canned sardines were exported (Lees, 1969). The pelagic fishery has always been situated around Walvis Bay and Lüderitz, and currently they fish mainly for juvenile horse mackerel, which is situated in the north (Hampton, 2003). Therefore the main ports of fishing for this fleet in the spatial model were Lüderitz and Walvis Bay.

In 1960, Hart and Currie (1960) reported that the pelagic fishes were "already being increasingly exploited and among them the South African pilchard takes first place as the basis of extensive fisheries at various points along the coast. Following closely in importance are fisheries for the 'maasbanker' (*Trachurus trachurus*), stockfish (*Merluccius capensis*) and snoek (*Thyrsites atun*), and many sharks are taken principally for their liver oil". In the early 1960s, the pilchard industry changed to trawling and small-scale line fishing, and two factories started freezing and salting fish for sale and export (Holtzhausen *et al.*, 2001). The canneries increased from 5 to 6 in 1961 and exported 4.7 million cartons of sardines that year (Lees, 1969). In 1963 the factories increased to 8 and in 1964 the fishery experimented with catching anchovy; the 7 boats that fished specifically for anchovy caught only 718 tonnes, while 4.5 million cartons of sardine were exported (Lees, 1969). By 1967 the quotas of the factories increased from 90,000 tonnes to 99,600 tonnes each, and two factory ships were also fishing off Namibia. In 1968 the factory quotas increased to 120,000 tonnes each, the factory ships had a combined catch of 630,000 tonnes and the Russian vessels took 300,000 tonnes of sardine (Lees, 1969).

Since the decline of these species in the early 1980s, the pelagic fishery has concentrated on juvenile horse mackerel, and operating with a mesh size between 11 and 23 mm they usually catch horse mackerel less than one year old (Vaske, 2001). Since 1990, the purse seine fishery is entirely Namibian-owned and consists of steel- and wooden-hulled vessels that operate out of Walvis Bay from mid-February to the end of August (Hampton, 2003). In 2000 the fleet consisted of 30 registered vessels between 21 and 49 m (99–614 tonnes), but by 2001 only 14 of these vessels were operational due to scarce fish (Hampton, 2003). The fleet has declined from 35 to 45 vessels in the 1980s to fewer than 15 vessels by 2000 in response to declining total allowable catches (TACs) (Boyer and Oelofsen, 2004). In 1999 there were still 40 vessels in operation, and that number had decreased to 13 by 2002 (Boyer and Oelofsen, 2004). These vessels are active for just a few months of the year and catch less than 10 tonnes per GRT (Gross Registered Tonnes) each year, while in the mid 1970s they caught 90 tonnes per GRT (Boyer and Oelofsen, 2004). Also, most of the Namibian canning and fishmeal plants are idle for much of the year (Boyer and Oelofsen, 2004). If the purse seine fleet catches more than 5% juvenile sardine, the area is closed to fishing for several weeks, although discarding of young sardine does take place (Boyer and Oelofsen, 2004). With the rights to exploit small pelagic fish, limited quotas for sardine and juvenile horse mackerel are issued, but there are no limitations on how much anchovy, round herring, chub mackerel and pelagic goby (*Suffoglobius bibarbatus*) is caught (Boyer and Oelofsen, 2004).

Effort time series for the purse seine fishery was estimated from the fleet hold capacity obtained for the fleet from 1956 to 1975 from Fuller and Prommer (2000), and the effort obtained from 1975 to 1987 from le Clus *et al.* (1988) (Figure 1).For 1988 to 2003 the effort was estimated to be related to the catch by using the average effort-to-catch ratio for 1980 to 1987, and the estimated effort showed a similar trend to the TACs set for the fleet from 1990 to 2001 (Nicols, 2004).

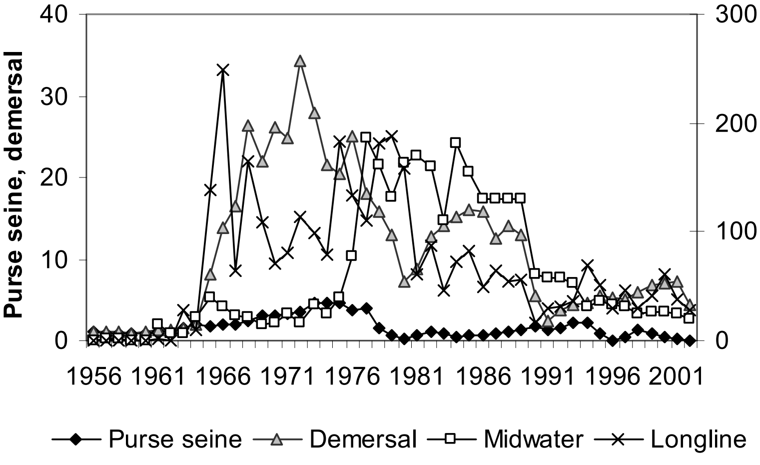


Figure 1. Effort time series (relative to 1956) used to drive the northern Benguela model for the purse seine, demersal, midwater and longline fleets.

2. Midwater trawl fishery

Klingelhoeffer (2006) suggests that the midwater trawl fishery started in the 1960s and catches mostly horse mackerel (Bauleth-D'Almeida *et al.*, 2001), which is mostly situated in the northern part of the ecosystem. However, no specification was made on the ports for this fishery and fishing is allowed anywhere in the spatial model.

The midwater trawl fleet uses nets of 60 mm mesh to target adults horse mackerel (17–48 cm), which occur offshore of the 200 m isobath, while the purse seine fleet uses nets of 12 mm mesh to catch juvenile horse mackerel of 6–20 cm inshore of the 200 m isobath (Bauleth-D'Almeida *et al.*, 2001). By 2001 the midwater fleet consisted of 25 large vessels from 75 m to 120 m with a maximum GRT of 7,765 tonnes; they process the catches at sea (Hampton, 2003). They are operational throughout the year. Most of the catch is frozen and transshipped to reefer vessels for export as a relatively low value product to West Africa, while 10% is reduced to fish meal and 5% is dried and salted ashore for export to African countries (Hampton, 2003). Bycatch of other species makes up about 2% of the catch of horse mackerel (Hampton, 2003). If catches of hake or young horse mackerel exceed 5% of the catch the fleet must leave the area (Boyer and Oelofsen, 2004).

To get an effort time series for the midwater trawl fishery, some calculations and assumptions had to be made. From the FAO catch statistics (FishStat), the nations fishing for Cape horse mackerel in 1986–1989 included South Africa, USSR, Cuba, Bulgaria, Romania, Japan, Israel, Angola, DRC, Poland, Spain, Portugal, Iraq and Namibia, while in 1990 the nations included South Africa, Russia (former USSR), Cuba, Bulgaria, Romania, Japan, Israel, Germany, Latvia, Lithuania, Estonia, Georgia, Ukraine and Namibia. In addition, the number of boats fishing from 1990 to 2004 was given by Klingelhoeffer (2006) starting at 100+ in 1990 down to 24 in 2004, while the effort by the most important fleets (USSR, Poland, Romania and Bulgaria) for 1973–1986 was given by Butterworth *et al.* (1990). Thus if one assumes that because there were the same number of nations fishing from 1986 to 1990, the number of boats in 1986 would be similar to the 100+ boats in 1989, and if their standardized effort did not change much over that time, then the number of boats can be calculated back to 1973 from the effort. In addition, if one uses total catch instead of effort, the number of boats is not significantly different; therefore, for 1955–1972 the same calculation was used but using catch instead of effort to back calculate the effort (Figure 1). This gives a very similar number of boats as the effort calculation for 1972–1986. However, to get an effort of 1 in 1956, the number of boats in 1986–1990 has to be increased to 130.

3. Demersal fishery

Klingelhoeffer (2006) suggests that a demersal trawl fishery was initiated in the 1950s and that the demersal trawl fishery targeting hake was dominated by Spain (Klingelhoeffer, 2006). By 1965 one hake processing plant was operational in Walvis Bay and by 1967, this had increased to 3 processing plants (Lees, 1969).

On the shelf, directed bottom trawling is carried out for hake, monkfish (*Lophius* spp.) and sole (*Austroglossus microlepis*) by a fleet of Namibian registered freezer and wet-fish trawlers based in Walvis Bay or Lüderitz, varying from 20 to 74 m in length and from 84 to 1,780 GRT (Stuttaford 1999 in Hampton, 2003). There were 111 such vessels in 2000. The larger vessels are capable of trawling to depths off the edge of the shelf or greater than 500 m (Hampton, 2003). The hake vessels operate throughout the year between the legal minimum depth of 200 m and the shelf edge and fish both by day and (less frequently) by night (Hampton, 2003). As the fleet includes both freezer and factory trawlers (Van der Westhuizen, 2001), it was assumed to fish over the whole area of the spatial model using the ports of Walvis Bay and Lüderitz for operational purposes.

Hake are principally caught by bottom trawling freezer/factory and wet-fish trawlers, but they are also caught by longlines and as bycatch in the monkfish and sole fishery and by the horse mackerel fishery (Van der Westhuizen, 2001). The hake fishery is the major contributor to employment in the fishing sector, and by 2000 there were about 4,500 shore-based and 2,500 sea-based employees in the hake fishery (Van der Westhuizen, 2001). The sector's contribution to the GDP was 1.7% in 1990 and more than 10% in 1999 (Van der Westhuizen, 2001).

The most abundant bycatch species in the hake-directed trawls are monkfish, kingklip, horse mackerel and snoek (Anon., 2001 in Hampton, 2003). Bottom trawlers used for hake fishing were used to estimate the percentage composition by weight of the main demersal taxa by survey between 1992 and 1996 (Hamukuaya *et al.*, 2001). This study found that on average 95% of the catch made by the demersal trawl consisted of teleosts, 3% of chondrichthyans and 2% of invertebrates, which included cephalopods, crabs, stomatopods, shrimps and lobsters (Hamukuaya *et al.*, 2001). These ratios were therefore used to estimate the catch of sharks and invertebrates from the trawl fleet. The breakdown of the teleosts and chondrichthyans show that cape hake dominate both the shelf and slope assemblages, but that shallow water hake (*Merluccius capensis*), horse mackerel and the goby dominate the shelf and upper slope area where the oxygen content is often low (Hamukuaya *et al.*, 2001).

The monkfish and sole vessels are generally smaller than the hake trawlers and do not operate as far from the coast, although they also fish throughout the year (Hampton, 2003). These high value fish are mainly exported to Europe in various frozen forms and the most abundant bycatch species in the trawls directed at monkfish and sole is hake (Hampton, 2003).

In 1994 an experimental license was given to one fishing company to fish in water exceeding 700 m for monkfish, deep water catfish (*Lepidion capensis*), warty dory (*Allocyttus verrucosus*), spiky dory (*Neocyttus rhomboidalis*), alfonsino (*Beryx splendens*), jewel squid (*Histioteuthis* spp.) and trachichthyids (*Hoplostethus* spp.) (Boyer *et al.*, 2001b). Viable fishing populations of orange roughy (*Hoplostethus atlanticus*) were found at 4 fishing grounds separated by 200 km (Boyer *et al.*, 2001b). The vessels that fish for orange roughy and alfonsino vary in length between 28 and 55 m, and they trawl down to depths of 600–900 m with heavy-duty trawl gear (Hampton, 2003). This fishery is too deep to be in this model, as the fish are not included in this ecosystem.

No effort time series was available for the demersal fleet, but the number of boats catching hake from 1991 to 2000 was obtained from Van der Westhuizen (2001) and showed a linear relationship with the biomass in that time period. Thus it can be assumed that the effort was linearly related to biomass for the whole time period (Figure 1).

4. Longline fishery

The most important longline fisheries for large pelagic species are those for tuna, particularly longfin or albacore tuna (*Thunnus alalunga*) and bigeye tuna (*T. obesus*), swordfish (*Xiphias gladius*) and large pelagic sharks. These species are caught by a fleet of Namibian and foreign bait-and-pole vessels and by foreign longliners. Most of the bait boat catches are made in the extreme south of Namibia, in contrast to the longline catches, which are more widely spread latitudinally and are generally further offshore, often outside of the Namibian exclusive economic zone (EEZ) (Hampton, 2003). Japanese and Taiwanese longliners have been fishing for tuna off Southern Africa since the early 1950s (Ryan *et al.*, 2002). In general the longline fleet is widespread and further offshore than the bait boats, which catch mainly in the south (Hampton, 2003). Thus, the fleet was operational throughout the whole spatial model area.

Hake are caught by 24 Namibian-owned deep longliners that operate from Walvis Bay and Lüderitz throughout the year (Hampton, 2003). The hake longline fishery started in the mid-1980s (Hampton, 2003). These catches are processed and exported as fresh fish to the lucrative European market (Hampton, 2003). Between 5,000 and 10,000 tonnes of hake are caught annually by the longliners (Hampton, 2003). The longliners have little effect on the sea bottom, but the effect on seabirds such as gannets and albatrosses is severe (Hampton, 2003).

Tuna is caught by approximately 30 local and foreign-owned pole or longline vessels (Hampton, 2003). The rights for tuna and swordfish fishery have recently been extended to include all large pelagics, and as there are no TACs for sharks they are being targeted and several thousand tonnes are now caught annually (Boyer and Oelofsen, 2004). As no estimate of effort was available for the tuna longline vessels and we have effort only for 1998–2003 for the hake longline vessels, we assumed that effort was related to catch for the longline vessels and specifically to the tuna catch as the hake catch was comparatively small (Figure 1). This is supported as, for the 5 years that the number of hake vessels are available (Nicols, 2004) it shows the same trend as the effort estimated from the tuna-catch derived effort.

5. Crab fishery

The red crab (*Chaceon maritae*) fishery started in 1973 and by 1974 there were 17 Japanese vessels and one mother vessel of 1,500 gross tonnes targeting this species (Beyers and Wilke, 1980). Effort declined due to marketing problems and by 1979 only 5 vessels were operating (Beyers and Wilke, 1980). By 2001 the number of vessels targeting this species had declined to 2 (Hampton, 2003). Beehive-type traps are used on a longline, with each vessel carrying 1,200 traps (Beyers and Wilke, 1980). The entire red crab catch is processed at sea and exported to Japan (Hampton, 2003). Crabs are caught in the north (Hampton, 2003) and are usually found in deep water with their main area of capture between 18°S and 21°S (Le Roux, 2001). The number of crab vessels per year from 1973 to 1986 was obtained from Melville-Smith (1988) and from 1998 to 2003 from Nicols (2004). A straight linear projection was made between the 5 boats in 1986 and the 3 boats in 1998 to give an effort series for this fleet (Figure 2).

6. Lobster fishery

The lobster (*Jasus lalandii*) fishery started in the 1930s. Rock lobster is caught in summer on shallow reefs off southern Namibia and taken in hoop nets from dinghies and in lobster traps set by 20 larger vessels (Hampton, 2003). Most of the lobster is cooked and exported to Japan (Hampton, 2003). The hub of the lobster fishery is Lüderitz, which was specified as the port of landing for this fishery in the spatial model.

Lobster effort time series in trap-days*10³ were obtained from Grobler and Noli-Peard (1997) for 1958 to 1996; we assumed that the effort in 1956–1957 was similar to that of 1958 (Figure 3). Pulfrich *et al.* (2003) give estimates of catch per unit effort (CPUE) from 1995 to 1999, which were used in conjunction with the catch to estimate an effort that was linearly scaled to those in Grobler and Noli-Peard (1997). For 2000–2003 the effort was assumed to be correlated with the catch and scaled accordingly.

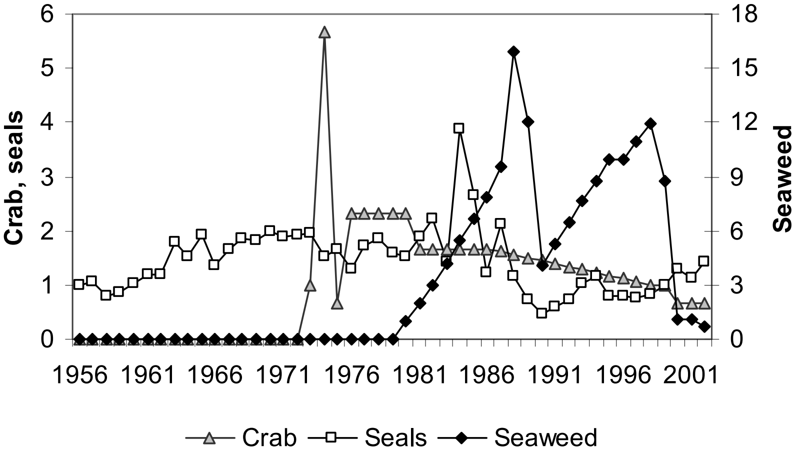


Figure 2. Effort (relative to the first year) with catch in the crab, seal and seaweed fisheries.

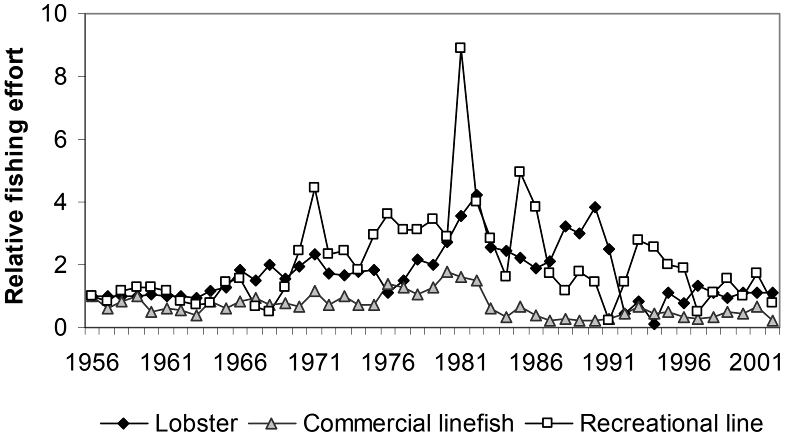


Figure 3. Effort (relative to 1956) in the lobster, commercial and recreational line fishery.

7. Commercial line fishery

The commercial line fishery uses rod–and–reels or hand lines with baited hooks for recreational fishers from the shore or from ski boats, or commercially from ski boats and line boats (Holtzhausen and Kirchner, 2004). Line boats are approximately 20 m long and carry up to 16 fishers using hand lines with two hooks each; they catch mostly kob, steenbras and snoek (Holtzhausen and Kirchner, 2004). By 2002 there were 20 firms registered as permit holders in the line fishing industry of which 7 were ski boat operators and 13 larger vessels (Stage and Kirchner, 2005). The commercial line fishery operates about 10 vessels in inshore waters up and down the coast from Walvis Bay (Zeybrandt and Barnes, 2001). The first catches from the line boats were recorded in 1964 for kob and in 1973 for steenbras (Holtzhauzen (1999) and Krichner (1998) in Holtzhausen *et al.*, 2001).

Ski boats are approximately 5–6 m long and carry between 4 and 6 fishers who work with one rod and reel each. They do not usually catch steenbras, but they catch all other species, while shore anglers do not usually catch snoek, but also catch most everything else (Holtzhausen and Kirchner, 2004). As we do not have any estimate of the commercial line fishery effort, it was assumed to be related to the catch of all kob, steenbras and snoek in the model (Figure 3).

The main areas that are open to the line fishery include the West Coast Recreational Area (WCRA), which stretches from the Ugab River mouth at 21°S to Sandwich Harbour at 23.5°S, with some fishing being possible in the Skeleton Coast Park north of the WCRA; however, no fishing is possible in the Namib Naukluft Park and Diamond Areas to the south (Holtzhausen and Kirchner, 2004).

8. Recreational line fishery

The most important recreational angling fish off Namibia are kob, West Coast steenbras, galjoen (*Dichistius capensis*), blacktail (*Diplodus sargus*) and various shark species such as the spotted gully shark (*Triakis megalopterus*), coppershark (*Carcharhinus brachyurus*), cowshark (*Notorynchus cepedianus*) and smooth houndshark (*Mustelus mustelus*) (Holtzhausen and Kirchner, 2004). Shore angling occurs along approximately 260 km of the Namibian coastline, between Sandwich Harbour to the mouth of the Ugab River (Zeybrandt and Barnes, 2001). Over 90% of the angling taking place in the WCRA in the vicinity of Walvis Bay, Swakopmund and Henties Bay (Stage and Kirchner, 2005), although there are also small sites north at Torra Bay and Terrace Bay in the Skeleton Coast Park and south near Lüderitz (Zeybrandt and Barnes, 2001). A small proportion of angling (<5% of effort and <3% of catches) is done for subsistence (Kirchner *et al.*, 2000). In the spatial model the main recreational fishing took place in the WCRA, at Torra Bay and Terrace Bay in the north and at Lüderitz in the south.

According to Holtzhausen *et al.* (2001), recreational fishery along the Namibian shoreline was anecdotally quite good prior to 1990, but no catch or effort data was available for the fishery except for the estimates obtained from Holtzhausen and Kirchner (2004) that indicated that the angling catch was about one third of the commercial catch for kob and steenbras. The effort of the recreational fishery (Figure 3) was assumed to be similar to the catch for all linefish species estimated by the Sea Around Us (www.seaaroundus.org) and other sources (see linefish below). The recreational shore angler pays most per fish and is therefore most valuable to the Namibian economy, while the commercial line fishery is worth only 1/7th the value of recreational fishery (Holtzhausen *et al.*, 2001). Barnes *et al.* (2004) studied the economic value of the recreational fishery and found that approximately 8,300 anglers spend a total of 173,000 days angling, and each angler spends about N$3,400 for a total expenditure between N$23 million and N$31 million or 2–4% of the total fishing sector.

9. Seal fishery

Seal harvesting has taken place in southern Africa since the seventeenth century, and legal controls were implemented in 1893 (Butterworth *et al.*, 1995). The first sealing company in Namibia started in 1895 at Cape Cross and by the end of that year the company had shipped 70 workers from Britain, Germany and South Africa (Berry, 2002). The company, Damaraland Guano Company, started off collecting guano and expanded into harvesting seals soon after (Berry, 2002). Data was available on the pup harvest since 1900 (David, 1989) and bulls since 1901 (Butterworth *et al.*, 1995). Winter harvesting is focused on the yearlings and during summer it is limited to the bulls (Hart and Currie, 1960). Cows were only harvested in the late 1980s and early 1990s (Butterworth *et al.*, 1995). Legislation controlling the utilization of seals in Namibia was introduced in 1922 (Berry, 2002). Seal pelts and genitalia are exported, while oil and meat are also produced (Wickens *et al.*, 1991). The seal fishery occurs mainly at Cape Cross (21.5°S) (Wickens *et al.*, 1991) and was entered into the spatial model this way. No effort was available for the seal fishery, and it was assumed to be related to the catch of seals (Figure 2).

10. Seaweed harvest

Formal seaweed harvesting started in 1980 (Hampton, 2003), although prior to that informal harvesting was taking place. Beach-cast *Gracilaria* are collected and supplemented with *Gracilaria* growing on longlines (Hampton, 2003). A company was established in Lüderitz in 1992 that can process up to 6,000 tonnes of seaweed annually to the agar stage, and good prices are obtained on the world market because the gel strength is very high (Hampton, 2003). The company, Taurus Atlantic Seaweeds, cultures *Gracilaria* in a 40 ha plot in the Lüderitz lagoon (Anon., 2005). Thus the seaweed fishery only occurs in the Lüderitz bay area of the spatial model (Rotmann, 1987; Critchley *et al.*, 1991; Hampton, 2003). The annual production of *Gracilaria* is around 120 tonnes of dry weight per year, and the operation employs 50 people (Anon., 2005). The effort of this fishery was assumed to be related to the catch for the fishery (Figure 2).

Management

In June 1949 the South West African Administration, the government of what was then South West Africa, passed the Sealing and Fishing Ordinance, which gave the Administration considerable power over all fishing activities (Lees, 1969). It specified the maximum quantities of any specific fish species that could be treated in the factories, and it limited the number of fishmeal and oil reduction plants and floating processing factories (Lees, 1969). It provided for taxes on fish and fish products, closed seasons and sanctuaries and collected statistics from fishermen and factory owners (Lees, 1969). A laboratory was built in Lüderitz but closed down quickly, and by the 1960s research was carried out by the Marine Research Laboratory in Walvis Bay (Lees, 1969). In 1950 the first scientist was appointed and in 1952 the first research vessel, the *Namib II*, was launched (Lees, 1969). For the first few years anyone with a licensed boat could catch fish, and there were no restrictions on the tonnage landed, so that by 1952 there were 11 industrial sites in Walvis Bay and the fourth major factory was being built (Lees, 1969). There were also canneries in Lüderitz mainly for the canning of lobster (Lees, 1969). By the late 1960s there were 8 factories processing pelagic fish in Walvis Bay and 3 processing hake (Lees, 1969). The factories had a limit of 90,000 tonnes of pelagic fish until 1967 when the limit was increased to 99,600 tonnes and in 1968 to 120,000 tonnes (Lees, 1969). During that time 2 processing ships were also fishing off Namibia, and their TAC was limited to 570,000 short tons in 1969 (~520,000 tonnes) and 500,000 short tons (~450,000 tonnes) in 1970 (Lees, 1969). The Division of Sea Fisheries in Cape Town assumed control of the South West African research organization in 1969 (Lees, 1969).

From the 1970s to 1990 horse mackerel (and hake) was assessed by the International Commission for Southeast Atlantic Fisheries (ICSEAF) through the Standing Committee on Stock Assessment (Anon., 2001). The Ministry of Fisheries and Marine Resources of Namibia took over the assessment in 1990 (Anon., 2001). Scientists from the Ministry of Fisheries and Marine Resources based their recommendations on acoustic surveys and age- and length-based VPA estimates from commercial data (Maurihungirire, 2004).

Under ICSEAF a TAC for horse mackerel was introduced in 1980, intensifying fishing for this species, and regulatory measures were only imposed on the foreign fleet while unrestricted catches were allowed by the local purse seine fleet (Anon., 2001). The only limiting factor on the local fleet was the closed fishing season in August (Anon., 2001). The TAC was estimated based on an age-based VPA model (Bauleth-D'Almeida, 2001).

Since Namibian independence in 1990, fishing is limited through output controls that consist of individual non-transferable quotas, and catches must be landed at one of two fishing ports while transshipments at sea are not permitted (Boyer and Boyer, 2004). Catches are landed at one of two fishing ports under the control of fisheries inspectors, and patrol vessels, aerial patrols and on-board observers ensure that the legal requirements are met (Boyer and Boyer, 2004). Ninety percent of the landings are from TAC-controlled stocks and therefore the Namibian authorities can control the fishing pressure of these stocks (Boyer and Boyer, 2004). Scientific personnel from the Ministry of Fisheries and Marine Resources base their recommendations on acoustic and midwater trawl surveys, with TACs being recommended for sardine at 18% of the survey biomass at the end of the previous fishing season (Maurihungirire, 2004). In Namibia, no edible or marketable fish taken as bycatch may be discarded, and this is monitored by ship-board observers, with levies being paid on the bycatch that would discourage targeting of such species (Boyer and Boyer, 2004).

Subsequent to 1990, when Namibia declared their EEZ, a fishing mortality of $F=0.3$ year^{-1} was instituted for horse mackerel, which corresponded to an exploitation rate of 26% ($C/B=0.26$) (Anon., 2001). A quota was allocated to the pelagic fishery to prevent the removal of large quantities of juvenile horse mackerel, while bycatch, size and depth restrictions were instituted (Anon., 2001). Limitations were introduced on 1) bycatch to prevent high catches of juvenile hake and pilchard, 2) size and 3) depth, with restrictions of 200 m to curb high catches of juvenile hake, pilchard and juvenile horse mackerel (Bauleth-D'Almeida, 2001). It was proposed that the midwater fleet vacate an area whenever the proportion of horse mackerel <17 cm total length (TL) in a haul exceeded 5% by weight and high catches (5% per set) of horse mackerel <12 cm were discouraged (Bauleth-D'Almeida, 2001).

For hake, the TAC is based on trends in abundance during fishery-independent bottom trawl surveys while making adjustments to allow for fish off the bottom at night, as determined acoustically, with the TAC set at 20% of the estimated biomass of mature hake (Maurihungirire, 2004). In 1998 an Interim Management Procedure was implemented and the TAC was adjusted according to the mean change in the survey and catch rate indices for the previous 5 years (Butterworth and Geromont, 2001; Maurihungirire, 2004).

Red crab management is based on length-based cohort analysis and predictive models, with TACs recommended on the basis of a projection of future biomass of the stock as a function of the catch (Maurihungirire, 2004).

Namibia has developed a management plan for orange roughy, operational management plans for hake and seals and national plans of action (NPOA) are being drafted for seabirds and sharks (Boyer and Boyer, 2004). Illegal fishing within Namibia's EEZ is believed to have been virtually eliminated as only one incident has been recorded since 1995 (MFMR 2002a in Boyer and Boyer, 2004).

Economics

Fish exports from Namibia have increased from about N$830 million in 1992 to N$2,6 billion in 2000 (Boyer and Boyer, 2004). The value of the major industrial fisheries in Namibia in 2000 was given by Sumaila *et al.* (2002). In general, prices for species were obtained from Sumaila *et al.* (2007). Prices for sharks caught by longlines and the commercial line fishery were assumed to be similar to those obtained by the demersal trawl fishery, while sharks caught by the recreational fishery had higher prices. Recreational linefish prices were estimated based on the catch of linefish caught by the recreational fishery (approximately 1000 tonnes) times the value of the catch, approximately N$7 million, giving a price of N$12,363.59 per tonne. This price was also used for sharks caught by the recreational fishery. Tuna caught by the purse seine fleet was assumed to have the same price as those caught by the bait fishery. The export price per tonne for seaweed was US$1,250 in 1994. Prices for seals were obtained for 2000 from Hugo (2006) and all prices are given in Table 1.

Table 1. Landed value in Namibian dollars (N$) for the different species caught in the northern Benguela by fleet.

Group Name	Purse seine	Midwater trawler	Demersal	Long lines	Crab traps	Lobster	Com. line fishery	Recr. line fishery	Seal -ing	Other
Seals									621	
Sharks			6,597	6,597			6,597	12,364		
Tuna	7,479			24,150			7,479			
Snoek		3,158					6,597			
Other linefish							6,597	12,364		
Anchovy	371									
Sardine	834									
Gobies	371									
Other s. pelagics	371									
Mesopelagics	371									
Juv. h mackerel	397									
Adult h mackerel		2,065								
Juv. hake		3,158								
Adult hake			5,685							
Monkfish			7,220							
Other demersals			6,597							
Crabs					11,357					
Lobster						71,700				
Benthic producers										1,028

In terms of product value the fishery for kob and other angling species in Namibia is insignificant compared with the major commercial fisheries (Hampton, 2003). However, the recreational fishery is an important tourist attraction and generates considerable expenditure far in excess of the product value. Kirchner *et al.* (2000) estimated that between October 1997 and September 1998, some 8,800 anglers spent 173,000 days angling and had direct expenditures totaling almost N$30 million. Value added to gross national income within the shore-angling fishery during that period was estimated at N$14 million (Hampton, 2003). Foreign visitors contributed 55% of the expenditure, and ski boat fishermen contributed about N$2 million annually to Namibia's GDP, while the line boat fishery contributed about N$3.4 million (Kirchner, 1998 in Holtzhausen *et al.*, 2001). The total contribution by the line fishery to the GDP was N$35 million.

The total export value of trawled hake in 2000 was N$1.58 billion, more than the N$837 million in 1998, and 62% of this value was obtained from wet-fish hake and 38% from hake frozen at sea (Hampton, 2003). Monkfish exports in 2000 amounted to N$158.8 million, which is 10% more than in 1999. In 2000 horse mackerel exports from the midwater fishery were valued at N$596 million, and approximately 3% of the catch is consumed in Namibia (Hampton, 2003). The purse seine fishery exported N$117 million worth of sardine in 2000 compared to the N$320 million in 1998 (Hampton, 2003). Similarly, the export of horse mackerel from the pelagic fishery also declined from N$60 million in 1998 to N$15.8 million in 2000 (Hampton, 2003).

The rock lobster trap fishery contributed N$34 million in 2000 and N$26 million in 1999 (Hampton, 2003). The rock lobster fishery is important as it is a relatively low capital, labour intensive industry that provides employment in a part of the country that has very high unemployment (Hampton, 2003). The crab fishery amounted to N$35 million in 2000 and N$25.5 million in 1999 (Hampton, 2003). The value of all tuna exported from Namibia in 2000 was N$29 million compared to the N$16 million in 1999 (Hampton, 2003). Seaweed harvesting started in 1980 and in 2000 829 tonnes were harvested with an export value of N$3,850,000 (Hampton, 2003).

Profit and loss was estimated from data obtained from the annual fisheries income and expenditure report from the Ministry of Fisheries and Marine Resources for 1997, where the net profit divided by the total income from the fishery gave the percentage profit for each year (see Table 2 below). The profit for the seaweed industry was estimated at 13% by Rotmann (1987). For recreational line fisheries the profitability was estimated from the income of N$47.9 million and the profit of N$23.9 million obtained from Stage and Kirchner (2005). For seals and tuna we assumed a high profit margin of 40% (Table 2).

Table 2. Income, expenditure, profit and percentage profit for the different fleets in Namibia (Namibian $).

Fishery	Income	Expenditure	Net Profit/Loss	% profit
Purse seine	309,327,946	319,638,333	-10,310,387	-3
Midwater	242,779,080	219,722,050	23,057,030	9
Demersal	756,066,479	795,463,632	-39,397,153	-5
Longline tuna*				40
Crab	254,809,630	207,414,600	47,395,030	19
Lobster	26,896,000	22,514,520	4,381,480	16
Commercial line fishery	1,593,740	1,237,870	355,870	22
Recreational line	-	-	-	50
Seals*	-	-	-	40
Seaweed	-	-	-	13

* assumed

The number of jobs that each fleet supports was estimated from the Ministry of Fisheries and Marine Resources for the purse seine, midwater, demersal, crab, lobster and commercial line fisheries, while the data for the recreational fishery was obtained from Kirchner *et al.* (2000) and for tuna from Armstrong *et al.* (2004). For the seaweed industry a value of 50 jobs was obtained from Anon. (2005) while Critchley *et al.* (1991) estimated that the industry supported 250 jobs in 1986. These jobs were converted to jobs/catch value by dividing them by the value of each catch (Table 3). For seals, Hugo (2006) suggests that between 14 and 150 migrant and part-time workers cull seals from August to November.

Model compartments

In this section the different functional groups of the model is described including the input data used in the model construction, and where necessary the data used to split groups into adult and juvenile groups. In addition, the spatial distribution of groups are described as input data used for the Ecospace model (see habitat map in Figure 26).

Table 3. Number of jobs per catch value for each of the fleets operational in Namibia

Fishery	Jobs/value
Purse seine	52
Midwater	1
Demersal	9
Longline	96
Crab	42
Lobster	28
Commercial line fishery	14
Recreational line	25
Seals	46
Seaweed	6

1. Marine mammals

Hart and Currie (1960) found that there were not many whales in the Benguela and they attributed this to the cold water, since specifically sperm whales do occur in Saldanha Bay and north of the Benguela but not in the cold upwelling areas. The marine mammals (other than fur seals) off Namibia include southern right whales (*Eubalaena australis*), humpback and minke whales (*Balaenoptera acutorostrata*) and small Odontocetes (Roux *et al.*, 2001). Humpback whales (*Megaptera novaeangliae*) and Bryde's whales (*Balaenoptera edeni*) also occur off the west coast of southern Africa (Griffiths *et al.*, 2004). Sightings and surveys of southern right whales indicate that there were at least one adult and calf in 1971 and maybe about 10 adults and one calf in 1999, but there is no defendable trend in population size in the data (Roux *et al.*, 2001). Du Pasquier (1990, in Best, 2006) listed 7 whaling grounds on the west coast of southern Africa that were utilized by French whalers in the late eighteenth century, of which Walvis Bay (23°S), Elizabeth Bay (27°S) and Alexander Bay (28°S) are in Namibian waters. From these descriptions and Findlay *et al.* (1992), it is evident that to some extent marine mammals occur in all areas of the northern Benguela ecosystem.

The Odontocetes include dusky (*Lagenorhynchus obscurus*) and Heaviside's (*Cephalorhynchus heavisidii*) dolphins, with a biomass of 1,220 tonnes in the 1980s, although Shannon and Jarre-Teichmann (1999) quadrupled that biomass to include all other species of whales and dolphins. The bottlenose dolphin (*Tursiops truncatus*) was found near shore in the vicinity of Walvis Bay and further north, and the southern right whale dolphin (*Lissodelphis peronii*) is know to occur off Lüderitz (Findlay *et al.*, 1992). The production to biomass ratio (P/B, 1.0 year^{-1}) and production to consumption ratio (P/Q, 7.9%) as well as diet from the 1980s model was used: 1.4% anchovy, 1.4% sardine, 19.3% lanternfish, 6.9% goby, 11.7% small pelagics, 27.5% hake and 31.8% cephalopods (Shannon and Jarre-Teichmann, 1999). The juvenile hake was reduced to 10% and 17.5% added to adult hake in the diet composition.

2. Seals

There are 15 breeding and 4 non-breeding Cape fur seal (*Arctocephalus pusillus pusillus*) colonies along the Namibian coast (De Villiers *et al.*, 1997). According to Mecenero *et al.* (2006) who wrote on the spatial distribution of the diets of seals, there are two main areas of seal aggregations: Cape Cross (21°47'S and 13°57'E, with 187,000 seals in 2001) and Lüderitz (Van Reenen Bay, Atlas Bay and Wolf Bay, south of Lüderitz, around 27°S and 15°E, with 173,000 seals in 2001). These two areas and the 200 km forage range around them were classified as essential habitat for seals (Mecenero *et al.*, 2006). Hampton (2003) gave numbers of seals extrapolated from the aerial pup sensus, which showed that there were smaller hallouts for seals at Cape Frio and between Sandwich Harbour and Sylvia Hill not shown by Mecenero *et al.* (2006). Seals are therefore prevalent in the Skeleton Coast Park and the West Coast Recreational Area of the spatial model.

South African fur seals were harvested off Namibia since the nineteenth century, with between 75 and 296 tonnes of fish and oil (from shark liver, seals and whales) being exported from Sandwich Harbour between 1863 and 1876 (Kinahan, 1991). Sealing off Namibia was not controlled until 1922, when the Sealing and Fishing Proclamation was passed, and since 1973 sealing was managed under the Sea Birds and Seals Protection Act (David, 1989). The number of pups, bulls and cows harvested in all of southern Africa between 1901 and 1992, the modelled number of pups and total population between 1920 and 2013 and the average weight of pups (age 1=23 kg) and adults (90 kg) were obtained from Butterworth *et al.* (1995), while the average weight of bulls (150 kg) was obtained from Griffiths *et al.* (2004).

From Appendix II in Butterworth *et al.* (1995) it is estimated that between 1972 and 1993 on average 63% of the fur seal population lived on the Namibian coast. Catches of seal pups were given by David (1989) and by Butterworth *et al.* (1995) for pups, bulls and cows separately, but these estimates were for the whole population (including South Africa). The same ratio of 63% was applied to the catch and the average weights for pups, cows and bulls (Butterworth *et al.*, 1995) were used to calculate the total catch from 1950 to 1979 (Figure 4). From 1980 to 1990 the ratio between catches made in South Africa and Namibia obtained from Wickens *et al.* (1991) was used, and since 1990 no seals were caught in South Africa (Griffiths *et al.*, 2004). The catches of pups and bulls in Namibia between 1993 and 2001 were obtained from Griffiths *et al.* (2004), and the total number of seals caught in 2002 was obtained from Nicols (2004), but he did not indicate if they

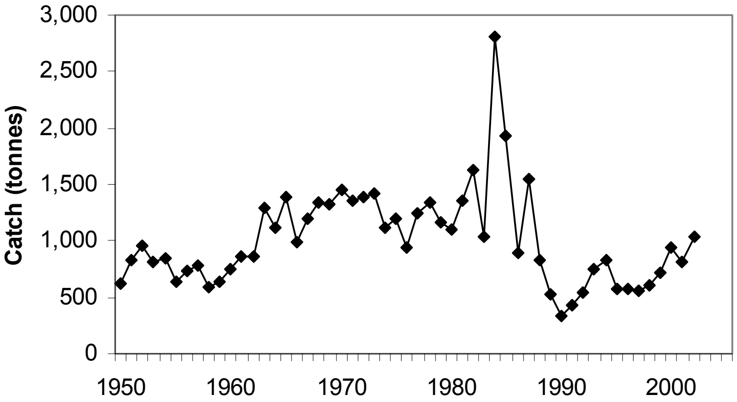


Figure 4. Catch (tonnes) of fur seals from 1950 to 2002 in the northern Benguela ecosystem.

were pups or adults. Using the ratio of pups to bulls (14:86) obtained from the catch for 1980-2001, the catch was estimated for 2002. Miller *et al.* (1996) found that thousands of seals are regularly trapped in trawl nets with 0.5% of the population dying this way (Wickens, 1994 in Miller *et al.*, 1996) and that 66% of the seal bycatch was trapped in midwater research vessels with only 34% trapped by bottom trawlers.

According to Shannon and Jarre-Teichmann (1999) the biomass was estimated at 51,763 tonnes. Using an average weight of 80 kg for adults with the Butterworth *et al.* (1995) time series gives a similar average biomass for the 1980s; thus that is used here, giving an increase biomass from 18,000 tonnes in 1950 to 90,000 tonnes in 2005. However, in the 1990s the population declined by more than a third due to lack of food, down from 922,396 seals in 1992–1993 to 476,074 in 2001–2002 (Roux, 1999 in Hampton, 2003). Assuming this was a linear decline and using a proportion of 78% adults in the population the total population was estimated until 2001 and assumed to be constant until 2003 (Figure 5). The estimate of biomass (0.289 t·km^{-2}) calculated from Butterworth *et al.* (1995) was too high to fit the model and it was reduced to 0.15 t·km^{-2}.

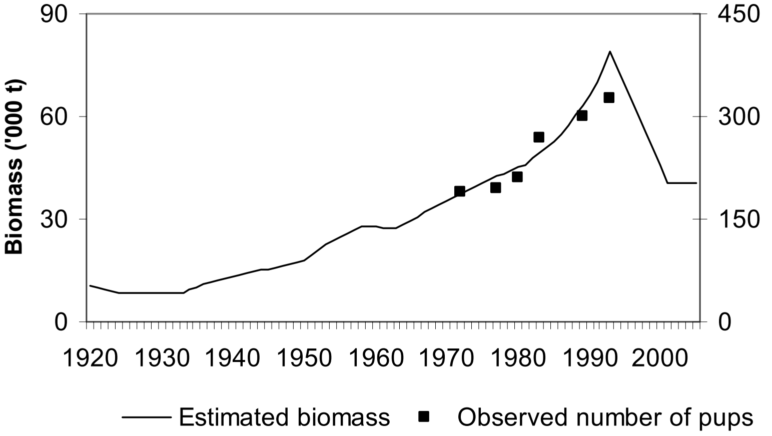


Figure 5. Biomass (*1000 tonnes) estimated and number of pups (thousands) observed for fur seals in the northern Benguela ecosystem.

The P/B ratio of 0.94 year^{-1} was obtained from Shannon and Jarre-Teichmann (1999) and according to Balmelli and Wickens (1994) the Q/B for seals is 19.4 year^{-1}. However, the P/B ratio of 0.94 year^{-1} was much too high and a P/B of 0.08 year^{-1} was used to fit the model. In addition a biomass accumulation of 0.005 t·km^{-2}·year^{-1} was included to increase the population to fit the model.

Much of the diet of seals is made up of fish; pelagic goby, horse mackerel and juvenile hake are the most important species (David, 1989 in Boyer and Hampton, 2001), but reports of fur seal predation on penguins have increased (Crawford *et al.*, 2001). Between 1974 and 1985 the diet was reported to be 3.6% anchovy, 23.6% horse mackerel, 2.6% sardine, 0.7% lanternfish, 52.9% goby, 4.6% snoek, 3.5% hake and 8.4% cephalopods (David, 1987). The 53% of gobies was divided between gobies and other small pelagics using the ratio of those two species in the diet suggested by Mecenero *et al.* (2006) giving a breakdown of 6% gobies and 47% small pelagics.

The diet given in Mecenero *et al.* (2006) had a much larger proportion of hake and sardine than that of the earlier years. Mecenero *et al.* (2005) found that only 0.1% of the frequency of the diet of female fur seals contained bird feathers, specifically those of penguins and cormorants, but reports that Rand (1959) in Mecenero *et al.* (2005) found 0.8%. Thus we added that percentage to the diet, and at first a value of 1% was used. According to Cury and Shannon (2004) and references therein, seals fed on sardines prior to the sardine decline and have since switched to goby, supplemented by myctophids in the southern part of the northern Benguela and horse mackerel in the central and northern parts.

To balance and fit the model the 4.6% snoek in the diet of seals was reduced to 2.6% and 0.01% added to linefish. Adult anchovy in the diet was increased from 3.7% to 50% to fit anchovy; adult sardine was increased to 10.1% and small pelagics were reduced to 3.7% to both these groups. The 23.6% of juvenile horse mackerel was reduced to 10% juveniles and 3.6% added to adult horse mackerel, adult sardine and adult anchovy respectively. Juvenile hake was reduced to 1% and 2.5% added to adult hake. The 8.4% of cephalopods were reduced to 3% and the rest added to sardine.

3. Birds

The gannets (*Morus capensis*) and cormorants (*Phalacrocorax capensis*) are widespread along the Namibian coast, but the penguins (*Spheniscus demersus*) tend to be found close to their breeding range and their northern limit is 25°S (Hampton, 2003). In addition to these species, the shy (*Thalassarche* *cauta*), black-browed (*T. melanophris*) and yellow-nosed (*T. chlororhynchos*) albatrosses and white-chinned petrel (*Procellaria aequinoctialis*) are also found (Ryan *et al.*, 2002), although they do not necessarily breed in Namibia. Cape gannets breed on islands off southern Namibia and Cape cormorants breed on the nearshore islands and guano platforms (Boyer and Hampton, 2001). African penguins also breed on islands off Namibia, and sardine and anchovy used to be their main prey, but now, as with cormorants, pelagic goby is more important as sardine is scarce (Crawford *et al.*, 1985). Cormorants are generally dependent on large, surface-schooling fish with anchovy and sardine being their preferred prey species (Crawford *et al.*, 1985).

Other bird species also found in Namibia include great, crowned (*Phalacrocorax coronatus*) and bank cormorants (*P. neglectus*), white pelicans (*Pelecanus onocrotalus*), kelp gulls (*Larus dominicanus vetula*), gaint petrels (*Macronectes giganteus*), Pintado petrels (*Daption capense*), great-winged petrels (*Pterodroma macroptera*), white-chinned prions (*Procellaria aequinoctialis*), Cory's shearwater (*Calonectris diomedea*), storm petrels (*Hydrobates pelagicus*), Sandwich terns (*Sterna sandvicensis*), Damara terns (*S. balaenarum*) and Arctic terns (*S. paradisaea*) (Crawford *et al.*, 1991; Best *et al.*, 1997).

Four islands off Namibia account for 97% of the population of African penguins in Namibia, namely Possession, Halifax, Ichaboe and Mercury islands (Kemper *et al.*, 2001). Since 1990 the breeding population decreased by 3.7% per year, which is shown by the active nests on these four islands (Kemper *et al.*, 2001). The general trend in penguin numbers from 1956 to 2000 is also given by Kemper *et al.* (2001), showing a decline of 2.8% per year from the approximately 100,000 adults in the 1950s (Figure 6). The decline between 1950 and 1985 is due to the exploitation of their eggs (Frost et al., 1976 in Kemper *et al.*, 2001) and scarcity of food (Kemper *et al.*, 2001). Similarly, gannets declined to 21% of their mid-1950s population, although cormorants seem to have increased to more than double the 1950s population (Crawford *et al.*, 1991). The changes in these species show that their biomass changed from 1,934 tonnes to 1,272 tonnes between the 1950s and 1980s. Crawford *et al.* (1991) give estimates of bird biomass of 1,867 tonnes in 150,000 km^2 and a P/B of 0.16 $year^{-1}$ with a Q/B of 120.3 $year^{-1}$. Using the change in biomass of the penguins, cormorants and gannets between the mid-1950s and 1980s, a biomass of 2,532 tonnes or 0.017 $t \cdot km^{-2}$ was estimated for the 1950s model if we assume that all other species stayed constant.

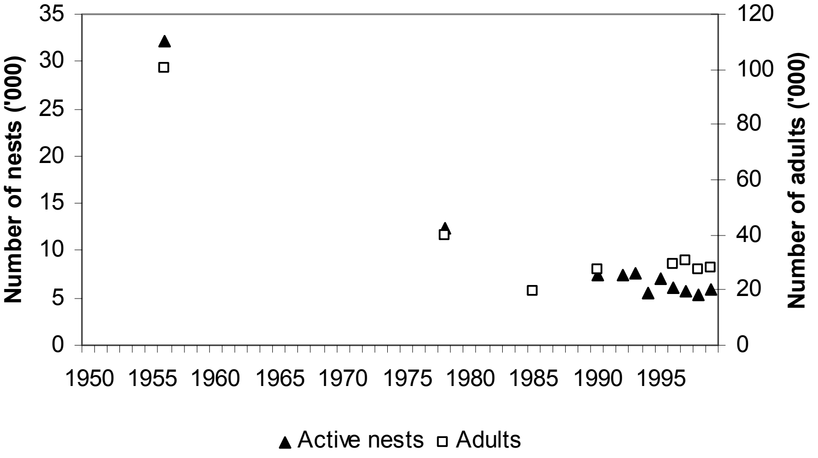


Figure 6. Number of penguin nests and adult penguins (thousands) in the northern Benguela ecosystem from 1950 to 2000.

Seabirds are often caught in longlines, specifically tuna longlines (Ryan *et al.*, 2002). The bycatch rate in the late 1990s on the west coast of South Africa was 0.48 birds killed per 1,000 hooks set (Ryan *et al.*, 2002), while the bycatch rate in the southern hemisphere is on average 0.4 birds per 1,000 hooks (Ryan *et al.*, 2002). In South Africa it was estimated that in the late 1990s between 19,000 and 30,000 birds, of which 70% were albatrosses, were caught annually (Ryan *et al.*, 2002), but no estimate is available for the Namibian longline fishery.

Penguins feed on shoaling epipelagic fish, such as anchovy and sardine, and regional trends in their abundance are associated with trends in their prey (Crawford *et al.*, 2001). As sardine have collapsed, the range of penguins in Namibia contracted northwards, with populations at Mercury and Ichaboe islands not being affected by the collapse of sardine as pelagic gobies provided alternative food at these two islands (Crawford *et al.*, 2001). The diet of seabirds was estimated at 0.3% copepods, 4.3% euphausiids, 4.4% cephalopods, 1.1% sardines, 21.4% anchovy, 0.5% horse mackerel, 5.3% mesopelagics, 46.6% gobies, 3.7% other pelagics, 10.3% hake, 0.2% seals and 0.1% seabirds (Shannon and Jarre-Teichmann, 1999). A small fraction of the diet of birds (0.001%) was assumed to be of seal pups on the colony, and the 21.4%

anchovy was increased to 25.3% to fit and the 46.6% of gobies was reduced to 42.9%. The 10% hake was reduced to 1% and 10.8% added to other demersals. As seabirds are a large group that includes both breeding and non-breeding seabirds, this group was assumed to occur in all areas of the spatial model.

4. Sharks

Three shark species were obtained from the demersal assemblages off Namibia in the 1990s, namely the soupfin shark (*Galeorhinus galeus*), African sawtail catshark (*Galeus polli*) and Izak catshark (*Holohalaelurus regani*) (Hamukuaya *et al.*, 2001). In addition, Macpherson and Gordoa (1992) caught dogfish (*Deania profundorum*), thornback skate (*Raja cf. clavata*), blancmange skate (*Raja wallacei*) and *Raja confundens*, yellowspotted catshark (*Scyliorhinus capensis*) and longnose spiny dogfish (*Squalus blainvillei*). Finally, Ebert (1996) found that the sevengill shark (*Notorynchus cepedianus*) was one of the more common species of elasmobranchs caught during angling competitions and they did not travel very far. As the shark group includes pelagic and benthic sharks, rays and skates, it is assumed that sharks occur in all areas of the spatial model.

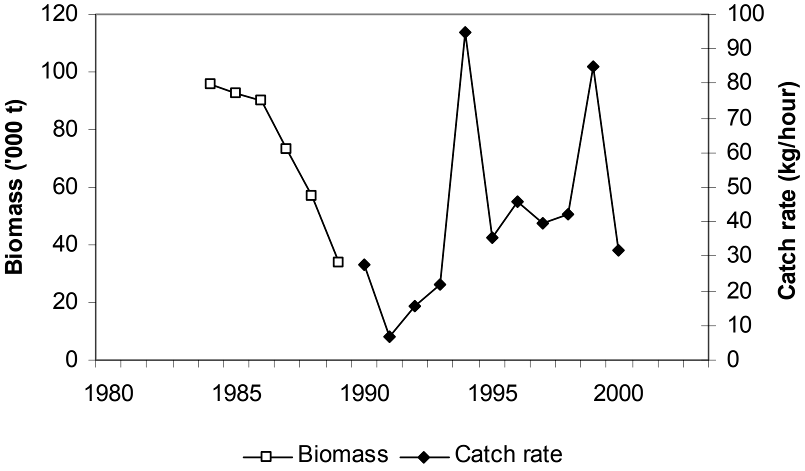


Figure 7. Biomass estimated (*1000 tonnes) and catch rates in kg/hour for sharks and skates in the northern Benguela ecosystem from 1980 to 2000.

Kinahan (1991) suggested that shark were already being fished off Namibia for liver oil in the 1800s and were fished out by 1885. The bycatch of sharks was obtained from the Sea Around Us webpage and divided into the demersal, midwater, hand line and other line fisheries in relation to the total catches for those fisheries in this database. The line fisheries were divided into longline and bait boat fisheries in the ratio that tuna were caught by those gears.

Biomass estimates for 1983–1990 (Figure 7) were obtained from Macpherson and Gordoa (1992) and were in the same range as the 67,180 tonnes reported by Shannon and Jarre-Teichmann (1999), with an average of 73,608 tonnes. This could be used as a first estimate for biomass, although the 1950 biomass might be higher due to reductions by the hake fishery and other demersal fisheries.

Bianchi *et al.* (2001) gave estimates of shark catch rates for 1990–2000 and Hamukuaya *et al.* (2001) found that in the early 1990s, Chondrichthyans on average made up 3.6% of the weight of the taxa caught in the demersal surveys, which could indicate that their biomass could be about 3.6% of that of all demersal species, including hake, monkfish, cephalopods, crabs and other demersal fish. Using 3.6% of the biomass of hake, monkfish, cephalopods and crabs only estimates a biomass of approximately 35,000 tonnes for the 1980s; thus a starting biomass similar to the average obtained from Macpherson and Gordoa (1992) was used, but the time series of biomasses were estimated from the biomasses of all other species as that is a relative estimate (Figure 7).

The P/B and P/Q and diet estimates used for the 1980s were also employed here: 0.5 year^{-1} and 25% respectively, and the diet consisted of 9.3% anchovy, 1.2% sardine, 1.2% horse mackerel, 11% small pelagics, 0.4% large pelagics (split into 0.15% snoek, 0.15% linefish, 0.1% tuna), 10% cephalopods, 41.5% demersals (which was divided into 10% monkfish and 31.5% other demersals), 0.4% hake, 10.4% macrobenthos (including crabs), 0.2% seals and 14.4% cannibalism (Shannon and Jarre-Teichmann, 1999). To fit the model the 0.2% seals had to be reduced to 0.1% and 0.1% was added to other marine mammals. Similarly, the demersals were reallocated to 5% monkfish and 36.5% other demersals. The macrobenthos was split between macrobenthos (5.4%) and crabs (5%).

5. Tunas and large pelagics

Albacore (*Thunnus alalunga*), yellowfin (*T. albacares*) and bigeye tuna (*T. obesus*) are all important tuna species in the catches off Namibia (Shannon and Jarre-Teichmann, 1999). Other species also recorded in the catches include northern bluefin tuna (*T. thynnus*), skipjack (*Katsuwonus pelamis*), Atlantic sailfish (*Istiophorus albicans*), Atlantic blue marlin (*Makaira nigricans*), Atlantic white marlin (*Tetrapturus albidus*) and swordfish (*Xiphias gladius*). All of these species are large pelagics that roam the world oceans from the shelf to the upper pelagic over the deep ocean; thus the tuna group was assumed to occur in the shelf, slope and deep ocean sections north and south of the Walvis Ridge in the spatial model.

Tuna has been fished since 1956 and the catches were obtained from the CATDIS dataset of ICCAT for all species including the marlins, sailfish and swordfish (www.iccat.es/downloads.htm) for the area 15°S–30°S and 10°E–15°E. The ICCAT data was broken down by fleets: longline, purse seine, bait boat and other gear (Figure 8). The catches of other large pelagics were obtained from the Sea Around Us database and added to the ICCAT data for this group. Biomass estimates for albacore in the South Atlantic were obtained from Punt *et al.* (1995) and only used as a relative biomass for this group (Figure 9).

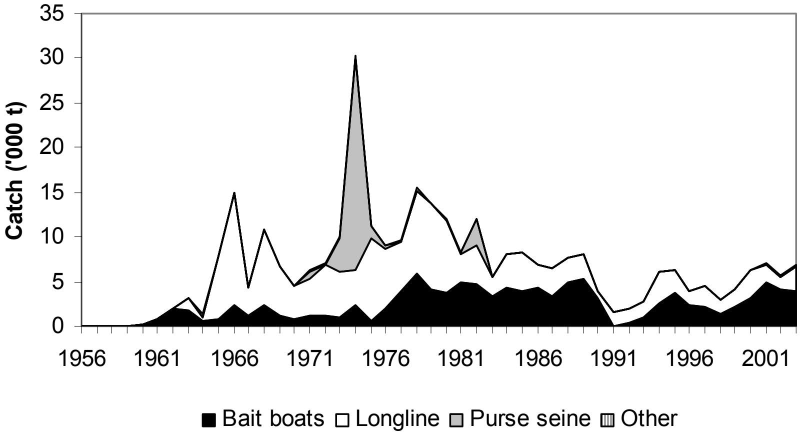


Figure 8. Tuna catch by fleet (*1000 tonnes) for the northern Benguela ecosystem.

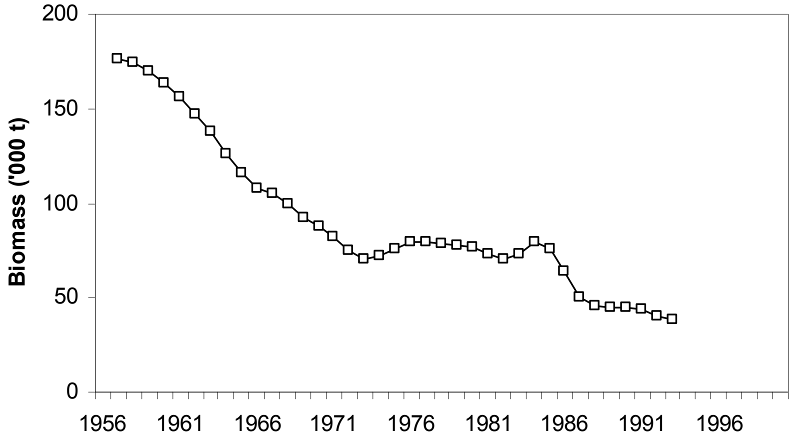


Figure 9. Biomass estimates (*1000 tonnes) for albacore tuna in the southeast Atlantic used as a proxy for tuna biomass in the northern Benguela ecosystem.

The natural mortality for tuna was assumed to be 0.2 year^{-1}, which was used for the P/B ratio and the P/Q was assumed to be 5%. The diet consisted of 20% euphausiids, 7% myctophids, 2% gobies, 15% anchovy, 15% sardine, 16% small pelagics, 5% horse mackerel, 15% cephalopods and 5% hake (Shannon and Jarre-Teichmann, 1999). No estimate of biomass was available, but to fit the model a biomass of 1 t·km^{-2} had to be assumed and the P/B increased to 0.25 year^{-1}. To fit the model the diet of tuna was changed to include 0.6% juvenile hake and 2.4% adult hake and 37.5% import had to be imported into the model as this group roams beyond the confines of the northern Benguela.

6. Snoek

Snoek (*Thyrsites atun*) is a pelagic predator that has been recorded from northern Angola to the east coast of South Africa (Griffiths, 2003). The distribution of snoek in the northern Benguela was described by Griffiths (2003) to span from south of Lüderitz to around Cape Frio and north, mainly on the continental shelf. It occurs in a depth range from 0 to 550 m (Froese, 2000); thus it was assumed to occur in the surf zone, on the shelf and on the slope of the whole spatial model of the northern Benguela ecosystem.

Snoek has been an important commercial species since the 1800s, caught first with hand lines and later with trawlers (Griffiths, 2003), with snoek caught as a bycatch in the midwater trawl fishery (Bianchi *et al.*, 1993). Between 1972 and 1980, 90% of the overall catch of snoek in the southeast Atlantic was taken in the area that sustains the Namibian and South African purse seine fisheries, with very little being caught in ICSEAF division 1.5 around the Lüderitz upwelling cell (Crawford and De Villiers, 1985). The general consensus was that there is only one stock of snoek on the west coast of southern Africa, but Griffiths (2003) suggested that the snoek found off Namibia and South Africa are separate sub-populations, although there could be extensive interaction between the populations.

No estimate of snoek biomass was available, but the total catch time series of snoek made with hand line and midwater trawls was obtained from Griffiths *et al.* (2004). Prior to 1972 snoek caught by the trawl fishery was discarded, and therefore there is no estimate of catches by the trawl fishery before 1972 (Griffiths *et al.*, 2004). From 2001 to 2003 estimates of snoek catches were obtained from the Sea Around Us database and were assumed to be made mostly by the hand line fishery (Figure 10). The P/B and P/Q ratios of 0.25 year^{-1} and 10% obtained from Shannon and Jarre-Teichmann (1999) were used.

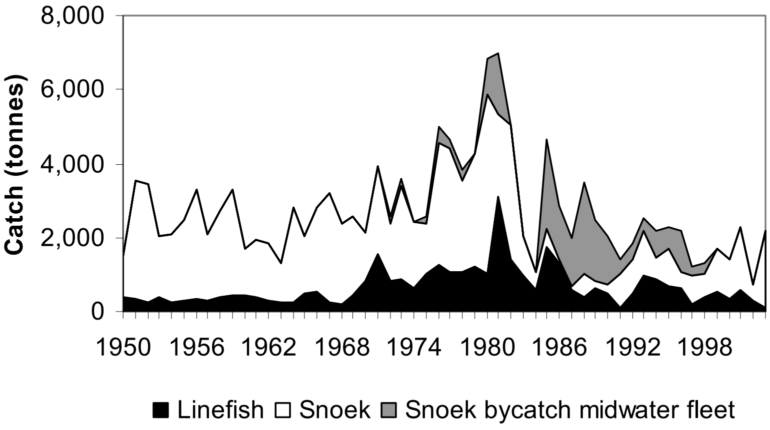


Figure 10: Catches of snoek and linefish (tonnes) made by the commercial line fishery and snoek bycatch by the midwater fleet.

Griffiths (2002) gives estimates of diet for snoek on the west coast of South Africa that include 12.6% macrobenthos, 3.5% euphausiids, 0.7% cephalopods, 12.3% anchovy, 17.5% sardine, 7.2% small pelagics, 16.1% mesopelagics, 5.4% horse mackerel, 9.8% demersals, 0.5% gobies and 14.3% hake. The 12.5% anchovy in the diet was reduced to 5% and the 16.1% mesopelagics were reduced to 5% with the difference added to mesozooplankton. The allocation for juvenile horse mackerel (5.4%) was reduced to 1% and 4.4% added to adult horse mackerel to balance juveniles. Juvenile hake was reduced to 0.3%, with 1% added to adult hake and the rest to macrozooplankton. The 9.8% demersals were reduced to 1% to balance that group. The 12.6% macrobenthos was split between 9% macrobenthos, 1% crabs and 2.6% lobster.

7. Linefish (steenbras and kob)

The two main species of linefish caught by the Namibian surf-and-rock recreational fishery and the commercial line fishery are steenbras (*Lithognathus aureti*) and kob (*Argyrosomus* spp.), but linefish also include the strepie (*Sarpa salpa*), breams (*Pagrus* spp.) and blacktail (*Diplodus* spp). Linefish are caught mainly in the West Coast Recreational Area, although there is also limited access to linefish in the Skeleton Coast Park, Namib Naukluft Park, Sperrgebiet and the surf zones north and south of these areas. Linefish occur mostly in the surf zone and on the shelf, but also over the slope areas on occasion (Froese and Pauly, 2000).

Both kob and steenbras have been caught since 1964 by the commercial fishery (Venter, 1988b), but also before that according to the Sea Around Us database. The catch of kob by the commercial fishery from 1964 to 2000 was obtained from Griffiths *et al.* (2004) and the catch of steenbras between 1964 and 1972 was obtained from Venter (1988b) and from 1973 to 1999 from Holtzhausen (1999). The catches of both kob and steenbras from 1950 to 1963, the catch of steenbras from 2000 to 2003 and kob from 2001 to 2003 and all catches of blacktail, breams and strepie were obtained from the Sea Around Us database (Figure 10). However, these catches were only for the commercial fishery as no recreational catches were available. Holtzhausen and Kirchner (2004) also give catches of kob by ski boat, line boat and anglers and catches of steenbras by anglers for 1995–2000.

Holtzhausen and Kirchner (2004) give the best estimate of silver kob and steenbras biomass in 2000 as 7,175 tonnes and 2,006 tonnes respectively and found that they were respectively 40% and 53% depleted from their unexploited states, giving a combined biomass in the 1950s of 21,722 tonnes. This value was used as a minimum biomass for this group and Holtzhausen *et al.* (2001) estimated a combined biomass of 9,872 tonnes for both species in 1995. The natural mortality of 0.23 for steenbras and 0.15 for kob was obtained from Holtzhausen *et al.* (2001), while Shin *et al.* (2004) estimated an M of 0.23 for kob, thus a P/B of 0.2 was assumed and a P/Q of 10% was taken from Shannon and Jarre-Teichmann (1999). Kob feeds on zooplankton (6.8%), anchovy (51%), sardine (0.6%), horse mackerel (3.3%), cephalopods (6.1%), macrobenthos (8.8%), hake (8.2%), cannibalism (0.4%), demersals (13.7%) and small pelagics (1.1%), and this diet was used for all linefish. The 8% juvenile hake was reduced to 5.5% and the rest added to macrozooplankton and the 13.7% demersals were reduced to 4.1% and the rest added to detritus to balance and fit the model. The 6.1% cephalopods was reduced to 3.3% and the rest added to macrozooplankton.

8. Juvenile anchovy

Crawford *et al.* (1989) found that juvenile anchovy aggregated north of about 24°S to about Henties Bay (22°S), and Mecenero *et al.* (2006) found that the Lüderitz area had smaller anchovies than around Cape Cross. Thus, juvenile anchovies were assumed to occur in the West Coast Recreational Area, Namib Naukluft Park, Sperrgebiet and on the southern shelf.

Anchovy was split in adults and juveniles at age 4 months, with a von Bertallanffy K value of 0.58 (Fishbase, Froese and Pauly, 2000, www.fishbase.org) and a W_{mat}/W_{∞} of 0.1. This weight at maturity was obtained from Fishbase (weight at L_{∞} of 16.6 cm = 18.3 g), the weight at age 0 from le Clus *et al.* (1988) and the length-weight relationship in Fishbase. Juvenile anchovy consume only phytoplankton.

9. Adult anchovy

Adult anchovy occur mainly in the north (Hewitson and Cruickshank, 1993), and Mecenero *et al.* (2006) found that larger anchovies were present in the scat of fur seals at Cape Cross. Le Clus *et al.* (1988) give the catches of anchovy in relation to their CPUE by 2° blocks from 17°S to 30°S for 1972–1987. From this paper, it seems that the main catches of anchovy were made between 22°S and 25°S, but the distribution of catches was more spread out than that of sardine, and the largest catches were between 23°S and 24°S (le Clus *et al.*, 1988). Thus, their non-preferred habitat includes the area from the Benguela-Angola front to Henties Bay (22°S) and from Sylvia Hill (25°S) to the Orange River.

According to Hampton (2003) anchovy was not caught much in Namibia before 1966, but after the collapse of the sardine fishery in the 1970s the catches increased substantially. Anchovy (*Engraulis japonicus*) only appears in the catch statistics from 1964 onwards, and catches of anchovy (Figure 11) from 1964 to 2000 were obtained from Willemse (2002), while the catches from 2001 to 2003 were obtained from the Sea Around Us database.

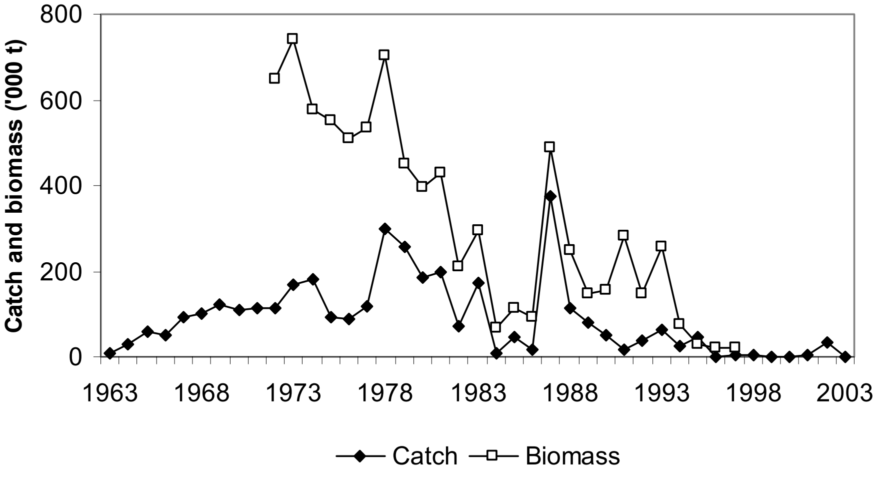


Figure 11. Catch and biomass (*1000 tonnes) of anchovy in the northern Benguela ecosystem.

A VPA was done on anchovy from 1972 to 1984 by le Clus (1985) in Crawford *et al.* (1987), but the data were only used for 1972–1979 (Figure 11). The data from 1980 to 1989 came from Hewitson and Cruickshank (1993) and from 1990 to 1995 were obtained from the Ministry of Fisheries and Marine Resources (Heymans, 1997). Hampton (2003) suggests that the biomass in 1996 and 1997 was around 20,000 tonnes and this is used here; however, after 1997 the survey design changed and no estimate of anchovy biomass is available. Even though no estimate of anchovy biomass was available an estimate of 5.7 t·km^{-2} was used as it fit the model best.

Adult anchovy P/B and Q/B ratios of 1.16 year^{-1} and 11.7% respectively were obtained from Shannon and Jarre-Teichmann (1999). The P/B for juveniles was estimated at 10 year^{-1}. To fit the model a P/B ratio of 0.85 year^{-1} was used for adult anchovy. Adult anchovy diet consists of 33% phytoplankton, 4% microzooplankton (detritus), 31% copepods and 32% euphausiids (Shannon and Jarre-Teichmann, 1999) and a small percentage (0.1%) of their diet was assumed to consist of juvenile sardine and juvenile gobies and 0.01% of their diet of juvenile jellyfish.

10. Juvenile sardine

Roy *et al.* (1992) suggest that the relationship between sardine year class strength and sea surface temperature is positive in the southern Benguela but negative in the northern Benguela. While looking at the scat samples of fur seals, Mecenero *et al.* (2006) found that both the Cape Cross and Lüderitz areas had large numbers of sardine. Crawford *et al.* (1989) showed that juvenile sardine aggregate north of about 24°S to about Henties Bay (22°S). However, there was a large area of spawning for sardine from 17°S to 21°S (le Clus, 1990), and O'Toole (1977) in Maurihungirire (2004) found that Namibian sardine spawn within 60 km of the coast between 21°S and the confluence of the Benguela and Angola currents in late summer or autumn in water above 19°C. Thus, in this model adult and juvenile sardine were assumed to occur in all areas of the spatial model except the deep ocean and slope areas.

Sardine was split into juveniles (12 months) and adults using the ratio of weight at age 1 (91 g) to weight at infinity (342 g) obtained from le Clus *et al.* (1988) and Fishbase respectively and a K value of 0.43 also obtained from Fishbase. For juveniles the P/B of 10 year^{-1} was assumed. Juvenile sardine consume only phytoplankton.

11. Adult sardine

Le Clus *et al.* (1988) give the catches of sardine in relation to their CPUE by 2° blocks from 17°S to 30°S for 1972–1987, which could be used to verify the estimates of catches by year for sardine. From Le Clus *et al.* (1988) it seems that the main catches of sardine were made between 17°S and 25°S, with the highest catches between 22°S and 23°S (le Clus *et al.*, 1988). Hewitson and Cruickshank (1993) also suggested that sardine is mainly found in the north. However, Mecenero *et al.* (2006) found that both the Cape Cross and Lüderitz areas had large numbers of sardine; thus adult sardine were assumed to occur in all areas of the spatial model except the deep ocean and the slope areas.

Catches of sardine from 1950 to 2000 (Figure 12) were obtained from Willemse (2002), for 2001 to 2002 from Nicols (2004) and for 2003 from the Sea Around Us database. Biomass estimates for sardine were obtained from Schwartzlose *et al.* (1999), le Clus *et al.* (1988) and Thomas (1986) for 1952 to 1983 and from 1984 to 1999 from Kreiner *et al.* (2001), while the biomass for 2000 and 2001 was obtained from Hampton (2003).

Shannon and Jarre-Teichmann (1999) used a P/Q of 10% which gives a Q/B ratio of 5.0 year^{-1}. Natural mortality was estimated at 0.59 year^{-1} in the 1960s (Newman, 1970 in Fossen *et al.*, 2001), and (Butterworth, 1983 in Fossen *et al.*, 2001) used 0.5 year^{-1} for his VPA, which is what was used here for adults. Fossen *et al.* (2001) estimated a value that varies between 0.77 and 2.38.

The diet of sardines consists of phytoplankton (56%), microzooplankton (detritus, 8%), copepods and euphausiids (18% each) (King and Macleod,

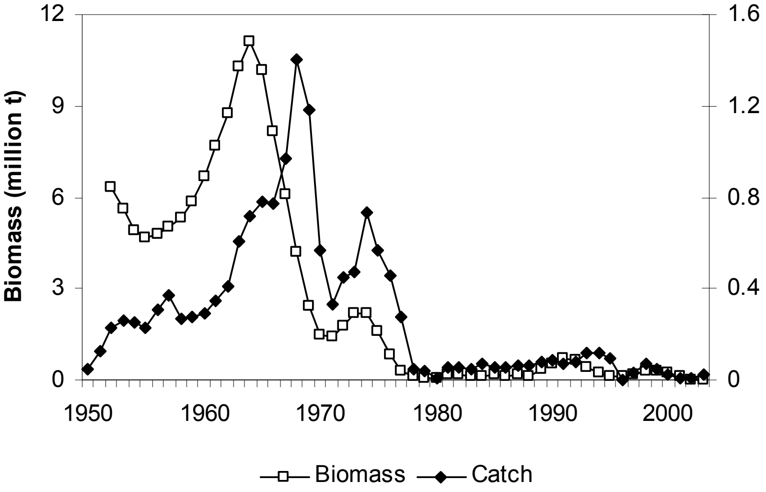


Figure 12. Catch and biomass (million tonnes) of sardine in the northern Benguela ecosystem.

1976 in Shannon and Jarre-Teichmann, 1999). A small percentage (0.1%) of their diet was assumed to consist of juvenile anchovy and juvenile gobies and 0.01% of their diet of juvenile jellyfish.

12. Juvenile gobies

Mecenero *et al.* (2006) found from scat samples of fur seals that the Cape Cross area has smaller gobies while the Lüderitz area has larger gobies, and Crawford *et al.* (1989) showed that juvenile gobies aggregate around Walvis Bay (17°S–20°S). However, in the spatial model of this ecosystem juvenile gobies were assumed to be distributed throughout the surf zone and shelf areas of the ecosystem but not on the slope. Migration of juveniles from the north to the south and adults from the south to the north were instituted.

Gobies were split into juvenile and adults at age 4 months, with a K of 0.4 and a W_{mat}/W_{∞} of 0.2 (Fishbase) and a P/B for juveniles of 7 $year^{-1}$. They only consume phytoplankton.

13. Adult gobies

Gobies are found up to 60 km offshore (Cruickshank *et al.*, 1980) and small gobies are more pelagic than larger individuals, which are mainly bottom dwellers and found further offshore (Crawford *et al.*, 1985), although seals do seem to feed on larger gobies near the surface at night (Mecenero *et al.*, 2006). Hamukuaya *et al.* (2001) showed that gobies were mostly found on the central shelf (20–200 m) and sometimes on the southern shelf (south of Elizabeth Bay at 27.5°S). Pelagic gobies were more important in the south, and the highest concentration of gobies was found between Lüderitz and Walvis Bay (Hewitson and Cruickshank, 1993). In the spatial model adult gobies were assumed to occur in the surf zone, shelf and slope areas of both the northern and southern part of the ecosystem but not in the deep ocean.

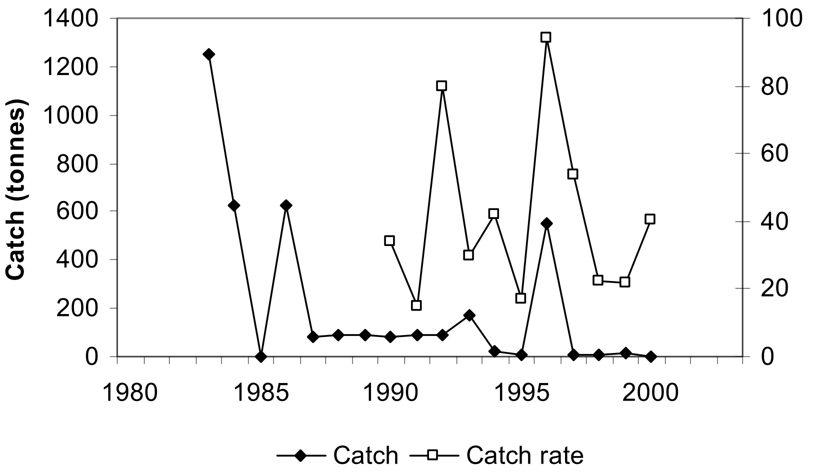


Figure 13. Catch (tonnes) and catch rate (kg/hour) for gobies in the northern Benguela ecosystem.

According to references in Melo and le Clus (2005), biomass estimates in the northern Benguela range between 0.6 and 1.45 million tonnes (Shannon and Jarre-Teichmann, 1999), but Hewitson and Cruickshank (1993) estimated 600,000 tonnes between 1978 and 1983, so that was used as a starting biomass and the P/B and P/Q was 0.9 $year^{-1}$ and 10% respectively (Shannon and Jarre-Teichmann, 1999). However, to fit the model the P/B and Q/B ratios for adult gobies were assumed to be 1.1 $year^{-1}$ and 15 $year^{-1}$ respectively. A biomass for adult gobies of 6.3 $t \cdot km^{-2}$ was used to fit gobies. Catch rates of gobies in the 1990s obtained from Bianchi *et al.* (2001) were used as a relative estimate biomass time series (Figure 13). Catches of gobies from 1983 to 2000 were obtained from Willemse (2002).

The diet of gobies consists of phytoplankton (93%), 1% copepods and 6% euphausiids (Crawford *et al.*, 1985). A small percentage (0.1%) of their diet was assumed to consist of juvenile anchovy and juvenile sardine and 0.01% of their diet of juvenile jellyfish.

14. Other small pelagics

Other small pelagics in this model included chub mackerel (*Scomber japonicus*) and round herring (*Etrumeus whiteheadi*) which have been caught since 1971 (Willemse, 2002). In addition, the Sea Around Us database shows that *Sardinella aurita*, other Sardinellas and other Carangidae, Sparidae and Engraulidae were also caught, and the total catch for this group was then obtained from the Sea Around

Us database (Figure 14). Also included in this group are the flying fish (Exocoetidae) and sauries (Scomberesocidae). The group was assumed to occur in all areas of the spatial model.

Very little is known about these species, but their catches were obtained from Willemse (2002), and their P/B and P/Q ratios were estimated at 0.6–0.9 year^{-1} and 10% respectively (Shannon and Jarre-Teichmann, 1999). No estimate of biomass was available and it was estimated using an ecotrophic efficiency of 95% for this group. Using the average diet of other small pelagics in chub mackerel and their biomass estimates obtained from Shannon and Jarre-Teichmann (1999), the average diet for this group was estimated at 55.8% copepods, 35% euphausiids, 2.1% jellyfish, 1.4% benthos, 0.5% anchovy, 0.3% cannibalism and 5% mesopelagics. The mesopelagics were reduced to 1% and the 4% added to mesozooplankton (copepods).

15. Mesopelagics

The most important mesopelagics in the northern Benguela are the lanternfish (*Lampanyctodes hectoris*) and the lightfish (*Maurolicus muelleri*) (Hewitson and Cruickshank, 1993). Lanternfish prefer water between 300 m and 1000 m deep and migrate vertically (Cruickshank, 1983). They live along the edge of the continental shelf but are concentrated from Walvis Bay to the Orange River about 30 km from the shore (Cruickshank, 1983). They are found mainly in the north, but mostly further offshore (Mecenero *et al.*, 2006); thus in the spatial model they were assumed to occur on the shelf, slope and over the deep ocean in both the northern and southern part of the ecosystem.

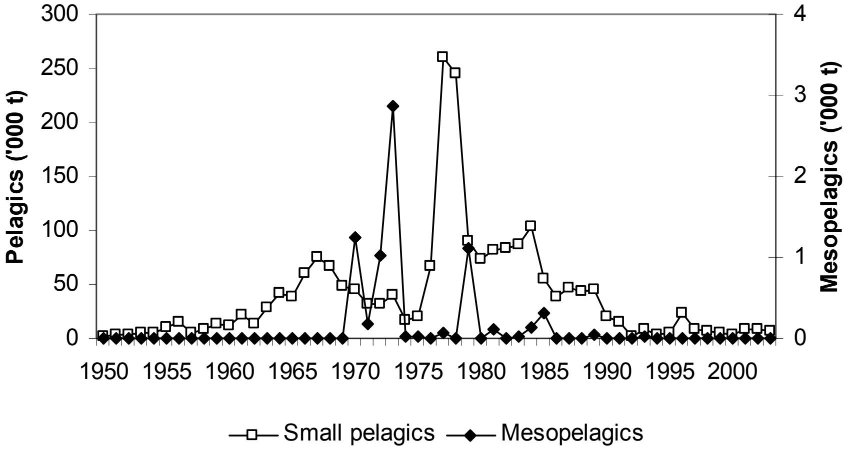


Figure 14. Catch (*1000 tonnes) for small pelagics and mesopelagics in the northern Benguela ecosystem.

Lanternfish have been recorded in the catches given by the Sea Around Us database from 1970 to 2003 (Figure 14). The lower limit for their biomass was 800,000 tonnes of lanternfish (Hewitson and Cruickshank, 1993) and 10,000 tonnes of lightfish (Shannon and Jarre-Teichmann, 1999) for the northern Benguela and their P/B and P/Q ratios were estimated at 1.23 year^{-1} and 10% respectively (Hewitson and Cruickshank, 1993). However, for this model of the 1950s the biomass of mesopelagics was estimated by using an ecotrophic efficiency of 95%. Their diet was assumed to be 40% copepods and 60% euphausiids (Hewitson and Cruickshank, 1993). They are caught as bycatch with an estimated catch of 1000 tonnes·year^{-1} (Shannon and Jarre-Teichmann, 1999) but no time series of catches were available.

16. Juvenile horse mackerel

Juvenile horse mackerel are important in the north, from 20°S to the Angolan border (Axelsen *et al.*, 2004). They are found from south of Conception Bay (around 25°S) all the way to the Angola-Benguela front at about 15°S (Axelsen *et al.*, 2004). This was confirmed by Crawford *et al.* (1989), who showed that juvenile horse mackerel aggregated close to Cape Frio. Mecenero *et al.* (2006) also found large numbers of horse mackerel in the scat samples of fur seals in the Cape Cross area, while the Lüderitz area had not much horse mackerel. According to Boyer and Hampton (2001) juveniles live inshore of the 100 m isobath and mature fish move offshore, while Axelsen *et al.* (2004) suggest that they occur inshore from the 200 m depth contour. Thus, in the spatial model juvenile horse mackerel was assumed to occur in the shelf and surf zone areas of the northern part of the system, as well as in the Skeleton Coast Park, West Coast Recreational Area and the Namib Naukluft Park, but not further south. Both juveniles and adults migrate along the shore and across the shelf break, but juveniles are mostly found closer inshore and adults offshore (Maurihungirire, 2004). Thus in the model juveniles were assumed to migrate south in the inshore waters and adults were assumed to migrate north in the offshore waters.

Horse mackerel was divided into adult and juveniles at age 2, with L_∞ of 51 cm, M of 0.4 and K of 0.13 or 0.15 (Anon., 2001). Krakstad and Kanandjembo (2001) give a range of values for L_∞ between 41.1 and 62.6, a range of K from 0.1 to 0.25, and a range of M from 0.22 to 0.53 obtained from the literature. The values obtained by Kampowski and Slosarczyk (1976) in Krakstad and Kannadjembo (2001) of L_∞=47 cm, K=0.25 and M=0.25–0.5 were used to balance the model of the 1950s. The W_{mat}/W_∞ ratio (0.066) was estimated from a W_{mat} of 92 g for 2-year-old fish (Klingelhoeffer, 2006) and W_∞ of 1,356 g at L_∞ of 55 cm calculated from the weight-length relationship of $W=0.0078 * L^{3.011}$ (Fishbase). To fit the model it was necessary to use a P/B of 1.7 $year^{-1}$ for juveniles.

Up to 2 years of age they feed near the surface and are zooplanktivorous with their diet consisting mainly of copepods, similar to that of sardine and anchovy (Venter, 1976 in Boyer and Hampton, 2001). Andronov (1983) suggested that even in 1963 most of the diet consisted of copepods.

17. Adult horse mackerel

Similar to juvenile horse mackerel, adults are found from about 25°S to the Angola-Benguela front, but they are mainly found offshore of the 200 m depth contour (Axelsen *et al.*, 2004). Hampton (2003) showed that adult horse mackerel are very prevalent offshore between 18°S and 21°S but, more importantly, inshore north of 18°S and between 21°S and 24°S. In the demersal assemblages, adult horse mackerel is found in the shelf areas, moving north and south over different years, with the main concentration south from the Kunene River (17.5°) to around Elizabeth Bay (27°S) but also occurring south to the Orange River in some years (Hamukuaya *et al.*, 2001). Horse mackerel spawn in warmer water west of the shelf break, and the nursery areas are adjacent to the spawning areas but closer to the shore (Maurihungirire, 2004). The distribution of horse mackerel in the spatial model included shelf and surf zone areas in both the northern and southern parts of the system, including the Skeleton Coast Park, the West Coast Recreational Area, the Namib Naukluft Park and the Sperrgebiet. The adults are found further offshore, and the migration of juveniles from north to south and of adults from south to north was included.

Biomass estimates of horse mackerel from 1966 to 2000 were obtained from Klingelhoeffer (2006) for both B0+ and B2+ and the difference was used as the biomass for juvenile horse mackerel. There were also VPA estimates for 1966–1985 from Crawford *et al.* (1987), for 1991–1993 from acoustic estimates obtained from the Ministry of Fisheries and Marine Resources, for 1994–2000 from Bauleth-D'Almeida *et al.* (2001), and, finally, Axelsen *et al.* (2004) give acoustic estimates of horse mackerel biomass from 1989 to 2003. However, the data obtained from Klingelhoeffer (2006) were used and interpolated from 1987 to 1991, and for 2001 the estimate was obtained from Hampton (2003) and divided into adults and juveniles by using an average of 72% adult weight in the population as given since 1994 (Figure 15). In addition, the fishing mortality from 1966 to 1986 and from 1991 to 2000 were also obtained from Klingelhoeffer (2006). There was a reduction in the mean age from 6.5 years to 1.9 years from 1968 to 1971 (Anon., 2001) after the start of the fishery.

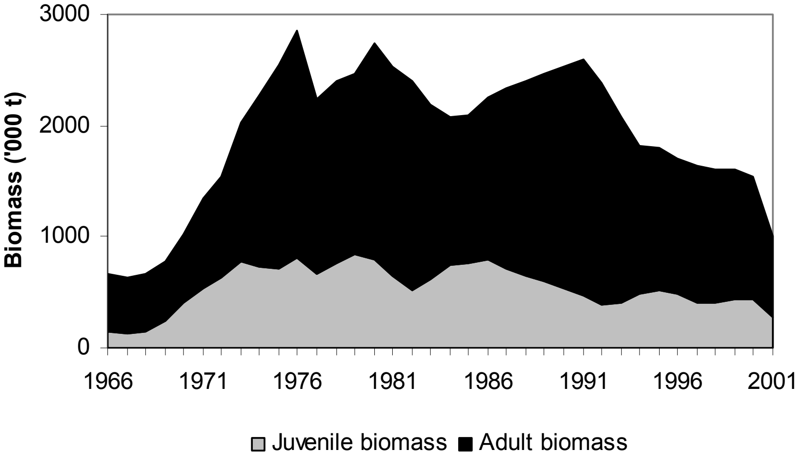


Figure 15. Biomass (*1000 tonnes) of adult and juvenile horse mackerel in the northern Benguela ecosystem.

Catches of adult horse mackerel (Figure 16) made by the midwater trawl fishery from 1955 to 1960 were obtained from Willemse (2002), while catches from 1961 to 2004 of the midwater trawl (adult) fishery and from 1970 to 2004 of the purse seine (juvenile) fishery were obtained from Klingelhoeffer (2006). According to Anon. (2001), the large Ukrainian fleet targeted horse mackerel since 1963. In addition, horse mackerel is also caught as a bycatch by the hake demersal fishery, and the data of these catches between 1980 and 2004 were obtained from Klingelhoeffer (2006).

As horse mackerel was probably always a bycatch of the demersal fleet, the average of the percentage of horse mackerel to hake in the 1980s was used (0.13%) with the catch of hake from 1964 to 1979 to calculate the bycatch for that time (Figure 16). For 1950–1970 the catch by the purse seine fleet was estimated as the difference between the catch obtained from the Sea Around Us database and the total catch of the midwater trawlers and demersal trawlers.

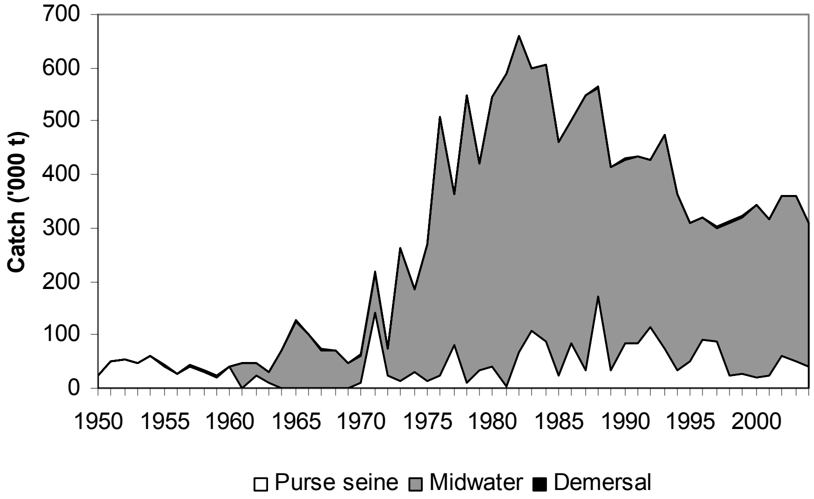


Figure 16. Catch (*1000 tonnes) of horse mackerel by the purse seine (juveniles), demersal and midwater fleets (adults).

The biomass of adult horse mackerel needed to be 7 t·km^{-2} to fit the model and it was necessary to use a P/B of 0.4 year^{-1} for adults. P/B and P/Q ratios for adult horse mackerel of 0.52 year^{-1} and 10% respectively were used by Shannon and Jarre-Teichmann (1999), which gives a Q/B ratio of 5.2 year^{-1} for adults. For juveniles a Q/B of 35 year^{-1} was used at first based on the estimates made by Shannon and Jarre-Teichmann (1999) based on work by Andronov (1985).

The diet of adult horse mackerel was 95% euphausiids off Namibia (Konchina, 1986; Boyer and Hampton, 2001), but they also feed on copepods and to a lesser extent on lantern fish (Andronov, 1983). Shannon and Jarre-Teichmann (1999) estimated the diet of adult horse mackerel to include 18% copepods, 78% euphausiids, 0.9% gobies, 0.1% cephalopods and 2% lanternfish, while Andronov (1983) estimates 43% each for copepods and euphausiids, 10% lanternfish, 0.5 cephalopods and 3.1% gobies. However, Andronov (1983) estimated percent abundance not percent mass, thus this model used the estimates of Shannon and Jarre-Teichmann (1999).

18. Juvenile hake

Two species of hake are prevalent off Namibia, namely Cape hake, *Merluccius capensis* and *M. paradoxus*. Burmeister (2005) indicates that *M. paradoxus* might be a single stock in South Africa and Namibia and not two separate stocks, so it might be difficult to model their ontogenetic split in the northern Benguela alone, as good recruitment would not necessarily have an effect on the Namibian *M. paradoxus* stock. *M. paradoxus* also does not spawn off Namibia and recruitment is only found in southern Namibia (Gordoa et al. 1995 in Maurihungirire, 2004).

Crawford *et al.* (1989) showed that juvenile hake aggregate north of about 24°S to about Henties Bay (22°S), but they are also found from about the Kunene (17°S) to Cape Cross (22°S) and from south of 24°S to Lüderitz. Mecenero *et al.* (2006) also found smaller hake in the scats of fur seals around Cape Cross, while the larger hake seemed to occur in the Lüderitz area. In the spatial model juvenile hake was assumed to occur on the slope and shelf of both the northern and southern areas of the model as they were not totally excluded from these areas by any references.

Shin *et al.* (2004) give estimates of K (0.046 year^{-1}) and Z_0 for age 0 fish (8 year^{-1}), while Botha (1971) in Burmeister (2005) indicates that hake adopt a demersal habitat at a length of 15–20cm at roughly an age of two years. The Z_0 for age 0 fish (8 year^{-1}) was used as the P/B for juveniles. However, this ratio is too high for juveniles up to 24 months, and it was reduced to 1.05 year^{-1} to be more realistic. Hake growth parameters of a=0.005 and b=3.11 were obtained from Fishbase, and with the L_∞ of 116 cm total length, a W_∞ of 13,165 g was estimated. Similarly, an average length at maturity of 40 cm was obtained from Fishbase and a W_{mat} of 480 g was estimated, giving a W_{mat}/ W_∞ ratio of 0.036.

Boyer and Hampton (2001) suggest that hake are opportunistic feeders, with young *M. capensis* and *M. paradoxus* feeding predominantly on planktonic crustaceans such as euphausiids, pelagic gobies and lanternfish. Huse *et al.* (1998) give estimates of *M. capensis* (which were mostly larger than 50 cm) and *M. paradoxus* (mostly smaller than 50 cm) diets, which were used as the adult and juvenile diets in conjunction with Pillar and Barange (1997) and Andronov (1983) to disaggregate the mixed contents and miscellaneous groups given in Huse *et al.* (1998). For juveniles the diet was broken down into: 81.5% euphausiids, 9.8% mesopelagics and 1.4% each for cephalopods, macrobenthos, small pelagics, anchovy and sardine. Roel and Macpherson (1988) found that the diet of hake is determined by the availability of prey and therefore this will change with balancing. In addition, this diet was based on percentage frequency of occurrence and not percentage weight. The juvenile diet was changed to balance and fit the model by reducing the mesopelagics in their diet from 9.8% to 1% and adding the rest to mesozooplankton.

19. Adult hake

Hampton (2003) showed that Cape hake (*M. capensis*) occurred in large numbers between 200 m and 500 m depth from the Kunene to Cape Frio and from about 23°S to north of Lüderitz, and south of Lüderitz to the Orange River, while deepwater hake (*M. paradoxus*) were more prevalent offshore (500–1000 m depth) between Cape Frio and 28°S with some lesser aggregations at the Orange River and Easter Point (25.5°S). This is similar to what was found by Maurihungirire (2004), that *M. paradoxus* seems to dominate where the continental slope is less steep and the shelf is narrow, while *M. capensis* is abundant on wider continental shelves. Punt *et al.* (1992) showed that Cape hake occur between 20°S and 30°S but that deepwater hake only occur north to about 25°S from South Africa. Similarly, Abelló *et al.* (1988) showed that shallow water hake occurred in larger numbers around Walvis Bay and the Orange River, while deepwater hake occurred in large numbers offshore from 26°S to the Orange River, although their study did not go further north than 23°S. Mecenero *et al.* (2006) found larger hake in the scats off Lüderitz than off Cape Cross in the north. In the spatial model adult hake was assumed to occur on the slope and in the deep waters of both the northern and the southern part of the model.

Shin *et al.* (2004) give estimates of M (0.5 for *M. capensis* and 0.4 for *M. paradoxus*) for adults and the average (0.45 year^{-1}) was then used as the P/B for adults. The Q/B ratio for juvenile hake was estimated at between 5.9 and 17.2 year^{-1} while Jarre-Teichmann *et al.* (1998) used 2.4 year^{-1} for hake aged 3 years and older and 8.0 year^{-1} for younger hake. These values are used for this model but Punt *et al.* (1992) estimate a value of ~3% per day (10.9 per year) and Jarre-Teichmann *et al.* (1998) used 11.6 year^{-1}.

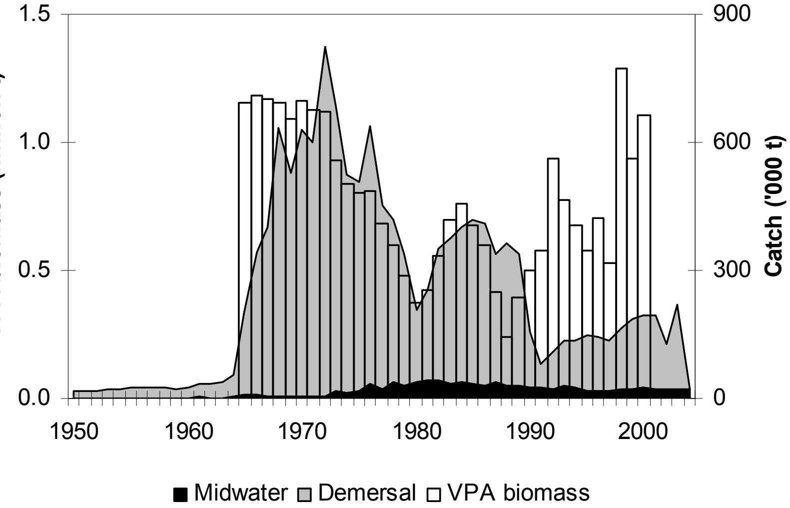


Figure 17. Hake biomass (million tonnes) estimated from VPA and catch (*1000 tonnes) made by the midwater and demersal fleets.

The catch statistics for hake have always been reported for the two species combined (Figure 17). Klingelhoeffer (2006) suggests that the demersal trawl fishery started in the 1950s and therefore catches from 1950 to 1963 were obtained from the Sea Around Us database. Similarly the catches from 2001 to 2003 were obtained from the Sea Around Us database, while from 1964 to 2000 the catches of hake were obtained from Willemse (2002). Hake is also caught as bycatch in the midwater trawl horse mackerel fishery, and according to Klingelhoeffer (2006), the bycatch ranged from 0.1%–2% for the Polish fleet during 1980–1984 to 18% for the Soviet fleet in 1990. Thus using an average of 7% of the landings of the midwater trawl fishery being hake gave an estimate of hake bycatch by the midwater horse mackerel fleet. As hake adopts a demersal habitat at age 2 (Botha, 1971 in Burmeister, 2005), this catch is assumed to be of juvenile hake. Hampton

(2003) found that by 2001 the bycatch was approximately 2% of the total midwater catch. Hake is also caught by the longline fleet, and in 1998 16,500 tonnes of hake were landed by this fleet (Hampton, 2003).

CPUE estimates for hake in the ICSEAF divisions were obtained from Butterworth and Rademeyer (2005), who indicated that the values from 1965 to 1980 were more reliable than those from 1981 to 1988 when there was misreporting of catches. Hake biomass for both species were estimated by VPA for ICSEAF divisions 1.3+1.4 from 1968 to 1984 and for division 1.5 from 1965 to 1984 (Leslie, 1986 in Crawford *et al.*, 1987), while Van der Westhuizen (2001) gives estimates of biomass from 1990 to 2000 (Figure 17). Hampton (2003) estimates that the 2001 spawning biomass for both species of hake combined was approximately 1.1 million tonnes (similar to that obtained for 2000 by Van der Westhuizen (2001)). For 1985–1989 estimates were obtained from Macpherson and Gordoa (1992) and were prorated to be in the same order of magnitude by using the value for 1984 obtained from VPA and the surveys. Butterworth and Geromont (2001) gave a stock assessment trajectory for hake 2+biomass if the estimates of the *Dr. Fridtjof Nansen* were assumed to be relative estimates of biomass. This trajectory from 1965 to 1999 was 5 times more abundant than the previous trajectory but did have a similar trend; thus it was used as a relative estimate of biomass. Surplus production models were used to estimate the biomass during the ICSEAF management phase, but there are concerns about the reliability of these assessments (Hampton, 2003). However, we used the values given by Butterworth and Geromont (2001) for the relative biomass for 2+, which gives a biomass of 24 $t \cdot km^{-2}$ in 1966, which we used for 1956 (Figure 17).

Punt *et al.* (1992) in Boyer and Hampton (2001) suggest that squid, epipelagic fish and lightfish and mesopelagic fish constitute a significant proportion of adult hake diet, but their main prey items are their own young and other demersal species. Shannon and Jarre-Teichmann (1999) assumed a diet of 50% macrozooplankton, 3% jellyfish, 1% cephalopods, 1% anchovy, 6% hake, 6% gobies, 4% macrobenthos, 18% mesopelagic fish, 10% other demersal fish and 1% horse mackerel. However, this was for adults and juveniles combined. Similar to the juvenile hake, the estimates given by Huse *et al.* (1998) for *M. capensis* (which were mostly larger than 50 cm) were used in conjunction with Pillar and Barange (1997) and Andronov (1983) to disaggregate the mixed contents and miscellaneous groups given in Huse *et al.* (1998). The adult diet was broken down into 26.9% euphausiids, 4.5% mesopelagics, 17.9% cannibalism, 6% demersals, 4.5% cephalopods, 4.5% horse mackerel and 4.5% each for macrobenthos, jellyfish, copepods, small pelagics, anchovy, sardine and snoek.

To balance and fit the model the diet of adult hake had to be changed substantially. The 4.5% snoek in the diet of adult hake was reduced to 1%, 0.01% added to linefish, 1% to adult horse mackerel and the remaining 3.499% to macrozooplankton. Anchovy was reduced from 1.4% to 1% to fit and balance this group. Similarly, mesopelagics and juvenile horse mackerel were reduced from 4.5% to 1% each and 1% was added to adult horse mackerel. Cannibalism of juveniles by adults was reduced to 0.5% and added to adults cannibalizing themselves. The 6% demersals was reduced to 0.5% and monk (0.05%) and macrozooplankton (4.5%) were added. Cephalopods were reduced from 4.5% to 0.5% and macrozooplankton added.

20. Monkfish

There are two species of monkfish in Namibia, namely *Lophius vomerinus* and *L. vaillanti* (Maartens and Booth, 2005). *L. vomerinus* is the more important species and occurs from northern Namibia (21°S) to the east coast of South Africa, while *L. vaillanti* occur north of Walvis Bay (Maartens and Booth, 2005). There are two separate spawning areas for *L. vomerinus*, one off Walvis Bay between 150 and 300 m depth, and one near the Orange River, at depths of 100–300 m (Maartens and Booth, 2005). Hampton (2003) showed that monkfish are caught mainly offshore, with large aggregations from the Angola-Benguela front extending south to 30°S, although there did seem to be interruptions at Sylvia Hill (25°S) and around the Orange River (29°S). Abelló *et al.* (1988) found an interruption in the monkfish stock at 27°S, around Elizabeth Bay, and a smaller reduction at Sylvia Hill. However, in this model the monk was assumed to occur on the whole coast, from the slope to the deep ocean.

Catch statistics for monkfish date back to 1974 when the two species were taken as bycatch in the hake fishery (Hampton, 2003). However, the Sea Around Us database gives catches back to 1967, and the Sea Around Us catches from 1967 to 1977 and 2001 to 2003 were used in conjunction with the catches from Willemse (2002) for the time period 1978–2000 (Figure 18). Maartens and Booth (2001) give estimates of the effort by the monkfish and sole fishery in days fished from 1991 to 1999.

Booth and Quinn (2006) use an age-structured maximum likelihood model to estimate the exploitable biomass of monkfish (*L. vomerinus*) from 1975 to 2004 and that was used as a biomass trend (Figure 18) for this species. To fit and balance the model a biomass of 0.6 t·km^{-2} was needed. For a P/B ratio the natural mortality of both species were obtained from Fishbase (at 8°C), which was 0.27 for *L. vaillanti* and 0.21 for *L. vomerinus*, giving an average P/B of 0.24 year^{-1}. A P/Q of 10% was assumed, similar to other demersals (Shannon and Jarre-Teichmann, 1999).

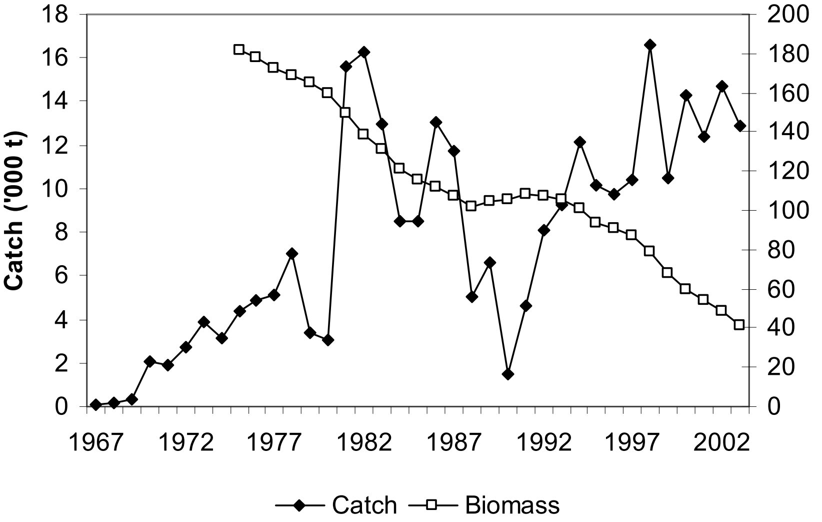


Figure 18. Catch and biomass (*1000 tonnes) of monkfish in the northern Benguela ecosystem.

Diet of monkfish was given by Walmsley *et al.* (2005) for the west coast of South Africa, and according to them, smaller individuals are found in shallower depths and there is a large overlap in distribution of the three size classes (<37 cm, 37–45 cm, and >45 cm); thus all size classes are exposed to fishing. Data on the size structure of monkfish indicate that 26.8% of landed monkfish were <37 cm in monkfish-directed trawls and 10.7% in hake directed trawls (Walmsley *et al.*, 2005). According to Macpherson (1985) in Boyer and Hampton (2001), hake is the main prey of monkfish and monkfish would take any hake up to their own size. The diet of monk was then estimated as 36.7% hake, 29.4% demersals, 6.6% horse mackerel, 0.2% gobies, 1% cannibalism, 12.3% small pelagics, 3.9% anchovy, 0.4% mesopelagics, 8.4% cephalopods and 1.2% macrobenthos (Walmsley *et al.*, 2005). The 0.2% gobies was increased to 10.2% and other demersals reduced to 5% to balance that group while adult horse mackerel was added (5%), small pelagics (19.7%) and mesopelagics were increased to 12.9%. The 36.7% hake was divided into 0.1% juveniles and 26% adult hake and small pelagics (10.6%). The 8.4% cephalopods was reduced to 3.4% and 5% added to macrobenthos.

21. Other demersals

The other groundfish species caught off Namibia (in order of abundance) include large eye dentex (*Dentex macrophthalmus*), grenadiers (*Trachyrinchus scabrus*), jacopever (*Helicolenus dactylopterus*), Atlantic greeneye (*Chlorophthalmus atlanticus*), Cape elephant fish (Josef) (*Callorhinchus capensis*), longfin bonefish (*Pterothrissus belloci*), Cape gurnard (Kaapse korhaan) (*Chelidonichthys capensis*), black slimehead (*Hoplostethus cadenati*), banded rattail (*Coelorinchus fasciatus*), grenadiers (*Nezumia* spp), thinlip splitfin (*Synagrops microlepis*), kingklip (cusk-eel) (*Genypterus capensis*), west coast sole (*Austroglossus microlepis*), silver scabbardfish (bottersnoek) (*Lepidopus caudatus*), Gunter's cuskeel (*Selachophidium guentheri*) and pencil cardinal (*Epigonus denticulatus*) (Hamukuaya *et al.*, 2001). To this group is also added the orange roughy (*Hoplostethus atlanticus*) and alfonsino (*Beryx splendens*). The groundfish assemblages of the northern Benguela have been divided into shelf and slope assemblages that were then subdivided into northern and southern assemblages as well (Hamukuaya *et al.*, 2001). However, for this project, as demersal fish are mostly combined in this group, they were assumed to occur everywhere in the ecosystem.

The relative abundance of the demersal species for 1990–2000 was estimated by Bianchi *et al.* (2001) and the biomass for demersals from 1983 to 1990 was obtained from Macpherson and Gordoa (1992). Thus, using the average biomass for 1990 (144,000 tonnes) obtained from Macpherson and Gordoa (1992) and the catch rate from Bianchi *et al.* (2001), a time series of biomass from 1983 to 2000 was obtained (Figure 19). However, no biomass was available for 1956 for this group and biomass was thus estimated by assuming an ecotrophic efficiency of 95%. Catches (Figure 19) for all demersals were obtained from the Sea Around Us database.

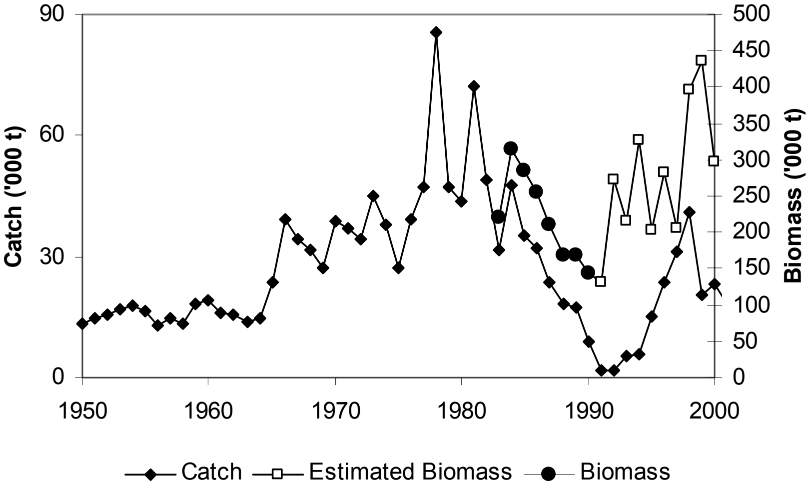


Figure 19. Catch and biomass estimated for demersal fish in the northern Benguela ecosystem (*1000 tonnes).

Shannon and Jarre-Teichmann (1999) assumed P/B and P/Q ratios of 1.0 year^{-1} and 10% respectively and a diet of 8.3% copepods, 32.4% euphausiids, 5.7% small pelagics, 1.9% myctophids, 2.2% gobies, 10.6% hake, 10.6% cannibalism, 13.3% cephalopods and 15% benthos. The 10.6% cannibalism was divided into 5% cannibalism, 1% monkfish, and detritus. The 10.6% hake was divided into 0.1% juvenile hake and 1% adult hake with the rest added to mesozooplankton. The 13.3% cephalopods was reduced to 0.01% and the rest added to detritus. The 15% macrobenthos was removed and 1% each added to lobster and crabs, with the rest added to detritus.

22. Cephalopods

The important cephalopods include *Loligo vulgaris reynaudii, Todarodes angolensis, Todaropsis eblanae, Lycoteuthis diadema, Sepia australis, Octopus* spp. and *Argonauta* spp. (Lipiński, 1992). In addition the flying squid (*Todarodes sagittatus*) and cuttlefish (*Sepia australis*) were found amongst the demersal trawls (Hamukuaya *et al.*, 2001). Abelló *et al.* (1988) showed that *T. sagittatus* occurred in deeper water between 23°S and 29°S, with the highest numbers around 24°S–25°S and 27°S. Similarly, Hamukuaya *et al.* (2001) showed that *T. sagittatus* occurred in demersal deep-water slope assemblages between 17°S and 29°S and that *S. australis* occurred on the shelf around the Orange River (29°S). Thus, as this group encompasses all cephalopods, it was assumed to occur everywhere in the spatial model.

Loligo v. reynaudii and *T. angolensis* sustained fisheries in the 1980s, with catches obtained from Lipiński (1992) for 1980–1988 and biomass estimated from 1983 to 1988 for *T. angolensis* specifically. These estimates were for a smaller area and in winter, so the biomass was lower than the total catch; thus the estimates were not used in the model, but biomass was estimated by assuming an ectrophic efficiency of 95%. For the periods 1950–1979 and 1989–2003 catches were estimated as 1.8% of the main catch of all demersal species including hake, other demersals and monkfish as suggested by Hamukuaya *et al.* (2001). The P/B and P/Q ratios were 1.5 year^{-1} and 10% respectively (Shannon and Jarre-Teichmann, 1999). To fit the model, the catch of cephalopods in the first year had to be halved to 0.002 t·km^{-2}·year^{-1}.

The diet of *T. angolensis* was calculated by Lipiński (1992) to include 5–10% euphausiids, 5–10% lightfish, 50–64% lanternfish, 5–8% hake, 2% other fish, 10% cephalopods, and 1% other organisms, while Shannon and Jarre-Teichmann (1999) included horse mackerel and gobies in the diet of all cephalopods. Therefore this model used a preliminary diet of 7.5% euphausiids, 64.5% lanternfish, 6.5% hake, 10% cannibalism, 5.5% horse mackerel and 6% gobies. The 6% gobies was increased to 10% to balance and the 64.5% of mesopelagics was reduced to 10% to balance that species. The difference was obtained from gobies, macro- (20%) and mesozooplankton (24.5%). Juvenile horse mackerel was reduced to 1% and the remainder added to macrozooplankton. The 6.5% juvenile hake was reduced to 0.1% and the remainder added to macrozooplankton. The 10% cannibalism was reduced to 1% and added to gobies and mesozooplankton.

23. Benthos

The biomass of benthos was estimated by using an ecotrophic efficiency of 95%. The P/B (1.2 year^{-1}) and P/Q (12%) of benthos in the southern Benguela was used (Jarre-Teichmann *et al.*, 1998) and the diet composition of 5% benthic producers, 15% benthos and 80% detritus was obtained from Shannon and Jarre-Teichmann (1999). The 15% benthos was reduced to 5% macrobenthos, 0.1% crabs and 0.1% lobster and the remainder added to detritus. As this was a combined group for all benthos, benthos were assumed to occur in all areas of the spatial model.

24. Crab

Deep-sea red crab (*Chaceon maritae*) occurs on the continental slope from 27°S northwards into Angola (Dias and Seita Machado, 1974 in Maurihungirire, 2004) at depths of 300–900 m (Melville-Smith, 1983). Thus, in the spatial model crabs were assumed to occur in the deep waters and on the northern slope.

The fishery for deep-sea red crab started in 1973 off Namibia, catching 3,877 metric tonnes (Beyers and Wilke, 1980) and expanded rapidly, with the largest annual catch of 10,000 tonnes being recorded in 1983 (Le Roux, 2001). Fishing effort increased in 1974 with 17 Japanese vessels and one mother vessel exploiting the stock, but during the next years the effort decreased and by 1979 only 5 vessels were active (Beyers and Wilke, 1980). Catch estimates (Figure 20) from 1980 to 1997 were obtained from Boyer and Hampton (2001) and from 1998 to 2002 from Nicols (2004). The catch estimate for 1973 (Beyers and Wilke, 1980) was used in conjunction with the catch in 1980 to calculate a linear increase in the catch for 1974 (the Sea Around Us catch was smaller than that of 1973 and the increased effort would have indicated an increased catch). Catch estimates from 1975 to 1979 and 2003 given by the Sea Around Us project were used.

In 1976 a South West African company entered the fishery, with 2 vessels in 1977 (Beyers and Wilke, 1980). The number of vessels in the crab fishery from 1973 to 1986 and the CPUE and effort from 1980 to 1986 were obtained from Melville-Smith (1988). In 1993 a depth restriction of 500 m was introduced, and it was reduced to 400 m later that year to prevent fishing vessels from operating at the shallow end of the species' range (Le Roux, 2001). Catches of deep-sea crab from 1980 to 2000 were obtained from Boyer and Hampton (2001).

The crab biomass (Figure 20) has declined from about 40,000 tonnes in the early 1980s to around 10,000 tonnes in the 1990s (Hampton, 2003). Thus, an estimate of 40,000 tonnes (0.22 t·km^{-2}) was used as a first biomass estimate for crabs in the 1950s. Population models, supplemented by surveys (which were conducted twice a year until 2000), indicate that the 2001 stock size was around 10,000 tonnes whole mass (Hampton, 2003). Estimates of crab biomass from 1990 to 1995 were obtained from the Ministry of Fisheries and Marine Resources (Heymans, 1997). The P/B (2.5 year^{-1}) and Q/B (8.6 year^{-1}) ratios were obtained from Heymans (1997). The P/B ratio was lowered to 1.2 year^{-1} to fit the model.

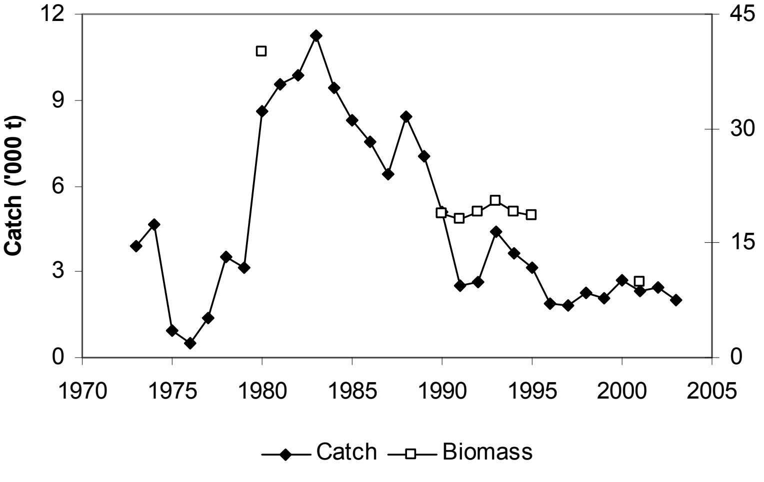


Figure 20. Catch and biomass of deep-sea crabs (*1000 tonnes).

Deep-sea crabs feed on skates (Macpherson, 1985 in Boyer and Hampton, 2001) and deep-sea (demersal) fish such as *Cottuncoloides macrocephalus* and *Alepocephalus rostratus* (Macpherson, 1983 in Boyer and Hampton, 2001). According to Beyers and Wilke (1980) the stomach contents of deep-sea crabs consisted of small shell fragments from goose barnacles, fish scales and the bones of small fish, while the remains of small crustaceans and unidentifiable digested food were the major constituents. Thus, this model assumed a diet of 33% macrobenthos, 33% demersal fish and 33% detritus. The demersals were reduced to 1% to balance the model and 1% was added to monkfish with the remaining 31% going to detritus.

25. Lobster

Lobster (*Jasus lalandii*) is associated with upwelling areas and occurs from South Africa to approximately 25°S (Hampton, 2003). They are most abundant off Lüderitz and the adjacent rocky shores (Hampton, 2003). Lobster was exploited from the early 1920s, and annual catches remained relatively high (9,000 tonnes) until the mid-1960s, and by the 1967 the fishery was near collapse (Pollock *et al.*, 2000). The fishery uses baited traps and hoop nets. Catches (Figure 21) of lobster from 1950 to 1957 were obtained from Crawford *et al.* (1989), from 1955 to 1957 from Pollock and Shannon (1987), from 1958 to 1989 from Boyer and Hampton (2001), from 1990 to 1997 from Pollock *et al.* (2000), from 1998 to 2002 from Nicols (2004) and for 2003 from the Sea Around Us database.

The fishable biomass of lobster has declined from around 10,000 tonnes in the early 1970s to 2,000–3,000 tonnes in 2001 (Grobler, 2000 in Hampton, 2003). Hampton (2003) suggested that the fishable biomass was between 3,000 and 4,000 tonnes in 2000. Barkai and Branch (1988) estimated the annual Q/B and P/Q of rock lobster to be 2.46 and 0.11 respectively. However, to fit the model a P/B of 1.2 year^{-1}, similar to that of macrobenthos was assumed and a P/Q of 0.3 was used to get a Q/B of 4 year^{-1}.

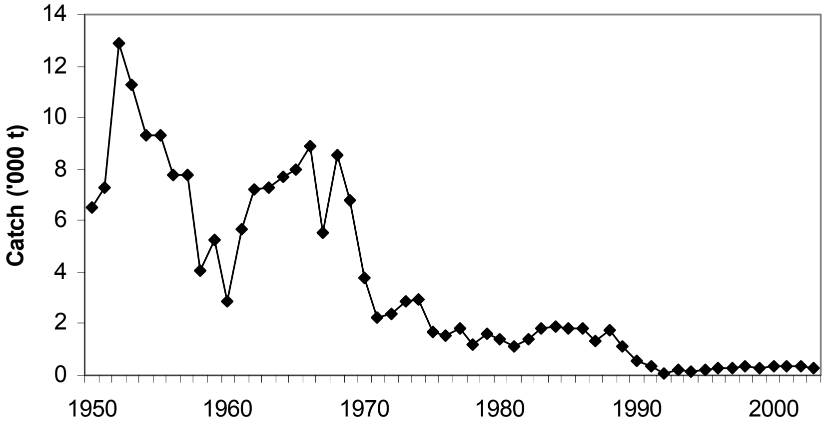


Figure 21. Catches of lobster (*1000 tonnes) made in the northern Benguela ecosystem from 1950 to 2002.

Rock lobster feed on mussels (ribbed mussels such as *Aulacomya ater*), echinoderms, gastropods, bryozoans, polychaetes and seaweed (Boyer and Hampton, 2001). They are preyed on by octopus, dogsharks, hagfish, young seals and cannibalism (Boyer and Hampton, 2001). This model used a diet of 50% macrozooplankton and 50% seaweed.

26. Juvenile jellyfish

Venter (1988a) found that there were abundant and widely distributed jellyfish off the coast of Namibia since the decrease in the pelagic fishing in 1972 and that the most abundant species were *Chrysaora hysoscella* and *Aequorea aequorea*. He showed that the main concentrations of jellyfish were between Cape Frio and south of Walvis Bay and mainly inshore. However, there were also some jellyfish further south and north and offshore around 21.5°S and at Walvis Bay (Venter, 1988a).

Fearon *et al.* (1992) found that jellyfish occur throughout the area they surveyed from 17°S to 29°S, with the lowest concentrations around 17°S–18°S and the highest concentrations of *Aequorea* in the north (19°S–22°S) and the highest concentrations of *Chrysaora* in the south (23°S–27°S). Sparks *et al.* (2001) found that both species are more prevalent in the north and *Chrysaora* specifically was very abundant in the north. Pagès (1992) showed that various cnidarians occurred in different areas of the northern Benguela, both offshore and onshore and in all the areas studied between 17.5°S and 26°S. Lynam *et al.* (2006) showed that *Chrysaora hysoscella* seems to occur mostly on the shelf and is widely distributed with hotspots around Möwe Bay (19°S), Swakopmund/Walvis Bay (22°S–23°S) and the Orange River (28°S–30°S). By contrast, *Aequorea forskalea* seems to occur further offshore, with definite hotspots at Cape Frio (18.5°S), a large area from Henties Bay (22°S) to south of Sandwich Harbour (24°S) and at the Orange River mouth (28°S–30°S). Thus both adult and juvenile jellyfish were assumed to occur in all areas of the model except the deep ocean.

Jellyfish was divided into adults and juveniles, and the P/B for juvenile jellyfish was estimated at 5 year^{-1}. The diet was assumed to consist only of phytoplankton.

27. Adult jellyfish

Venter (1988a) gave the distribution of jellyfish from the pelagic fish catches between 1981 and 1987. The catch of jellyfish from 1981 to 1987 was measured by Venter (1988a), who suggested that this was not an absolute estimate of catch, as it depends on the extent of damage caused during catching, transport and pumping procedures, on dumping and on the intensity of fishing activities. However, as the only estimate available, it was used as an indication of the fishing during that time. In addition, Venter (1988a) also indicates the percentage of the purse seine catch that consisted of jellyfish to be on average 14% for that time period. This model therefore assumes that from 1950 to 1972 the percentage of jellyfish in the catches increased linearly from 0% to 2% of the catches of anchovy and sardine (only), and from 1973 to 1979 it increased more substantially from 3% to 14% (the average for 1980–1988). From 1989 to 2003, we assumed that the jellyfish in the catch increased from 14% to 20% of the anchovy and sardine catches. These catches were still an order of magnitude higher than those given by Venter (1988a), so this was divided by 10 to get a first estimate of jellyfish catch (Figure 22).

Pagès (1992) found that the most abundant medusae in the northern Benguela in 1981–1982 were *Chrysaora hysoscella, Aequorea aequorea* and *Liriope tetraphylla*, with the most abundant siphonophores being *Muggiaea atlantica, Abylopsis tetragona* and *Bassia bassensis*. He differentiated three assemblages, one associated with coastal upwelling, the second with oceanic water and the third with species typical of shelf fauna (Pagès, 1992). *C. hysoscella* is known as a coastal species and *A. aequorea* a coastal shelf species, while *L. tetraphylla* is oceanic, *M. atlantica* is an inshore species and *Abylopsis tetragona* is an oceanic species (Pagès, 1992).

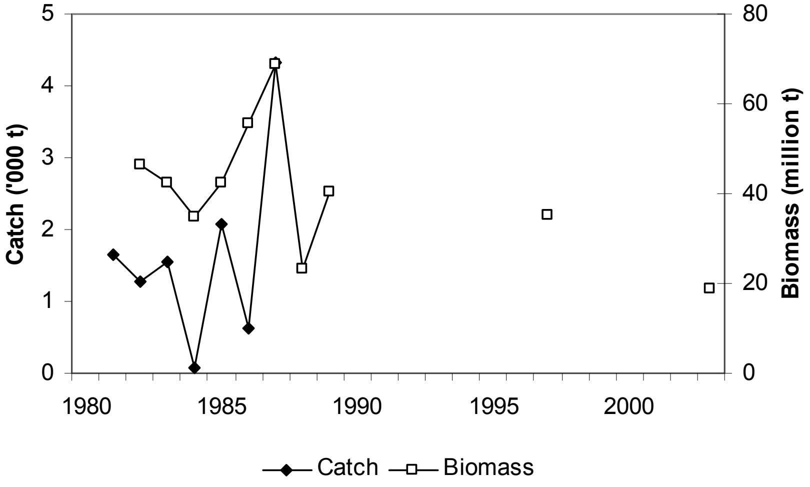


Figure 22. Catch (*1000 tonnes) and biomass (million tonnes) estimates of jellyfish.

Estimates of jellyfish biomass (Figure 22) from 1982 to 1989 were obtained from Fearon *et al.* (1992), while the biomass for 1997 to 1998 was estimated by Sparks *et al.* (2001), and Lynam *et al.* (2006) estimated a biomass of 106 tonnes·km^{-2} in 2003. However, the biomass in the 1950s was not known, and according to Lynam *et al.* (2006) large jellyfish was not prevalent prior to the heavy exploitation of pelagic fish in the Benguela, as "reports of extensive plankton sampling in the 1950s and 1960s do not mention large jellyfish, although numerous small gelatinous species (e.g. ctenophores) were observed". We can therefore assume that the biomass would have been very low in the 1950s and a value of 13.2 tonnes·km^{-2} was needed to fit the model.

The P/B and P/Q ratios for adults were estimated at 0.371 year^{-1} and 41% respectively (Shannon and Jarre-Teichmann, 1999). The diet of adults was estimated to consist of 24.7% phytoplankton, 25% bacteria (detritus), 25% microzooplankton (detritus) and 25% copepods (Shannon and Jarre-Teichmann, 1999) and we assumed that juvenile anchovy, sardine and gobies were 0.1% each.

28. Macrozooplankton

Early studies of the zooplankton of the northern Benguela showed that the area west and northwest of Walvis Bay had consistently high zooplankton biomasses and that there are two annual zooplankton peaks, one during the late spring and early summer (November–December) and the other during the autumn (March–May) (Shannon and Pillar, 1986). The SWAPELS cruises found that there were high concentrations of phytoplankton inshore and offshore peaks of zooplankton biomass (Shannon and Pillar, 1986). Estimates of zooplankton biomass were given in Shannon and Pillar (1986) for 1958–1959 as 2.04 gC·m^{-2} and for 1959–1962 as 1.34 gC·m^{-2} in Walvis Bay, for the area 19°S–23°S in 1971 as 0.96 gC·m^{-2} and in June–July as 0.63 gC·m^{-2}. This averages to about 18 t·km^{-2} for both meso- and macrozooplankton combined (Shannon and Pillar, 1986). However, the macrozooplankton biomass was estimated using an ecotrophic efficiency of 95% to balance the model.

Macrozooplankton include euphausiids, chaetognaths and hyperiid amphipods, with the euphausiids being the most important group (Heymans, 1997). Amphipods, siphonophores, ostracods, decapods and mysids are scarce (Timonin *et al.*, 1992). The important euphausiids include *Nyctiphanes capensis, Nematoscelis megalops, Thysanoessa gregaria, Euphausia lucens, E. tenera, E. recurva* and *E. hanseni* (Hart and Currie, 1960). Species of chaetognaths of importance include *Sagitta friderici, S. serratodentata, S. decipiens, S. minima, S. lyra* and *Eukrohnia hamata* (Hart and Currie, 1960). In addition, Hart and Currie (1960) also found Cladocera (*Evadne normandi, Podon polyphemoides*), Ostracoda (*Conchoecia* spp.), mysids (*Gastrosaccus sanctus, Boreomysis rostrata*), Cumacea (*Iphinoe* spp., *Upselaspis caparti*), Stomatopods (*Squilla armata*), planktonic mollusks (*Ianthina ianthina, I. globosa*) and Larvacea (*Oikopleura* and *Fritillaria*). Hutchings *et al.* (1991) estimated a biomass of 0.6 gC·m^{-2}, or 15 t·km^{-2} (using a C:wet weight ratio of 0.04) and P/B and P/Q ratios 13 year^{-1} and 41% respectively, while their diet included 60% phytoplankton and 40% copepods.

29. Mesozooplankton

The mesozooplankton of the northern Benguela is homogeneous, with copepods being dominant in terms of numbers and biomass (Timonin *et al.*, 1992). Hansen *et al.* (2005) found that 4 calanoid copepods dominated the zooplankton community off Walvis Bay in 2000, ranked in order of abundance as *Metridia lucens, Calanoides carinatus, Rhincalanus nasutus* and *Centropages* spp. The total copepod abundance was 520*10^{3} m^{-2} and according to Hansen *et al.* (2005) it compared well with the 236–446*10^{3} m^{-2} found in 1972, 700*10^{3} m^{-2} in 1979 and 300–800*10^{3} m^{-2} in 1986. Unterüberbacher (1964) in Shannon and Pillar (1986) gave an estimate of 0.828 gC·m^{-2} and Kollmer (1963) in Shannon and Pillar (1986) estimated 1.26 gC·m^{-2}; thus using the average of these two estimates and the carbon to wet mass ratio of 0.04 given by Hutchings *et al.* (1991) gives a biomass of 26 tonnes·km^{-2} between 1958 and 1962. This figure is used here and compares to the 25 tonnes·km^{-2} used by Shannon and Jarre-Teichmann (1999). This is also very similar to the value of 1.0 gC·m^{-2} estimated by Hutchings *et al.* (1991). The P/B and P/Q ratios were 40 year^{-1} and 30% respectively (Hutchings *et al.*, 1991). However, Cushing (1971) in Verheye *et al.* (1992) suggests a daily P/B of 0.02–0.03 or 9.1 year^{-1}. The diet of copepods includes 50:50 phytoplankton and detritus in our model (Hutchings *et al.*, 1991).

30. Benthic producers

Benthic producers in Namibia include the seaweed *Gracilaria gracilis*, which is harvested in Lüderitz Bay and the lagoon area and is used for the production of agar (Hampton, 2003). Kelp species such as *Laminaria pallida and L. schinzii* and *Ecklonia maxima* are also prevalent in the northern Benguela and used to a lesser extent (Hampton, 2003). Critchley *et al.* (1991) found that *Suhria vittata* is also exploited for export.

The organized harvesting of seaweed started in 1980 and beach-cast *Gracilaria* was exported for US$1,700 per tonne, but that declined to US$1,250 per tonne by 1994. Production increased from 310 tonnes dry weight in 1982 to 1,500 tonnes in 1988 (Hampton, 2003). Approximately 15,000 tonnes of *Gracilaria* are deposited on the shore in Lüderitz and collected for agar extraction each year (Critchley *et al.*, 1991). An agar extraction plant was relocated to Lüderitz in 1986 and it employed about 250 people. By 1991 it had a targeted output of 100 tonnes of agar powder per year, which was exported to Europe, South Africa and Mauritius (Critchley *et al.*, 1991). The agar powder has a moisture content of 10–16% and the agar content of *Gracilaria verrucosa* ranged from 16–30% of dry weight, with monthly yields of 5.3 tonne per month in 1988–1989, 7 tonne per month in 1989–1990 and 12 tonne permonth in 1990–1991 (Critchley *et al.*, 1991). The total dry weight extracted from 1986 to 1989 was given by Critchley *et al.* (1991) as approximately 810 tonnes, 982 tonnes, 1,640 tonnes and 1,244 tonnes from 1986 to 1989. This model assumed a linear increase in the catch from 1982 to 1986.

Harvests since 1990 have fluctuated between 423 and 1,029 tonnes dry weight, with the largest harvests being made in 1995 and 1996. We assumed that the 423 tonnes was in 1990 and the 1,029 tonnes in 1995 and 1996 and did a linear increase from 1990 to 1995. In 2000, 829 tonnes were harvested with an export value of N$3,850,000 (Hampton, 2003), and Nicols (2004) gives estimates of harvest from 1998 to 2002. A dry weight to wet weight ratio of 0.137 was used to calculate the wet weight (Hernández *et al.*, 2005). We assumed that there was a linear increase in catch from 1979 to 1982 and from 1982 to 1988 and that there was a linear decline from 1996 to 1998. No estimates of biomass or P/B were available for the 1950s, thus the values from the 1970s were used for P/B (0.5 year^{-1}) and an EE of 0.5.

31. Phytoplankton

The dominant phytoplankton or 'microplankton' obtained during the *William Scoresby* surveys include: *Stephanopyxis turris, Thalassiosira excentrica, T. subtilis, Planktoniella sol, Chaetoceros affine, C. compressum, C. constrictum, C. convulutum, C. debile, C. decipiens, C. difficile, C. didymum, Ceratium strictum, Rhizosolenia alata, R. hebetata, R. imbricata, Dactyliosolen mediterraneus, F. karstenii, Asterionella japonica, Nitzschia delicatissima, N. seriata, Peridium* spp., *Trichodesmium thiebautii* and Foramanifera (Hart and Currie, 1960). During 1950 the *William Scoresby* undertook a major oceanographic study off the coast of southern Africa and found that the depth of upwelling was down to 350 m in the fall (March) and 320 m in spring (October) (Hart and Currie, 1960). Even during this survey there were large areas of oxygen-depleted water in the Walvis Bay region (Hart and Currie, 1960) and Brongersma-Sanders (1948) in Hart and Currie (1960) reported large areas of fish kills from Walvis Bay to Conception Bay, while Reuning (1925) in Hart and Currie (1960) showed even larger fish kills in 1924–1925. These fish kills are related to calm weather or northerly winds, which create abnormal conditions in the vicinity of Walvis Bay (Hart and Currie, 1960).

Barange and Boyd (1992) showed that the main areas of high chlorophyll-a distribution between 1985 and 1989 were south of Cape Frio (18.5°S) to about Torra Bay (20.5°S) and from Swakopmund (22.5°S) to about Easter Point (25.5°S). These overlap with the areas of highest chlorophyll-a concentration shown by Pitcher *et al.* (1992) for 1971–1989, with highest concentrations between Cape Cross and just south of Cape Frio (21.5°S–19°S) from Swakopmund to Sandwich Harbour (22.5°S–23.5°S) and from 24.5°S north of Sylvia Hill to Lüderitz (26.5°S). These areas are mostly north of the main upwelling areas around Lüderitz (from 24°S–26.5°), north of Cape Cross (20°S–21.5°S) and around Cape Frio (18°S–19°S), according to Crawford *et al.* (1989). The upwelling cells were also given by Hamukuaya *et al.* (2001) from around Panther Head (28°S) to Dolphin Head at Easter Point (25.5°S), north of Cape Cross (20°S–21.5°S) and south of Cape Frio (18.5°S–19°S), indicating that the northern upwelling cell might have moved. In addition, Pitcher *et al.* (1992) showed that the highest offshore concentrations of chlorophyll-a were from the Kunene (17°S, and their most northerly data) to Cape Cross (21.5°S) and between 24°S and 28°S.

Wasmund *et al.* (2005) calculated the primary production and chlorophyll-a biomass of phytoplankton in 6 different water bodies in the Cape Frio area, and the average primary production was 1.6 gC·m^{-2}·d^{-1} (24,436 tww·km^{-2}·year^{-1}) and 56 mg·m^{-2} (117 tww·km^{-2}) respectively. Carr and Kearns (2003) give estimates of the primary production and biomass of phytoplankton between 1998 and 2000 for 6 areas off Namibia, with an average primary production of 4.25 gC·m^{-2}·d^{-1} (65,153 tww·m^{-2}·year^{-1}) and chlorophyll biomass of 6.83 mgC·m^{-3}. For 1997–1999 Carr (2002) estimates a production of 2.49 gC·m^{-2}·d^{-1} (40,057 tww·km^{-2}·year^{-1}) and Ryther (1969) estimates a value of 3.9 gC·m^{-2}·d^{-1} (59,787 tww·km^{-2}·year^{-1}) prior to 1969. Estimates of primary production given by references in Shannon and Pillar (1986) range from 0.8 gC·m^{-2}·d^{-1} at the Orange River to 2.5 gC·m^{-2}·d^{-1} at Walvis Bay to 5.1 gC·m^{-2}·d^{-1} at Walvis Bay, to 0.3 gC·m^{-2}·d^{-1} at Orange River, 0.9 gC·m^{-2}·d^{-1} at Lüderitz, 3.9 gC·m^{-2}·d^{-1} at Sylvia Hill, 1.2 gC·m^{-2}·d^{-1} at Walvis Bay, 0.6 at 21ºS and 3.2 gC·m^{-2}·d^{-1} at Cape Frio. This gives an average similar to the 2.58 gC·m^{-2}·d^{-1} of Schultz (1982) in Wasmund *et al.* (2005). In addition, Schultz (1982) in Wasmund *et al.* (2005) estimated a chlorophyll-a biomass of 258 mg·m^{-2}, or 433 t·km^{-2} using a C:wet weight ratio of 42 (Cushing *et al.*, 1958). The biomass was estimated using an average euphotic zone depth of 40 m, as Wasmund *et al.* (2005) suggests that the 1% light level was at 18–36 m in upwelling water and 30–60 m in subtropical waters, and the average depth of euphotic zones of the various water bodies they tested was approximately 40 m. This value is lower than the 600 t·km^{-2} estimated by Brown *et al.* (1991). The annual P/B ratio of 49.9 was estimated from the biomass and primary production (Schultz, 1982 in Wasmund *et al.*, 2005). This is much higher than the annual P/B of 30 estimated by Brown *et al.* (1991).

Environmental variation

Shelton and Crawford (1988) found that three major components of variability with different time periods characterize the Benguela system, namely upwelling events, seasonal changes and prolonged changes in normal advection patterns. The relative contribution of these different components to the overall variability of the system has not been resolved (Shelton and Crawford, 1988).

Benguela Niños occurred in 1934, 1949, 1963, 1974, 1984 (Shelton and Crawford, 1988) and 1995. These warm events are interspersed with cooler periods, suggesting a 10-year cycle, and correspond with heavy rains or flooding in parts of Namibia (Shannon *et al.*, 1986). The rainfall patterns in Namibia have an effect on the oxygen content of the bottom water along the Namibian coast. It has been postulated that groundwater with high silicate concentrations seeps into the coastal water at river mouths (Pollock *et al.*, 2000). In adjacent river catchments the rainfall regime changed from the 1960s. It increased during the late 1960s and the 1970s but decreased again during the 1980s and 1990s (Pollock *et al.*, 2000). Thus, a nutrient-driven change in ecosystem productivity might have started in the late 1960s with the consequence of increased production of oxygen-depleted bottom water in the area between 19°S and 25°S. This was synchronized with the collapse of the west coast pilchard stock and its replacement by anchovy and pelagic gobies (Crawford *et al.*, 1985; Pollock *et al.*, 2000). The recycling of silicate over the siliceous mudbelt between 19°S and 25°S might be maintaining the system in a hypertrophic mode with persistently high levels of diatom production and decay (Pollock *et al.*, 2000). Rainfall estimates from 1913 to 1997 were obtained from Pollock *et al.* (2000).

Two environmental anomalies occurred between 1993 and 1995: in 1993–1994 the shelf water off Namibia was hypoxic and extended over a larger area and lasted for a longer period than usual (Hamukuaya *et al.*, 1998). Then in February–March 1995 there was a strong Benguela Niño event, with warm water intruding onto the Namibian shelf (Cury and Shannon, 2004). Most stocks underwent large declines: sardine recruitment was poor (Boyer *et al.*, 2001a), hake migrated offshore (Hamukuaya *et al.*, 1998), monkfish catches decreased (Maartens, 1999 in Cury and Shannon, 2004), horse mackerel biomass decreased by 50% (Boyer and Hampton, 2001) and anchovy abundance declined further (Cury and Shannon, 2004).

Warm water intrusions into northern Namibia also have an effect on the ecosystem. Voges *et al.* (2002) give indications of how far south warm water intruded into Namibia from Angola, and Stander and De Decker (1969) in Shelton and Crawford (1988) indicated that in 1963 there was an intrusion of warm water from the northwest.

There is evidence that the distribution of hake in Namibian waters is affected by both oxygen deficiency and temperature, although adult hake are well adapted to low oxygen concentrations (Hampton, 2003). Oxygen levels are generally low over much of the Namibian shelf due to its depletion during the decomposition of excessive phytoplankton production and the advection into the region of oxygen-deficient water, with concentrations below 2 $\text{ml}\cdot\ell^{-1}$, formed off Angola (Shannon, 1985). Oxygen levels over a large part of the shelf can become intolerable, possibly causing major shifts in distribution and even increased mortality, if extensive and persistent enough. The juveniles, which are less tolerant to hypoxic conditions, are particularly vulnerable (Woodhead, *et al.* 1996 in Hampton, 2003). An example of a major effect on the resource occurred in 1993 and 1994, when pronounced and persistent hypoxic conditions off central and northern Namibia displaced *M. capensis* offshore, subjecting them to heavy mortality from predation by larger hake and trawling (Hamukuaya *et al.*, 1998).

There is evidence to suggest that low surface temperatures favor hake recruitment, or at least that the recruits are more abundant and occur at higher densities in cool periods, such as in 1992, when *M. capensis* recruitment in Namibia was the highest ever recorded (Stromme, 1996 in Hampton, 2003). Also, there has been a clear positive correlation between monthly catch rates and surface temperature in Namibia in certain years (e.g. 1994 through 1996), although in other years (e.g. 1993 and 1997) the correlation has been as clearly negative (Boyer *et al.,* 1998 and Gordoa *et al.,* 2000 in Hampton, 2003). The reasons for these apparent correlations are not understood. The vertical structure in temperature and oxygen concentration, particularly close to the bottom, is believed to have an effect on the vertical distribution of hake, which could indirectly affect their horizontal distribution (S. Sundby, *pers. comm.*) and perhaps even their abundance. The effect on trawl catch rates, and hence estimates of abundance, would be more direct, since even a small vertical migration away from the bottom will affect catch rates significantly (Hampton, 2003).

Anchovy catches were exceptionally good in 1987 due to the breakdown of the Lüderitz upwelling barrier, which enabled anchovy recruits from South Africa to be carried into the northern Benguela (Hampton, 2003). According to Jenkins (1979) in Shelton and Crawford (1988), lower SST, lower sea level and lower SE wind components were positively correlated with pilchard catches. The rock lobster decline in the late 1980s was due to changes related to oxygen fluctuations in bottom waters and was aggravated by overfishing (Hampton, 2003).

Time series of wind stress for the Lüderitz upwelling cell from 1960 to 2002 were obtained from Klingelhoeffer (2006) and from 1906 to 1984 for the area 20°S–25°S:5°E–10°E from Shannon and Taunton-Clark (1988). Similarly for the same time period, sea surface temperature for the same area and for the whole coastal area were also obtained from Shannon and Taunton-Clark (1988). Sea surface temperature and pseudo–wind stress anomalies were obtained from Shannon and O'Toole (2003) from 1946 to 1990 and the sea surface anomaly was negatively correlated with the forcing function estimated by the model (Figure 23).

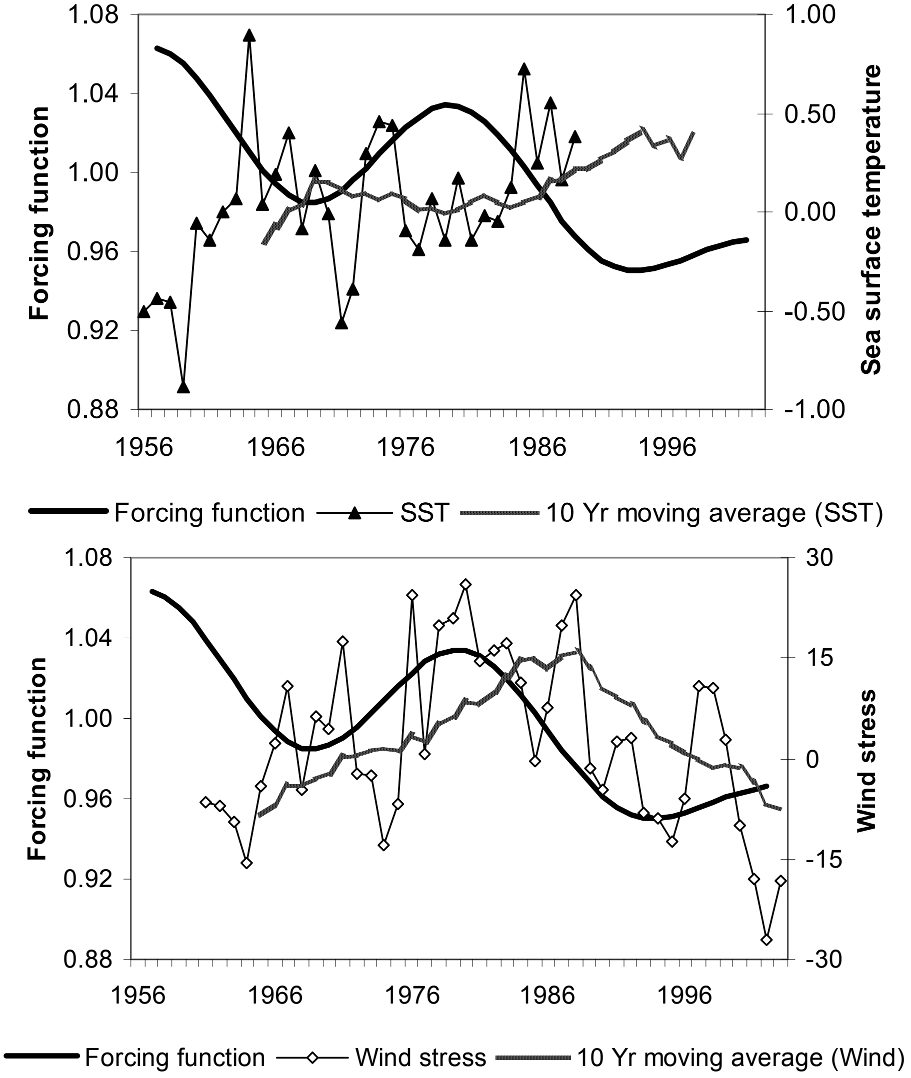


Figure 23. Estimates of the forcing function estimated by the model based on the data : Top graph - Sea surface temperature (SST) anomaly. Bottom graph – wind stress.

MODEL FITTING RESULTS

To fit the model, the catches of tuna, seaweed and lobster were forced thereby acting as a simple stock reduction model for those groups. For sharks, anchovy, monkfish, demersals and crabs only some of the catches were forced where no biomass was available to estimate a fishing effort. For the species that were not fished in 1956 the catches in their first year were entered and then taken out at a negative biomass accumulation to start the effort calculations correctly. In addition, to fit the model the catch of cephalopods in the first year had to be halved to 0.002 t·km^{-2}·year^{-1} and a catch and discard of 0.002 t·km^{-2}·year^{-1} needed to be added to juvenile horse mackerel to increase their catches in the fitted model. The input variables of the balanced model are given in Table 4, the catches used for the 1956 Ecopath model in Table 5 and the diet in Appendix A.

The model was driven by the effort time series given in the fisheries section above, and the model was fitted to the time series by the algorithm that changes the vulnerabilities for each fo the interactions between predators and prey and by using feeding time adjustment rates of 0.5 for juvenile anchovy, sardine, gobies, and juvenile and adult jellyfish (Table 4). In addition a forcing function was estimated which was negatively correlated (R^2=-0.434, α=0.05, DF = 33) with the sea surface anomaly given by Shannon and O'Toole (2003) and the summer sea surface temperatures at Lüderitz (R^2=-0.426, α=0.05, DF = 39) used in Heymans (2004). The forcing function was also positively correlated to the wind stress anomaly (R^2=0.341, α=0.05, DF = 43) used by Klingelhoeffer (2006). The sea surface temperature anomaly and wind stress as well as the forcing function estimated by the model are given in Figure 23. Even though both these environmental variables were correlated with the forcing function obtained from the model, neither were directly applied to the model as they do not span the whole time period. The fitted model results are given in Figure 24 (biomass) and Figure 25 (catch).

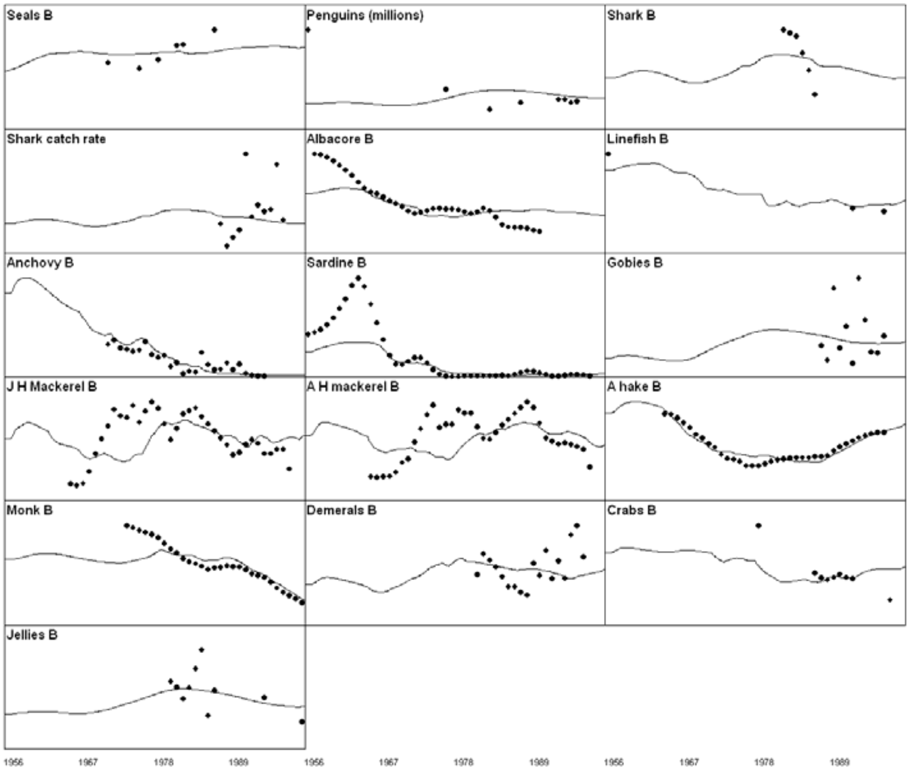


Figure 24. Fit of the northern Benguela model (lines) to the biomass estimates given in the literature (dots).

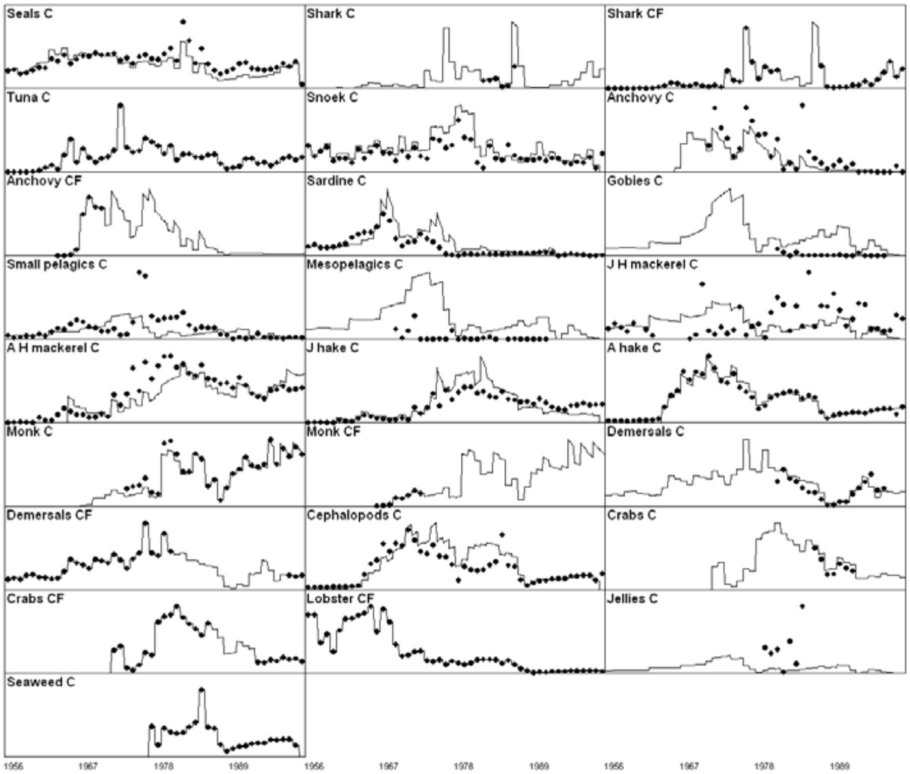


Figure 25. Fit of the model (lines) to the catches of the various species in the northern Benguela ecosystem.

The model was able to reproduce the general decline in pelagics, specifically anchovy, quite well, but was not able to reproduce the large increase in sardine in 1960 that was estimated by VPA (Figure 24). This could indicate more of a failure of the VPA model than of the ecosystem model, as VPA can overestimate the initial biomasses in order to have large catches (Figure 25). The good fit of the hake and monkfish biomass in the model to the data are related to the high catches in the system, and the model was able to reproduce the catches of those two groups very well, as well as the catches of other demersal fish species and crabs (Figure 25). Where the model is unable to fit the data is in the gobies, small pelagics and mesopelagics, where we have very little information on the biomass of these groups to drive the model. For the predators such as seals, sharks and snoek the model reproduces the catch series quite well even when we do not have good biomass estimates.

Table 4. Ecosystem groupings, trophic level (TL), biomass (t·km^{-2}) production to biomass (P/B) and consumption to biomass (Q/B) ratios, ecotrophic efficiencies (EE), catches (t·km^{-2}·yr^{-1}) and vulnerabilities (Vul.) by predator used in the northern Benguela ecosystem in 1956. Values in italics have been estimated by Ecopath.

Group name	TL	Biomass	P/B	Q/B	EE	Catch	Vul.
Marine Mammals	4.23	0.027	1	*12.66*	*0.030*		2.00
Seals	3.84	0.150	0.08	19.44	*0.890*	0.005	2.00
Birds	3.54	0.017	0.16	120.3	*0.838*		2.00
Sharks	4.09	0.411	0.5	*2*	*0.577*	0.0002	2.00
Tuna	3.9	1.000	0.25	*5*	*0.005*	0.005	1.50
Snoek	3.66	*0.664*	0.25	*2.5*	0.950	0.017	5.60
Other linefish	3.74	0.121	0.2	*2*	*0.585*	0.007	1.00
Anchovy juvenile	2	0.005	10	103.9	*0.704*		1000.00
Anchovy adults	2.76	5.700	0.85	11.6	*0.785*	0.003	2.05
Sardine larvae	2	0.023	10	48.45	*0.378*		10.00
Sardine adults	2.43	26.000	0.53	5	*0.398*	1.722	1000.00
Gobies larvae	2	0.004	7	144.2	*0.631*		2.00
Gobies adults	2.09	6.300	1.1	15	*0.877*	0.007	5.13
Other small pelagics	3.17	*9.206*	0.75	*7.5*	0.950	0.079	2.00
Mesopelagics	3.24	*3.820*	1.23	*12.3*	0.950	0.007	1.00
Juvenile horse mackerel	3	0.934	1.7	15.18	*0.821*	0.152	2.00
Adult horse mackerel	3.34	7.000	0.4	5.2	*0.390*	0.007	2.00
Juvenile hake	3.38	0.482	1.05	11.27	*0.891*		2.00
Adult hake	3.35	24.000	0.4	2.4	*0.407*	0.134	2.00
Monkfish	4.02	0.600	0.24	*2.4*	*0.787*	0.001	1.75
Other demersals	2.78	*1.158*	1	*10*	0.950	0.073	2.00
Cephalopods	3.43	*1.023*	1.5	*15*	0.950	0.002	2.00
Macrobenthos	2.06	*7.826*	1.2	*10*	0.950		2.00
Crabs	2.4	*0.210*	1.2	8.6	0.950	0.022	1.50
Lobster	2.53	*0.235*	1.2	*4*	0.950	0.043	2.00
Jellyfish juveniles	2	0.002	5	11.16	*0.354*		2.00
Jellyfish adults	2.25	13.200	0.37	0.90	*0.826*	0.001	3.00
Macrozooplankton	2.4	*13.302*	13	*32.5*	0.950		2.00
Mesozooplankton	2	26.000	40	*133*	*0.316*		2.00
Benthic producers	1	*0.584*	15	-	0.500	0.006	-
Phytoplankton	1	433.44	49.9	-	*0.101*		-
Detritus	1	1.000	-	-	*0.087*		-

Ecospace model

Base map and habitat types

An Ecospace model of the northern Benguela, off the coast of Namibia (15°S–29°S, 10°E–17°E) was constructed to look at the effectiveness of current MPAs and the possible placement and number of MPAs in the future. The base map was obtained from the global GIS database query in Ecospace with a resolution of 6 minutes. The base map had 140 rows and 70 columns with a cell length of 10 km and 2 steps per degree (Figure 26). The base map depths were then exported to Excel and divided into 11 specific habitats based on depths <30 m as surf zones, 30–200 m as shelf areas, 200–500 m as slope areas and >500 m as deep areas. In addition the northern and southern parts of the coast were split at the Walvis Ridge. There are 3 marine protected areas in the northern Benguela, namely the Skeleton Coast Park in the north, the Namib Naukluft Park south of Walvis Bay, and the Diamond Sperrgebiet, south of Lüderitz (Figure 26). These areas are only closed to fishing from the shore and in the surf zone, but fishing in areas deeper than 30 m is allowed at present. The ports of Walvis Bay and Lüderitz are both used by the purse seine and demersal trawlers, while the lobster fishery and seaweed harvesting only occur around Lüderitz and the seal fishery only at Cape Cross. The midwater trawlers, longliners and crab fisheries are all operated from distant ports and with freezer trawlers. Linefish are caught by the commercial linefish fleet mostly from Walvis Bay, Swakopmund and Henties Bay (just north of Walvis Bay) and by the recreational fishery around Lüderitz and in the West Coast Recreational Area between Walvis Bay to Cape Cross.

Table 5. Catches ($t \cdot km^{-2} \cdot yr^{-1}$) by the purse seine (PS), midwater (MWT), demersal (DT), longline (LL), crab, lobster, commercial line (Com L), recreational line (Rec L), seal and seaweed (SW) fisheries. Italics are discards vs. landings.

Group name	PS	MWT	DT	LL	Crab	Lobster	Com L	Rec L	Seal	SW
Seals		*0.0005*	*0.0003*						0.004	
Sharks		*0.0001*	*0.00002*	0.00002			*0.0001*	0.000001		
Tuna	0.004			0.0003			0.0004			
Snoek		0.00001					0.017			
Other linefish							0.002	0.0046		
Anchovy adults	0.003									
Sardine adults	1.722									
Gobies adults	0.007									
Other S pelagics	0.079									
Mesopelagics	0.007									
J. h mackerel	0.152		*0.0002*							
A. h mackerel		0.0045								
Juvenile hake		*0.002*								
Adult hake			0.1340							
Monkfish			*0.0005*							
Other demersals			*0.0727*							
Cephalopods			*0.0020*							
Crabs					0.022					
Lobster						0.0434				
Jellyfish adults	0.001									
Benthic prod.										0.006
Total	1.976	0.007	0.210	0.0003	0.022	0.043	0.019	0.005	0.004	0.006

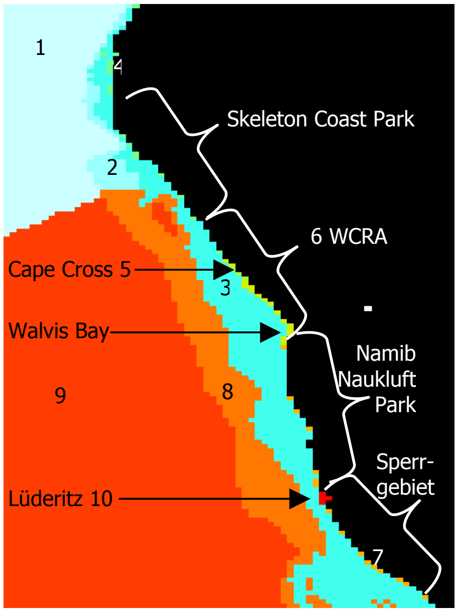


Figure 26. Base map of the northern Benguela ecosystem with numbers defined in the text.

Habitat information was available for some species and fisheries from the literature and these are described in the compartment descriptions in the text above. The habitat preferences of the different species are given in Table 6 and the various fisheries have been defined by area in Table 7. This information was used to define the habitats used in this model, which included the:

1) Deep areas north of the Walvis Ridge (>500 m, 15.2% of the area);
2) Northern slope (200–500 m, 1.6% of the area);
3) Shelf (30–200 m, 13.4%);
4) Northern surf zone (<30 m, 0.3%);
5) Cape Cross (<0.1%);
6) West Coast Recreational Area (0.3%);
7) Southern surf zone (< 30 m, 0.3%);
8) Southern slope (200–500 m, 10.9%);
9) Deep areas south of the Walvis Ridge (>500 m, 57.9%);
10) Lüderitz harbour (<0.1%).

Dispersal

The dispersal parameters in Ecospace were used to confine species to their known habitat. For most species the base dispersal rate was kept at the default value of 300 $km \cdot yr^{-1}$, while the relative dispersal in bad habitat was left at the default value of 5 $km \cdot yr^{-1}$, 100 $km \cdot yr^{-1}$ for species that are more pelagic and have specific areas of occurrence (adult and juvenile anchovy, sardine, gobies and juvenile horse mackerel) and 1,000 $km \cdot yr^{-1}$ for crabs and lobsters because they only occur in very specific areas in the ecosystem. In addition the relative vulnerability to predators in bad habitat was increased from the base value of 2 to 100 for juvenile and adult anchovy, sardine, gobies, as well as for juvenile horse mackerel, crabs and lobsters. Finally the relative feeding rate in bad habitat was reduced to 0 for these species from 0.01, which was the default for all other groups.

Table 6. Preferred habitats for the various groups in the northern Benguela. CC = Cape Cross and WCRA = West Coast Recreational Area.

Group	All	Deep N	Slope N	Shelf	Surf N	CC	WCRA	Surf S	Slope S	Deep S	Lüderitz
Marine mammals	+										
Seals					+	+	+				
Birds	+										
Sharks	+										
Tuna		+	+	+					+	+	
Snoek			+	+	+	+	+	+	+		+
Other linefish			+	+	+	+	+	+	+		+
Anchovy juveniles				+	+	+	+	+			+
Anchovy adults				+	+	+	+	+			+
Sardine juveniles				+	+	+	+	+			+
Sardine adults				+	+	+	+	+			+
Gobies juveniles				+	+	+	+	+			+
Gobies adults			+	+	+	+	+	+	+		+
Other s pelagics	+										
Mesopelagics		+	+	+					+	+	
Juv. h mackerel				+	+	+	+	+			+
Adult h mackerel			+	+					+		
J hake			+	+					+		
A hake		+	+						+	+	
Monkfish		+	+						+	+	
Other demersals	+										
Cephalopods	+										
Macrobenthos	+										
Crabs		+	+								
Lobster							+	+			+
Jellyfish juvs	+										
Jellyfish adults	+										
Macrozooplankton	+										
Mesozooplankton	+										
Benthic producers							+	+			+
Phytoplankton	+										
Detritus	+										

Table 7. Distribution of the fishery in the northern Benguela Ecospace model. CC = Cape Cross and WCRA = West Coast Recreational Area.

Fleet	All	Deep N	Slope N	Shelf	Surf N	CC	WCRA	Surf S	Slope S	Deep S	Lüderitz
Purse seine				+							
Midwater trawler		+	+	+					+	+	
Demersal		+	+	+					+	+	
Longlines		+	+	+					+	+	
Crab traps		+									
Lobster											+
Commercial line					+	+	+	+			+
Recreational line					+	+	+	+			+
Seal fishery						+					
Seaweed											+

Advection

Advection patterns are given by Carr and Kearns (2003) and currents by Stenevik *et al.* (2003). Phytoplankton and mesoplankton were advected in the model. In general, the wind vectors on this part of the coast are from north to south, with northwesterly winds being prevalent offshore. The wind forcing varies between 0.08 and 1.2 $m^2 \cdot s^{-1}$ (Carr and Kearns, 2003). Due to the Coriolis force, sea surface currents move the water offshore and upwelling occurs. The spatial model of the northern Benguela ecosystem is given in Figure 27.

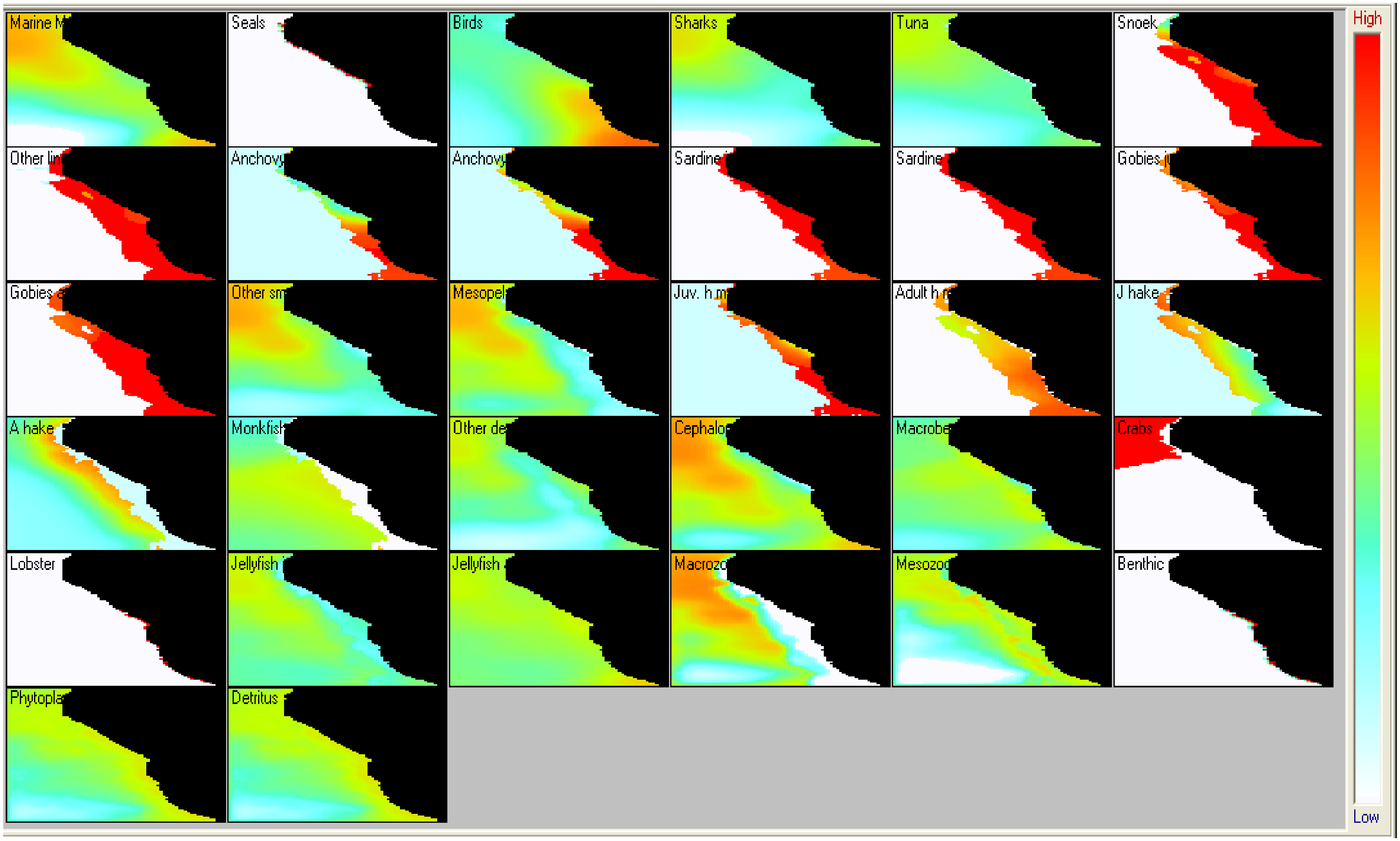


Figure 27. Result of the Ecospace run for biomass in the northern Benguela ecosystem.

ACKNOWLEDGEMENTS

The authors wish to thank Kevin Stephanus and Susan Alexander for their contribution to the data used in this report. The work was funded by the European Union through the INCOFISH project (www.incofish.org).

REFERENCES

Abelló, P., Gordoa, A., Manriquez, M., Masó, M. and Macpherson, E. 1988. Biomass indices and recruitment levels for hake and other commercial species in ICSEAF Division 1.4 and 1.5: Results from the Spanish Benguela XI research cruise (1987). Collection of Scientific Papers of the international Commision of South East Atlantic Fisheries 15(1): 7-21.

Andronov, V.N. 1983. Feeding of Cape horse mackerel (*Trachurus trachurus capensis*) and Cape hake (*Merluccius capensis*) off Namibia in January 1982. Collection of Scientific Papers of the international Commision of South East Atlantic Fisheries 10(1): 1-6.

Andronov, V.N. 1985. Feeding of Cape horse mackerel *Trachurus trachurus capensis* Castelnau, in the Namibian area. Collection of Scientific Papers of the international Commision of South East Atlantic Fisheries 12(1): 1-16.

Anon. 2001. Proceedings of an international workshop on the research and management of horse mackerel in Namibian waters. pp. 45++ *in* Payne, A.I.L., editor. Ministry of Fisheries and Marine Resources, Swakopmund, Namibia.

Anon. 2005. A review of aquaculture policy and institutional capacity in the BCLME region, with recommended regional policy options. BCLME Project LMR/MC/03/01, EFA Enviro-Fish Africa, The Consortium 67 p.

Armstrong, C.W., Sumaila, U.R., Erastus, A. and Msiska, O. 2004. Benefits and costs of the Namibianisation policy. pp. 203-214 *in* Sumaila, U.R., Steinshamn, S.I., Skog, M. and Boyer, D.C., editors. Ecological, economic and social aspects of Namibian fisheries. Eburon, Netherlands.

Axelsen, B.E., Krakstad, J.-O. and Bauleth-D'Almeida, G. 2004. Aggregation dynamics and behaviour of the Cape horse mackerel (*Tracurus trachurus capensis*) in the northern Benguela - implications for acoustic abundance estimation. pp. 135-164 *in* Sumaila, U.R., Steinshamn, S.I., Skog, M. and Boyer, D.C., editors. Ecological, economic and social aspects of Namibian fisheries. Eburon, Netherlands.

Balmelli, M. and Wickens, P.A. 1994. Estimates of daily ration for the South African (Cape) fur seal. South African Journal of Marine Science 14: 151-157.

Barange, M. and Boyd, A.J. 1992. Life history, circulation and maintenance of *Nyctiphanes capensis* (Euphausiacea) in the northern Benguela upwelling system. South African Journal of Marine Science 12: 95-106.

Barkai, A. and Branch, G.M. 1988. Energy requirements for a dense population of rock lobsters *Jasus lalandii*: Novel importance of unorthodox food sources. Marine Ecology Progress Series 50: 83-96.

Barnes, J., Zeybrandt, F., Kirchner, C., Sakko, A. and MacGregor, J. 2004. Economic valuation of the recreational shore fishery: a comparison of techniques. pp. 215-230 *in* Sumaila, U.R., Steinshamn, S.I., Skog, M. and Boyer, D.C., editors. Ecological, economic and social aspects of Namibian fisheries. Eburon, Netherlands.

Bauleth-D'Almeida, G. 2001. Development and application of management procedures for horse mackerel, *Trachurus capensis*, in the Namibian waters: 1990-2001. pp. 1-9 *in* Payne, A.I.L., editor. Proceedings of an international workshop on the research and managment of horse mackerel in Namibian waters. Ministry of Fisheries and Marine Resources, Swakopmund.

Bauleth-D'Almeida, G., Krakstad, J.-O. and Kanandjembo, A. 2001. Comparison of horse mackerel length frequencies obtained from research vessels and commercial midwater trawlers: implications for biomass estimation. South African Journal of Marine Science 23: 265-274.

Berry, H.U. 2002. Cape Cross: Past and present. The Authors, P&M Bridgeford, Walvis Bay, 44 p.

Best, P.B. 2006. The presence of right whales in summer on the west coast of South Africa: the evidence from historical records. African Journal of Marine Science 28: 159-166.

Best, P.B., Crawford, R.J.M. and Van der Elst, R.P. 1997. Top predators in Southern Africa's marine ecosystem. Transactions of the Royal Society of South Africa 52: 177-225.

Beyers, C.J.D.B. and Wilke, C.G. 1980. Quantitative stock survey and some biological and morphometric characteristics of the deep-sea red crab *Geryon quinquedens* off South West Africa. Fisheries Bulletin of South Africa 13: 9-19.

Bianchi, G., Hamukuaya, H. and Alvheim, O. 2001. On the dynamics of demersal fish assemblages off Namibia in the 1990s. South African Journal of Marine Science 23: 419-428.

Bianchi, G., Carpenter, K.E., Roux, J.-P., Molloy, F.J., Boyer, D. and Boyer, H.J. 1993. The living marine resources of Namibia. FAO species identification field guide for fishery purposes. FAO, NORAD, Rome, 250+ p.

Booth, A.J. and Quinn, T.J.I. 2006. Maximum likelihood and Bayesian approaches to stock assessment when data are questionable. Fisheries Research 80: 169-181.

Boyer, D. and Boyer, H. 2004. The large volume small pelagic fisheries of the Southeast Atlantic: Angola, Namibia and South Africa. pp. 67-94 *in* Swan, J. and Gréboval, D., editors. Report of the International workshop on the Implementation of International

Fisheries Instruments and Factors of Unsustainability and Overexploitation in Fisheries, Mauritius, 3-7 February 2003. FAO Fisheries Report No. 700. FAO, Rome.

Boyer, D.C. and Hampton, I. 2001. An overview of the living marine resources of Namibia. South African Journal of Marine Science 23(A Decade of Namibian Fisheries Science): 5-35.

Boyer, D.C. and Oelofsen, B. 2004. Co-Management: Namibia's experience with two large-scale industrial fisheries - sardine and orange-roughy. pp. 333-356 *in* Sumaila, U.R., Steinshamn, S.I., Skog, M. and Boyer, D.C., editors. Ecological, economic and social aspects of Namibian fisheries. Eburon, Netherlands.

Boyer, D.C., Boyer, H.J., Fossen, I. and Kreiner, A. 2001a. Changes in abundance of the northern Benguela sardine stock during the decade 1990-2000, with comments on the relative importance of fishing and the environment. South African Journal of Marine Science 23: 67-84.

Boyer, D.C., Kirchner, C.H., McAllister, M.K., Staby, A. and Staalesen, B.I. 2001b. The orange roughy fishery of Namibia: lessons to be learned about managing a developing fishery. South African Journal of Marine Science 23: 205-221.

Brown, P.C., Painting, S.J. and Cochrane, K.L. 1991. Estimates of phytoplankton and bacterial biomass and production in the northern and southern Benguela ecosystems. South African Journal of Marine Science 11: 537-564.

Burmeister, L. 2005. Is there a single stock of *Merluccius paradoxus* in the Benguela ecosystem? African Journal of Marine Science 27: 23-32.

Butterworth, D.S. and Geromont, H.F. 2001. Evaluation of a class of possible simple interim management procedures for the Namibian hake fishery. South African Journal of Marine Science 23: 357-374.

Butterworth, D.S. and Rademeyer, R.A. 2005. Sustainable management initiatives for the southern African hake fisheries over recent years. Bulletin of Marine Science 76: 287-319.

Butterworth, D.S., Hughes, G. and Strumpfer, F. 1990. VPA with *ad hoc* tuning: implementation for disaggregated fleet data, variance estimation, and application to the Namibian stock of Cape horse mackerel *Tracurus trachurus capensis*. South African Journal of Marine Science 9: 327-357.

Butterworth, D.S., Punt, A.E., Oosthuizen, W.H. and Wickens, P.A. 1995. The effects of future consumption by the Cape fur seal on catches and catch rates of the Cape hakes. 3. Modelling the dynamics of the Cape fur seal *Arctocephalus pusillus pusillus*. South African Journal of Marine Science 16: 161-183.

Carr, M.-E. 2002. Estimation of potential productivity in Eastern Boundary Currents using remote sensing. Deep-Sea Research II 49: 59-80.

Carr, M.-E. and Kearns, E.J. 2003. Production regimes in four Eastern Boundary Current systems. Deep-Sea Research II 50: 3199-3221.

Crawford, R.J.M. and De Villiers, G. 1985. Snoek and their prey-interrelationships in the Benguela upwelling system. South African Journal of Science 81: 91-97.

Crawford, R.J.M., Shannon, L.V. and Pollock, D.E. 1987. The Benguela ecosystem. Part IV. The major fish and invertebrate resources. Oceanography and Marine Biology Annual Review 25: 353-505.

Crawford, R.J.M., Shannon, L.V. and Shelton, P.A. 1989. Characteristics and management of the Benguela as a large marine ecosystem. pp. 169-219 *in* Sherman, K. and Alexander, L.M., editors. Biomass yields and geography of large marine ecosystems, American Association for the Advancement of Science Symposium 111. Westview Press, Inc., Boulder, Colorado.

Crawford, R.J.M., Ryan, P.G. and Williams, A.J. 1991. Seabird consumption and production in the Benguela and Western Agulhas ecosystems. South African Journal of Marine Science 11: 357-375.

Crawford, R.J.M., Cruickshank, R.A., Shelton, P.A. and Kruger, I. 1985. Partitioning of a goby resource amongst four avian predators and evidence for altered trophic flow in the pelagic community of an intense perennial upwelling system. South African Journal of Marine Science 3: 215-228.

Crawford, R.J.M., David, J.H.M., Shannon, L.J., Kemper, J., Klages, N.T.W., Roux, J.-P., Underhill, L.G., Ward, V.L., Williams, A.J. and Wolfaardt, A.C. 2001. African penguins as predators and prey - coping (or not) with change. South African Journal of Marine Science 23: 435-447.

Critchley, A.T., Rotmann, K.W.G. and Molloy, F.J. 1991. The Namibian seaweed industry: Present and potential. Bioresource Technology 38: 137-143.

Cruickshank, R.A. 1983. Lanternfish ecology in the Benguela current system. South African Journal of Science 79: 149-150.

Cruickshank, R.A., Cooper, J. and Hampton, I. 1980. Extension to the geographical distribution of pelagic goby *Sufflogobius bibarbatus* off South West Africa and some mensural and energetic information. Fisheries Bulletin of South Africa 13: 77-82.

Cury, P. and Shannon, L.J. 2004. Regime shifts in upwelling ecosystems: observed changes and possible mechanisms in the northern and southern Benguela. Progress in Oceanography 60: 223-243.

Cushing, D.H., Humphrey, G.F., Banse, K. and Laevastu, T. 1958. Report of the Committee on Terms and Equivalents. Rapports et Procès-verbaux des Réunions du Conseil Permanent International pour l'Exploration de la Mer 14: 15-16.

David, J.H.M. 1987. Diet of the South African fur seal (1974-1985) and an assessment of competition with fisheries in southern Africa. South African Journal of Marine Science 5: 693-713.

David, J.H.M. 1989. Seals. pp. 288-302 *in* Payne, A.I.L. and Crawford, R.J.M., editors. Oceans of life off Southern Africa. Vlaeberg Publishers, Cape Town.

De Villiers, D.J., Oosthuizen, W.H., Roux, J.-P. and Kotze, P.G.H. 1997. Population structure of a non-breeding colony of the Cape fur seal *Arctocephalus pusillus pusillus* at Cape Frio, Namibia. South African Journal of Marine Science 18: 295-298.

Ebert, D.A. 1996. Biology of the sevengill shark *Notorynchus cepedianus* (Peron, 1807) in the temperate coastal waters of Southern Africa. South African Journal of Marine Science 17: 93-103.

Fearon, J.J., Boyd, A.J. and Schülein, F.H. 1992. Views on the biomass and distribution of *Chrysaora hysoscella* (Linne, 1766) and *Aequorea aequorea* (Forskal, 1775) off Namibia, 1982-1989. Scientia Marina 56(1): 75-85.

Findlay, K.P., Best, P.B., Ross, G.J.B. and Cockcroft, V.G. 1992. The distribution of small odontocete cetaceans off the coasts of South Africa and Namibia. South African Journal of Marine Science 12: 237-270.

Fossen, I., Boyer, D.C. and Plarre, H. 2001. Changes in some key biological parameters of the northern Benguela sardine stock. South African Journal of Marine Science 23: 111-121.

Froese, R., Pauly, D. 2000. FishBase 2000: concepts, design and data sources. [Distributed with 4 CD-ROMs]; www.fishbase.org, 346 pp. *in*. ICLARM, Los Baños, Philippines.

Fuller, B. and Prommer, I. 2000. Population-Development-Environment in Namibia. Background readings. Interim Report IR-00-31, International Institute for Applied Systems Analysis, Laxenburg, Austria, 326 p.

Griffiths, C.L., Van Sittert, L., Best, P.B., Brown, A.C., Clark, B.M., Cook, P.A., Crawford, R.J.M., David, J.H.M., Davies, B.R., Griffiths, M.H., Hutchings, K., Jerardino, A., Kruger, N., Lamberth, S., Leslie, R.W., Mellville-Smith, R., Tarr, R. and Van der Lingen, C.D. 2004. Impacts of human activities on marine animal life in the Benguela: A historical overview. Oceanography and Marine Biology Annual Review 42: 303-392.

Griffiths, M.H. 2002. Life history of South African snoek, *Thyrsites atun* (Pices: Gempylidae): a pelagic predator of the Benguela ecosystem. Fisheries Bulletin 100: 690-710.

Griffiths, M.H. 2003. Stock structure of snoek *Thyrsites atun* in the Benguela: a new hypothesis. African Journal of Marine Science 25: 383-386.

Grobler, C.A.F. and Noli-Peard, K.R. 1997. *Jasus lalandii* fishery in post-independence Namibia: monitoring population trends and stock recovery in relation to a variable environment. Marine and Freshwater Research 48: 1015-1022.

Hampton, I. 2003. Harvesting the sea. pp. 43-80 *in* Anon., editor. A marine state of Environment Report: Namibia's Marine Environment. Namibian Ministry of Environment and Tourism.

Hamukuaya, H., O'Toole, M.J. and Woodhead, P.M.J. 1998. Observations of severe hypoxia and offshore displacement of Cape hake over the Namibian shelf in 1994. South African Journal of Marine Science 19: 57-59.

Hamukuaya, H., Bianchi, G. and Baird, D. 2001. The structure of demersal assemblages off Namibia in relation to abiotic factors. South African Journal of Marine Science 23: 397-417.

Hansen, F.C., Cloete, R.R. and Verheye, H.M. 2005. Seasonal and spatial variability of dominant copepods along a transect off Walvis Bay (23°S), Namibia. African Journal of Marine Science 27: 55-63.

Hart, T.J. and Currie, R.I. 1960. The Benguela Current. Discovery Report 31: 123-298.

Hernández, I., Fernández-Engo, M.A., Pérez-Lloréns, J.L. and Vergara, J.J. 2005. Integrated outdoor culture of two estuarine macroalgae as biofilters for dissolved nutrients from *Sparus aurata* waste waters. Journal of Applied Phycology 17: 557-567.

Hewitson, J.D. and Cruickshank, R.A. 1993. Production and consumption by planktivorous fish in the Northern Benguela Ecosystem in the 1980s. South African Journal of Marine Science 13: 15-24.

Heymans, J.J. 1997. Network analysis of the carbon flow model of the northern Benguela ecosystem, Namibia. PhD. University of Port Elizabeth, now Nelson Mandela Metropolitan University, Port Elizabeth Pages p.

Heymans, J.J. 2004. The effects of internal and external control on the northern Benguela ecosystem. pp. 29-52 *in* Sumaila, U.R., Steinshamn, S.I., Skog, M. and Boyer, D.C., editors. Ecological, economic and social aspects of Namibian fisheries. Eburon, Netherlands.

Heymans, J.J. and Baird, D. 2000. Network analysis of the northern Benguela ecosystem by means of NETWRK and ECOPATH. Ecological Modelling 131: 97-119.

Holtzhausen, J.A. 1999. Population dynamics and life history of westcoast steenbras (*Lithognathus aureti* (Sparidae)), and management options for the sustainable exploitation of the steenbras resource in Namibian waters. PhD. University of Port Elizabeth, Port Elizabeth Pages p.

Holtzhausen, J.A. and Kirchner, C.H. 2004. Management regulations of Namibian angling fish species. pp. 113-134 *in* Sumaila, U.R., Steinshamn, S.I., Skog, M. and Boyer, D.C., editors. Ecological, economic and social aspects of Namibian fisheries. Eburon, Netherlands.

Holtzhausen, J.A., Kirchner, C.H. and Voges, E. 2001. Observations on the linefish resources of Namibia, 1990-2000, with special reference to west coast steenbras and silver kob. South African Journal of Marine Science 23: 135-144.

Hugo, F. 2006. Sea Shepherd News Release: Seal Alert appeals to CITES to take action for South African seals. pp. Letter to CITES *in*. Sea Shepherd Conservation Society.

Huse, I., Hamukuaya, H., Boyer, D.C., Malan, P.E. and Strømme, T. 1998. The diurnal vertical dynamics of Cape hake and their potential prey. South African Journal of Marine Science 19: 365-376.

Hutchings, L., Pillar, S.C. and Verheye, H.M. 1991. Estimates of standing stock, production and consumption of meso- and macrozooplankton in the Benguela ecosystem. South African Journal of Marine Science 11: 499-512.

Jarre-Teichmann, A., Shannon, L.J., Moloney, C.L. and Wickens, P.A. 1998. Comparing trophic flows in the southern Benguela to those in other upwelling ecosystems. South African Journal of Marine Science 19: 391-414.

Kemper, J., Roux, J.-P., Bartlett, P.A., Chesselet, Y.J., James, J.A.C., Jones, R., Wepener, S. and Molloy, F.J. 2001. Recent population trends of African penguins *Spheniscus demersus* in Namibia. South African Journal of Marine Science 23: 429-434.

Kinahan, J. 1991. The historical archaeology of nineteenth century fisheries at Sandwich Harbour on the Namib coast. Cimbebasia 13: 1-27.

Kirchner, C.H., Sakko, A.L. and Barnes, J.I. 2000. An economic valuation of the Namibian recreational shore-angling fishery. South African Journal of Marine Science 22: 17-25.

Klingelhoeffer, E.W. 2006. Population dynamics and the development of a sustainable fishery for the Cape horse mackerel *Trachurus capensis* (Castelnau, 1861), in the northern Benguela current upwelling system. PhD. Nelson Mandela Metropolitan University, Port Elizabeth Pages p.

Konchina, Y.V. 1986. Distribution and feeding of the South African horse mackerel and hake in the Namibian shelf waters. Collection of Scientific Papers of the international Commision of South East Atlantic Fisheries 13(2): 7-18.

Krakstad, J.-O. and Kanandjembo, A. 2001. A summary of the fishery and biology of Cape horse mackerel (*Trachurus capensis*) in Namibian waters. pp. 1-15 *in* Payne, A.I.L., editor. Proceedings of an international workshop on the research and managment of horse mackerel in Namibian waters. Ministry of Fisheries and Manrine Resources, Swakopmund.

Kreiner, A., Van der Lingen, C.D. and Fréon, P. 2001. A comparison of condition factor and gonadosomatic index of sardine *Sardinops sagax* stocks in the northern and southern Benguela upwelling ecosystems, 1984-1999. South African Journal of Marine Science 23: 123-134.

le Clus, F. 1990. Impact and implications of large-scale environmental anomalies on the spatial distribution of spawning of the Namibian pilchard and anchovy populations. South African Journal of Marine Science 9: 141-159.

le Clus, F., Melo, Y.C. and Cooper, R.M. 1988. Impact of environmental perturbations during 1986 on the availability and abundance of pilchard and anchovy in the northern Benguela system. Collection of Scientific Papers of the international Commision of South East Atlantic Fisheries 15(2): 49-70.

Le Roux, L. 2001. The impact of emigration on population estimates of deep-sea red crab *Chaceon maritae* off Namibia. African Journal of Marine Science 23: 61-66.

Lees, R. 1969. Fishing for fortunes: The story of the fishing industry in Southern Africa - and the men who made it. Purnell, Cape Town, 283 p. I only have some pages, not the whole document.

Lipiński, M.R. 1992. Cephalopods and the Benguela ecosystem: Trophic relationships and impact. South African Journal of Marine Science 12: 791-802.

Lynam, C.P., Gibbons, M.J., Axelsen, B.E., Sparks, C.A.J., Coetzee, J., Heywood, B.G. and Brierley, A.S. 2006. Jellyfish overtake fish in an heavily fished ecosystem. Current Biology 16: 492-493.

Maartens, L. and Booth, A.J. 2001. Quantifying commercial catch and effort of monkfish *Lophius vomerinus* and *L. vaillanti* off Namibia. South African Journal of Marine Science 23: 291-306.

Maartens, L. and Booth, A.J. 2005. Aspects of the reproductive biology of monkfish *Lophius vomerinus* off Namibia. African Journal of Marine Science 27: 325-329.

Macpherson, E. and Gordoa, A. 1992. Trends in the demersal fish community off Namibia from 1983 to 1990. South African Journal of Marine Science 12: 635-649.

Maurihungirire, M. 2004. Transboundary issues in the purse-seine, trawl and crustacean fisheries of the Southeast Atlantic. pp. 151-164 *in* Payne, A.I.L., O'Brien, C.M. and Rogers, S.I., editors. Management of shared fish stocks. Blackwell Publishers, Oxford.

Mecenero, S., Kirkman, S.P. and Roux, J.-P. 2005. Seabirds in the diet of Cape fur seals *Arctocephalus pusillus pusillus* at three mainland breeding colonies in Namibia. African Journal of Marine Science 27: 509-512.

Mecenero, S., Roux, J.-P., Underhill, L.G. and Bester, M.N. 2006. Diet of Cape fur seals *Arctocephalus pusillus pusillus* at three mainland breeding colonies in Namibia. 1. Spatial variation. African Journal of Marine Science 28: 57-71.

Melo, Y.C. and le Clus, F. 2005. Growth and reproduction of the pelagic goby *Sufflogobius bibarbatus* off the Orange River, southern Africa. African Journal of Marine Science 27: 265-273.

Melville-Smith, R. 1983. Some observations on the abundance of deep-sea red crab *Geryon maritae* in Namibian waters using photography. South African Journal of Science 79: 144.

Melville-Smith, R. 1988. The commercial fishery for and population dynamics of red crab *Geryon maritae* off South West Africa, 1976-1986. South African Journal of Marine Science 6: 79-75.

Miller, C.M., Oosthuizen, W.H. and Wickens, P.A. 1996. Cape fur seals trapped in trawling gear: age structure, sex ratio, seasonality and distribution. South African Journal of Marine Science 17: 105-111.

Nicols, P. 2004. Marine fisheries management in Namibia: Has it worked? pp. 319-332 *in* Sumaila, U.R., Steinshamn, S.I., Skog, M. and Boyer, D.C., editors. Ecological, economic and social aspects of Namibian fisheries. Eburon, Netherlands.

Pagès, F. 1992. Mesoscale coupling between planktonic Cnidarian distribution and water masses during a temporal transition between active upwelling and abatement in the northern Benguela system. South African Journal of Marine Science 12: 41-52.

Pillar, S.C. and Barange, M. 1997. Diel variability in bottom trawl catches and feeding activity of the Cape hakes off the west coast of South Africa. ICES Journal of Marine Science 54: 485-499.

Pitcher, G.C., Brown, P.C. and Mitchell-Innes, B.A. 1992. Spatio-temporal variability of phytoplankton in the southern Benguela upwelling system. South African Journal of Marine Science 12: 439-456.

Pollock, D.E. and Shannon, L.V. 1987. Response of rock-lobster populations in the Benguela ecosystem to environmental change - a hypothesis. South African Journal of Marine Science 5: 887-899.

Pollock, D.E., Cockcroft, A.C., Groeneveld, J.C. and Schoeman, D.S. 2000. Chapter 5: The commercial fisheries for *Jasus* and *Palinurus* species in the south-east Atlantic and south-west Indian Oceans. pp. 105-120 *in* Phillips, B.F. and Kittaka, J., editors. Spiny lobsters: Fisheries and culture. Blackwell Science Ltd., Oxford.

Pulfrich, A., Parkins, C.A. and Branch, G.M. 2003. The effects of shore-based diamond-diving on intertidal and subtidal biological communities and rock lobsters in southern Namibia. Aquatic Conservation: Marine and Freshwater Ecosystems 13: 233-255.

Punt, A.E., Leslie, R.W. and Du Plessis, S.E. 1992. Estimation of the annual consumption of food by Cape hake *Merluccius capensis* and *M. paradoxus* of the South African west coast. South African Journal of Marine Science 12: 611-634.

Punt, A.E., Butterworth, D.S. and Penney, A.J. 1995. Stock assessment and risk analysis for the South Atlantic population of albacore *Thunnus alalunga* using an age-structured production model. South African Journal of Marine Science 16: 287-310.

Roel, B.A. and Macpherson, E. 1988. Feeding of *Merluccius capensis* and *M. paradoxus* off Namibia. South African Journal of Marine Science 6: 227-243.

Romanov, E. 2001. History of Ukranian fisheries in the South-eastern Atlantic and YugNIRO database for this area. *in* Payne, A.I.L., editor. Proceedings of an international workshop on the research and managment of horse mackerel in Namibian waters. Ministry of Fisheries and Manrine Resources, Swakopmund.

Rotmann, K.W.G. 1987. The collection, utilization and potential farming of red seaweeds in Namibia. Hydrobiologia 151/152: 301-305.

Roux, J.-P. and Shannon, L.J. 2004. Ecosystem approach to fisheries management in the northern Benguela: the Namibian experience. African Journal of Marine Science 26: 79-93.

Roux, J.-P., Best, P.B. and Stander, P.E. 2001. Sightings of southern right whales (Eubalaena australis) in Namibian waters, 1971-1999. Journal of Cetacean research and management Special Issue 2: 181-185.

Roy, C., Cury, P. and Kifani, S. 1992. Pelagic fish recruitment success and reproductive strategy in upwelling areas: environmental compromises. South African Journal of Marine Science 12: 135-146.

Ryan, P.G., Keith, D.G. and Kroese, M. 2002. Seabird bycatch by tuna longline fisheries off Southern Africa, 1998-2000. South African Journal of Marine Science 24: 103-110.

Ryther, J.H. 1969. Photosynthesis and fish production in the sea. Science, New Series 166: 72-76.

Schwartzlose, R.A., Alheit, J., Bakun, A., Baugartner, T.R., Cloete, R., Crawford, R.J.M., Fletcher, W.J., Green-Ruiz, Y., Hagen, E., Kawasaki, T., Lluch-Belda, D., Lluch-Cota, S.E., MacCall, A.D., Matsuura, Y., Nevárez-Martínez, M.O., Parrish, R.H., Roy, C., Serra, R., Shust, K.V., Ward, M.N. and Zuzunaga, J.Z. 1999. Worldwide large-scale fluctuations of sardine and anchovy populations. South African Journal of Marine Science 21: 289-347.

Shannon, L.J. and Taunton-Clark, J. 1988. Interannual and decadal changes in sea surface temperature and relative wind stress in the South-East Atlantic this century. pp. 49-51 *in* MacDonald, I.A.W. and Crawford, R.J.M., editors. Long-term data series relating to southern African's renewable natural resources. Foundation for Research Development, Pretoria.

Shannon, L.J. and Jarre-Teichmann, A. 1999. A model of trophic flows in the Northern Benguela upwelling system during the 1980s. South African Journal of Marine Science 21: 349-366.

Shannon, L.V. 1985. The Benguela ecosystem. Part I. Evolution of the Benguela, physical features and processes. Oceanography and Marine Biology Annual Review 23: 105-182.

Shannon, L.V. and Pillar, S.C. 1986. The Benguela ecosystem. Part III. Plankton. Oceanography and Marine Biology Annual Review 24: 65-170.

Shannon, L.V. and O'Toole, M.J. 2003. Sustainability of the Benguela ex Africa semper aliquid novi. pp. 227-253 *in* Hempel, G. and Sherman, K., editors. Large Marine Ecosystems of the World: Trends in Exploitation, Protection and Research. Elsevier.

Shannon, L.V., Boyd, A.J., Brundrit, G.B. and Taunton-Clark, J. 1986. On the existence of an El Niño-type phenomenon in the Benguela system. Journal of marine Research 44(3): 495-520.

Shelton, P.A. and Crawford, R.J.M. 1988. Analysis of time series of seabird guano harvested off southern Africa. pp. 51-53 *in* MacDonald, I.A.W. and Crawford, R.J.M., editors. Long-term data series relating to southern African's renewable natural resources. Foundation for Research Development, Pretoria.

Shin, Y.-J., Shannon, L.J. and Cury, P.M. 2004. Simulations of fishing effects on the southern Benguela fish community using an individual-based model: learning from a comparison with Ecosim. African Journal of Marine Science 26: 95-114.

Sparks, C., Buecher, E., Brierley, A.S., Axelsen, B.E., Boyer, H. and Gibbons, M.J. 2001. Observations on the distribution and relative abundance of the scyphomedusan *Chrysaora hysoscella* (Linné, 1766) and the hydrozoan *Aequorea aequorea* (Forskål, 1775) in the northern Benguela ecosystem. Hydrobiologia 451: 275-286.

Sparks, D.L. 1984. Namibia's coastal and marine development potential. African Affairs 83: 477-496.

Stage, J. and Kirchner, C.H. 2005. An economic comparison of the commercial and recreational linefisheries in Namibia. African Journal of Marine Science 27: 577-584.

Stenevik, E.K., Skogen, M.D., Sundby, S. and Boyer, D.C. 2003. The effect of vertical and horizontal distribution retention of sardine (*Sardinops sagax*) larvae in the Northern Benguela - observations and modeling. Fisheries Oceanography 12: 185-200.

Sumaila, U.R., Ninnes, C. and Oelofsen, B. 2002. Management of shared hake stocks in the Benguela marine ecosystem. pp. 143-158 *in* FAO, editor. Papers presented at the Norway-FAO Expert Consultation on the Management of Shared Fish Stocks, Bergen, Norway 7-10 October 2002. FAO Fisheries Report No. 695. FAO, Rome.

Sumaila, U.R., Marsden, A.D., Watson, R. and Pauly, D. 2007. Global ex-vessel fish price database: construction and applications. Journal of Bioeconomics, in press.

Thomas, R.M. 1986. The Namibian Pilchard: The 1985 season, assessment for 1952-1985 and recommenations for 1986. ICSEAF Collectin of scientific Papers of the International Commision for Southeast Atlantic Fisheries 13: 245-269.

Timonin, A.G., Araschkevich, E.G., Drits, A.V. and Semenova, T.N. 1992. Zooplankton dynamics in the northern Benguela ecosystem, with special reference to the copepod *Calanoides carinatus*. South African Journal of Marine Science 12: 545-560.

Van der Westhuizen, A. 2001. A decade of exploitation and management of the Namibian hake stocks. South African Journal of Marine Science 23: 307-315.

Vaske, B. 2001. Some comments on the biological effects of the small-meshed purse-seine fishery. *in* Payne, A.I.L., editor. Proceedings of an international workshop on the research and managment of horse mackerel in Namibian waters. Ministry of Fisheries and Marine Resources, Swakopmund.

Venter, G.E. 1988a. Occurrence of jellyfish on the west coast of South West Africa/Namibia. pp. 54-61 *in* MacDonald, I.A.W. and Crawford, R.J.M., editors. Long-term data series relating to southern African's renewable natural resources. Foundation for Research Development, Pretoria.

Venter, J.D. 1988b. Fluctuations in the catches of some linefish species off South West Africa/Namibia, 1964-1986. pp. 62-64 *in* MacDonald, I.A.W. and Crawford, R.J.M., editors. Long-term data series relating to southern African's renewable natural resources. Foundation for Research Development, Pretoria.

Verheye, H.M., Hutchings, L., Huggett, J.A. and Painting, S.J. 1992. Mesozooplankton dynamics in the Benguela ecosystem, with emphasis on the herbivorous copepods. South African Journal of Marine Science 12: 561-584.

Voges, E., Gordoa, A., Bartholomae, C.H. and Field, J.G. 2002. Estimating the probability of different levels of recruitment for Cape hakes *Merluccius capensis* off Namibia, using environmental indices. Fisheries Research 58: 333-340.

Walmsley, S.A., Leslie, R.W. and Sauer, W.H.H. 2005. The biology and distribution of the monkfish *Lophius vomerinus* off South Africa. African Journal of Marine Science 27: 157-168.

Wasmund, N., Lass, H.-U. and Nausch, G. 2005. Distribution of nutrients, chlorophyll and phytoplankton primary production in relation to hydrographic structures bordering the Benguela-Angola frontal region. African Journal of Marine Science 27: 177-190.

Wickens, P.A., David, J.H.M., Shelton, P.A. and Field, J.G. 1991. Trends in harvests and pup numbers of the South African fur seal: Implications for management. South African Journal of Marine Science 11: 307-326.

Willemse, N.E. 2002. Major trends in the marine fisheries catches of Namibia, 1950-2000. Norwegian College of Fisheries Science, University of Tromsø, Tromsø.

Zeybrandt, F. and Barnes, J.I. 2001. Economic characteristics of demand in Namibia's marine recreational shore fishery. South African Journal of Marine Science 23: 145-156.

Appendix A: Diet matrix of the northern Benguela model in 1956.

	Group	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
1	Marine mammals				0.001											
2	Seals			0.00001	0.001											
3	Birds		0.00008	0.001												
4	Sharks				0.144											
5	Tuna				0.001											
6	Snoek		0.026	0.003	0.002											
7	Other linefish		0.0001		0.002											
8	Anchovy juveniles											0.0001		0.0001		
9	Anchovy adults	0.014	0.5	0.253	0.093	0.091	0.05	0.562							0.005	
10	Sardine juveniles									0.001				0.0001		
11	Sardine adults	0.014	0.101	0.011	0.012	0.091	0.175	0.007								
12	Gobies juveniles									0.0001		0.0001				
13	Gobies adults	0.069	0.059	0.429		0.012	0.005									
14	Other s pelagics	0.117	0.106	0.037	0.11	0.097	0.145	0.012							0.003	
15	Mesopelagics	0.193	0.007	0.053		0.042	0.05								0.01	
16	Juv. h mackerel		0.1	0.005			0.01	0.036								
17	Adult h mackerel		0.036		0.012	0.05	0.044									
18	J hake	0.1	0.01	0.01		0.006	0.003	0.055								
19	A hake	0.175	0.025		0.004	0.024	0.099									
20	Monkfish				0.05											
21	Other demersals			0.108	0.365		0.01	0.041								
22	Cephalopods	0.318	0.03	0.044	0.1	0.091	0.007	0.033								
23	Macrobenthos				0.054		0.09								0.014	
24	Crabs				0.05		0.01									
25	Lobster						0.026									
26	Jellyfish juvs									0.00001		0.00001		0.00001		
27	Jellyfish adults														0.021	
28	Macrozooplankton			0.043		0.121	0.165	0.254		0.32		0.18		0.06	0.35	0.6
29	Mesozooplankton			0.003			0.111			0.31		0.18		0.01	0.597	0.4
30	Benthic producers															
31	Phytoplankton								1	0.33	1	0.56	1	0.93		
32	Detritus									0.038		0.08				
33	Import					0.375										

Appendix A continued: Diet matrix of the northern Benguela model in 1956.

	Group	16	17	18	19	20	21	22	23	24	25	26	27	28	29
1	Marine mammals														
2	Seals														
3	Birds														
4	Sharks														
5	Tuna														
6	Snoek				0.001										
7	Other linefish				0.0001										
8	Anchovy juveniles												0.001		
9	Anchovy adults			0.018	0.01	0.039									
10	Sardine juveniles												0.001		
11	Sardine adults			0.018	0.045										
12	Gobies juveniles														
13	Gobies adults		0.009	0.018	0.045	0.102	0.021	0.1							
14	Other s pelagics				0.045	0.197	0.054	0.1							
15	Mesopelagics		0.02	0.01	0.01	0.129	0.018	0.1							
16	Juv. h mackerel				0.01	0.066		0.01							
17	Adult h mackerel				0.01	0.05									
18	J hake				0.005	0.001	0.00099	0.001							
19	A hake				0.05	0.26	0.009								
20	Monkfish				0.0005	0.01	0.00094			0.01					
21	Other demersals				0.005	0.05	0.009			0.01					
22	Cephalopods		0.001	0.014	0.005	0.034	0.00094	0.01							
23	Macrobenthos			0.018	0.045	0.062			0.05	0.333	0.5				
24	Crabs						0.009		0.001						
25	Lobster						0.009		0.001						
26	Jellyfish juvs														
27	Jellyfish adults				0.045										
28	Macrozooplankton		0.79	0.816	0.311		0.304	0.394							
29	Mesozooplankton	1	0.18	0.088	0.358		0.11	0.285					0.25	0.4	
30	Benthic producers								0.05		0.5				
31	Phytoplankton											1	0.247	0.6	0.5
32	Detritus						0.455		0.898	0.647			0.5		0.5
33	Import														

MODELLING THE FOOD WEB IN THE UPWELLING ECOSYSTEM OFF CENTRAL CHILE (33°S–39°S) IN THE YEAR 2000[1]

Sergio Neira
Zoology Department, University of Cape Town, Rondebosh 7701, Cape Town, South Africa;
Email: sergio.neiraalarcon@uct.ac.za

Hugo Arancibia
Departamento de Oceanografía, Universidad de Concepción, Casilla 160-C, Concepción, Chile

ABSTRACT

We describe the main steps in the construction of a food web model representing trophic relationships for the main fishery resources in the upwelling system off central Chile. We use biological and fishing data for the most important functional groups covering the year 2000 and the Ecopath with Ecosim software. The model includes 31 functional groups, from primary producers to top predators such as marine birds and mammals. This paper presents a comprehensive description of the study area, the functional groups included and the source of the data needed to parameterize the model. We also present key assumptions in the modelling process derived from the lack of information on basic life history parameters for functional groups.

INTRODUCTION

Marine populations are tightly linked to their physical and biological environment. This basic ecological principle is normally disregarded by traditional single-species fisheries management, by considering stocks as discrete and independent units (Walters and Martel, 2004). A side effect of this assumption is that fishing mortality was considered to be the only factor explaining stock dynamics. This myopic approach cannot assess or predict the effects of environmental and trophic (predator and prey) controls on marine populations, which are as important as fishing in explaining stock fluctuations (Cushing, 1982; Sinclair *et al.*, 1997; Bax, 1991, 1998).

Therefore, it is likely that ignoring interactions between stocks and the ecosystem, from where landings are removed, played a significant role in the worldwide overexploitation crisis of fisheries (Pauly *et al.*, 2003). The global call for an ecosystem approach to fisheries (EAF) implies that future stock assessment and management should not rely exclusively on single species approaches (FAO, 2003). In addition, EAF pre-supposes an incremental knowledge on the key aspects of the 'ecology of the ecosystem', which is expected to play an important role in future stock recovery and fisheries sustainability (Botsford *et al.*, 1997; Link, 2002a, b; Pikitch *et al.*, 2004).

Changes in predator-prey interactions and energy/mass flows among trophic levels are important aspects of ecosystem structure (Elton, 1927; Lindeman, 1942). An increasing body of literature indicates that these two ecosystem properties are negatively altered by fishing (Pauly and Christensen, 1995; Pauly *et al.*, 1998a; Worm *et al.*, 2006). Therefore, the understanding of ecosystem trophodynamics should be an important aspect of EAF.

The development of trophic interaction, food web and ecosystem models that appear capable of making useful predictions about ecosystem-based policy issues, ignored in single-species assessment and policy

---

[1] Cite as: Neira, S. and Arancibia, H. 2007. Modelling the food web in the upwelling ecosystem off central Chile (33°S–39°S) in the year 2000, p. 71–86. *In*: Le Quesne, W.J.F., Arreguín-Sánchez, F. and Heymans, S.J.J. (eds.) INCOFISH ecosystem models: transiting from Ecopath to Ecospace. Fisheries Centre Research Reports 15(6). Fisheries Centre, University of British Columbia [ISSN 1198-6727].

recommendations, are regarded as potential improvement for fisheries stock assessment and management (Walters and Martell, 2004).

The Ecopath with Ecosim model and software (EwE; Christensen and Pauly, 1992; Walters *et al.*, 1997; Pauly *et al.*, 2000) represents a well-known approach to analyse predator-prey relationships and energy flows (i.e., who eats whom? and how much?) in aquatic ecosystems. EwE's friendly interface and easily parameterized framework has resulted in dozens of published models describing aquatic ecosystems all over the globe (Christensen and Pauly, 1993; Christensen and McLean, 2004; www.ecopath.org).

Previous representations of the food web in the upwelling system off central Chile have been published (Neira and Arancibia, 2004) describing system conditions in the early 1990s, i.e., healthy stocks and no severe changes in environmental conditions. By the mid- to late 1990s, however, the system experienced changes in fishing and environmental forcing. The most important changes were related to the ENSO event in 1997–1998, the strongest of the 20th century (MacPhaden, 1999), and sequential stock collapses of horse mackerel *Trachurus symmetricus* (1997), red squat lobster *Pleuroncodes monodon* (2000) and hake *Merluccius gayi* (2004). In the late 1990s, the dominant species of small pelagic fish, common sardine (*Strangomera bentincki*) and anchovy (*Engraulis ringens*), suffered heavy fishing pressure. In addition, unusual invasions of jumbo squid (*Dosidicus gigas*) have been reported since the early 2000s (Arancibia *et al.*, 2007).

It is likely that these changes affected energy flows and prey-predator relationships through the food web resulting in an altered community structure. In this paper we describe an Ecopath model constructed to analyze food web structure off central Chile at the beginning of the 2000s. We consider that this model will allow future comparisons with both previous models constructed for the Chilean system (i.e., Neira and Arancibia, 2004) and other upwelling systems.

This report describes the data sources and calculations used to parameterize an Ecopath model of the upwelling system off central Chile (USCCh).

METHODS

The USCCh model includes biological and fishing information of the main functional groups inhabiting the study area, with emphasis on fishing resources, their prey and predators in the year 2000. The food web model was constructed using EwE version 5.1. Below we present a comprehensive description of the study area, the functional groups included and the source of the data needed to parameterize the model. We also present key assumptions in the modelling process derived from the lack of information for selected functional groups.

Study area

The study area corresponds to the upwelling system off central Chile (USCCh; Figure 1) that is located in the southern section of the Humboldt Current System, which is one of the four major eastern boundary ecosystems of the world. The USCCh supports one of the highest levels of primary productivity recorded for the open ocean (19.9 g C m^{-2} d^{-1}; Daneri *et al.*, 2000) and globally significant landings (>4.5 million tons in 1995). Despite this high biological productivity, the state of exploited stocks is far from healthy (Arancibia and Neira, 2003). In fact, the main target species have been fully exploited or even overexploited for many years, leading to a series of recent stock collapses, for example of horse mackerel (1998), red squat lobster and yellow squat lobster (1999) and hake (2004).

The USCCh, as considered in this modelling exercise, extends from 33°S to 39°S and from the coastline up to 30 nautical miles westward, covering a total area of approximately 50,000 km^2. This geographical unit corresponds to the 'Mediterranean District' and is ecologically independent from the 'Peruvian Province' and the 'Austral District' located northward and southward, respectively (Camus, 2001). The main oceanographic and biogeographic patterns that characterize the study area are a rather narrow continental shelf (<30 nautical miles), strongly seasonal upwelling (September to March) and high levels of primary productivity (Strub *et al.*, 1998; Daneri *et al.*, 2000; Escribano *et al.*, 2003).

Oceanographically, four main water masses are present in the USCCh: Subtropical Surface Water (STSW), Subantarctic Water (SAW), Antarctic Intermediate Water (AAIW), and Equatorial Subsurface Water (ESSW) (for a review of the physical and chemical characteristics of each water mass, see Strub *et al.,* 1998). Wind-driven coastal upwelling brings the ESSW to the surface in the coastal zone, causing a persistent and characteristic shallow oxygen minimum zone (>0.5 ml $O_2.l^{-1}$). Based on the correlation between the low frequency coastal modes and the Pacific and Atlantic sea surface temperature (SST), Montecinos *et al.* (2003) suggest that the coastal SST comprises two main large-scale climate processes affecting the study area. At the inter-annual scale, the main source of variability is the El Niño Southern Oscillation cycle. At the long-term scale, an inter-decadal oscillation occurs at a basin-wide, and maybe even global, scale.

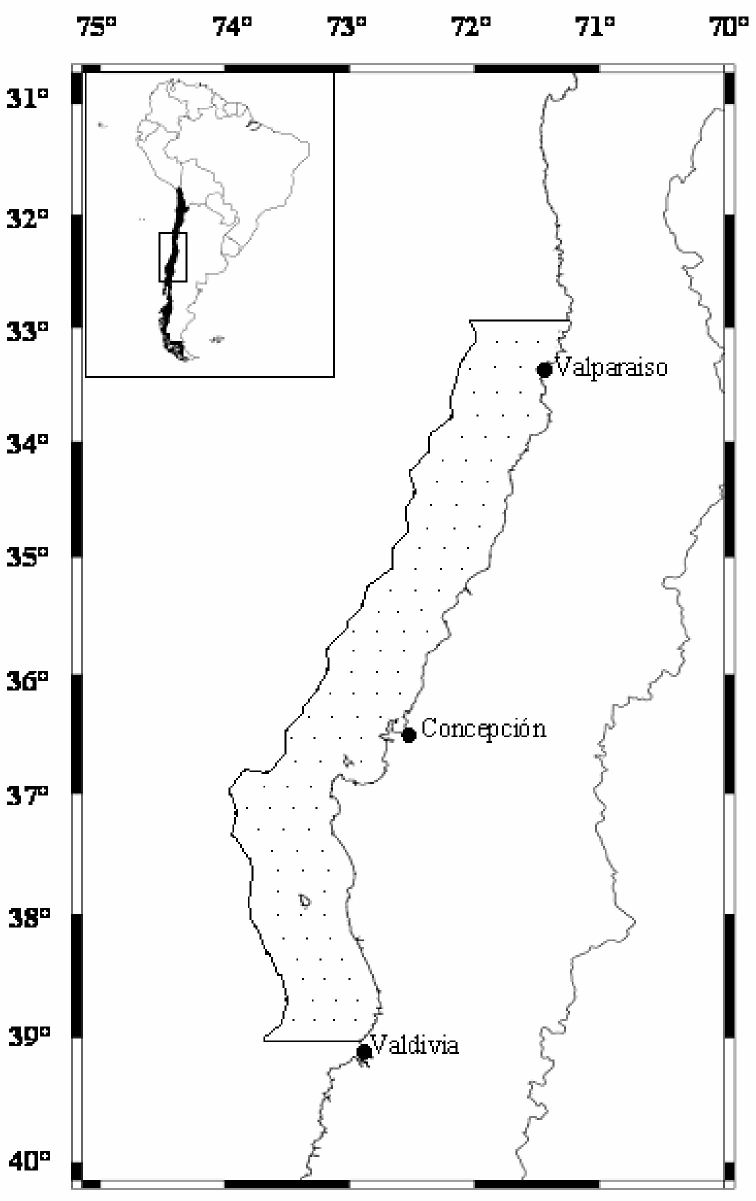


Figure 1. Study area corresponding to the upwelling system off central Chile (highlighted zone) extending from 33° to 39°S and from the line coast up to 30 nautical miles westward.

In terms of the main biological components, the USCCh sustains a diverse and productive food web. The phytoplankton group is dominated by large diatoms for most of the year (Avaria and Muñoz, 1982), while the zooplankton is dominated by herbivorous copepods and euphausiids. Jellyfish (Hydrozoa) also constitute an important group in the plankton domain (Palma and Rosales, 1995). Macrocrustaceans are significant benthic components and some species such as red squat lobster (*Pleuroncodes monodon*), yellow squat lobster (*Cervimunida johni*) and pink shrimp (*Heterocarpus reedi*) support important fisheries. The fish community is dominated by pelagic species. Small pelagic fishes such anchovy (*E. ringens*) and the endemic common sardine (*S. bentincki*) are present at high biomass levels off central Chile and dominate landings. These species seem to feed primarily on phytoplankton and secondarily on zooplankton (Arrizaga *et al.*, 1993). The horse mackerel (*T. symmetricus*) is a major fishery resource in the study area. This highly migratory species performs large-scale migrations in the Pacific Ocean. Off Chile, horse mackerel feed mainly on euphausiids (Miranda *et al.*, 1998). The demersal fish community is dominated by hake (*M. gayi*) both in biomass and landings. Hake inhabits mid-depth waters (100–400 m) and feeds on euphausiids, galatheid crustaceans and small pelagic fish (Meléndez, 1983; Arancibia, 1989; Cubillos *et al.*, 2003) and is highly cannibalistic (Arancibia *et al.*, 1998).

The USCCh also represents an independent management unit, comprising the main fishing ground for the Chilean purse seine and trawling fleets, both industrial and small scale operations and accounting for approximately 75% of the total landings in Chile (Neira and Arancibia, 2004; Neira *et al.*, 2004). The industrial fishery, based on fish and crustacean species, started in the 1940s, when demersal trawlers targeted hake. However, landings of this fleet were significant only from the mid-1950s onwards. By the early 1960s, an industrial pelagic fishery came into operation, targeting small pelagic fishes, mainly common sardine and anchovy. At the same time, an industrial fleet operated on a medium-sized pelagic fish, namely horse mackerel, with landings of this species becoming significant from 1975 onwards.

Description of functional groups

In this section we describe the main taxonomic groups covered using the letters A–G and the functional groups (*in italics*) included in the model representing the food web in the upwelling system off central Chile for the year 2000. The data sources for the input parameters are presented in Table 1.

A. Top predators

Top predators are important in food webs since they affect the abundance of other species either directly (by preying on them or competing with them) or indirectly (by removing other predators). Because of that, changes in higher trophic levels result in cascading effects that can spread through the entire food web (Frank *et al.*, 2005). Top predators are also important for conservation policies since many of them (i.e., sharks, marine mammals and marine birds) are considered charismatic groups that are indirectly affected by overfishing of their prey. In spite of accurate data, we considered three 'generic' groups as top predators in the system: cetaceans, sea lions and marine birds.

Cetaceans

Taking into account the spatial scale of the model (30 nautical miles to the west) we only considered species with coastal distribution. Following Aguayo-Lobo *et al.* (1998), this functional group includes the dolphins (*Cephalorhyncus eutropia* Gray, 1846) and killer whales (*Orcinus orca* Linnaeus, 1758). No estimates of abundance, biomass, DC, P/B nor Q/B exist for this species in central Chile. Therefore, we use values for these parameters informed for similar species in comparable ecosystems.

Sea lions

The common sea lion (*Otaria flavescens* Shaw, 1800) is by far the most conspicuous species inhabiting the Chilean coast (Siefeld, 1999). Time series data of catches and abundance for this species in the study area are scarce. The first records indicate an intensive activity during the early 1900s. For example, in only one site (Santa Maria Island, 37°0.3'S; 73°31'W), 52,000 individuals were caught between 1921 and 1922 (Osgood, 1943). Currently, the common sea lion population in the study area is estimated at only 17,000 individuals (Doppler Ltda., 1997).

Marine birds

The functional group labelled 'marine birds' includes species such as seagulls (*Larus dominicanus*), the Humboldt penguin (*Spheniscus humboldtii*), pelicans (*Pelicanus tagus*) and cormorants (*Phacalocorax* spp.). No estimates of abundance, biomass, DC, P/B nor Q/B exist for these species in central Chile. Therefore, we use values for these parameters informed for similar species in comparable ecosystems.

B. Fishes

Fishes play a very important role in ecosystems as prey, predators and target species for many fisheries. The trophic role of fishes is largely a function of their size, with big fishes normally eating small fishes. However, the high diversity in anatomical and physiological adaptations exhibited by this group *leads* to a wide range of dietary specializations (i.e., herbivores and carnivores). This results in fishes occupying almost all trophic levels in the food web.

We split the fish community in two major categories, bony fishes and chondrichthyans. Bony fishes were split in three main categories based on their habitat and feeding traits: pelagic fish, mesopelagic fish and demersal fish. Due to lack of data we only consider demersal chondrichthyans. Below are the main characteristics of selected fish functional groups.

Pelagic fish

We split this broad category in three main groups: small- (mainly planktivores), medium- (planktivores and piscivores), and large-sized (mainly piscivores) fish. The constituent species in each category are described below.

Small pelagic fish: common sardine and anchovy

We include the two dominant species (in terms of biomass and landings) of small pelagic fish in the study area, common sardine and anchovy. Common sardine is endemic to central Chile, while anchovy presents a wider distribution ranging from southern Ecuador to southern Chile. Both species aggregate in mixed schools distributed in shallow coastal waters (between 0 and 70 meters and <20 nautical miles from the shore).

Medium pelagic fish: horse mackerel and hoki

We include two species in this sub-category: horse mackerel and hoki (*Macruronus magellanicus* Lönnberg, 1907). Horse mackerel is distributed in the Pacific Ocean from the eastern boundary off Peru and Chile up to the western boundary off New Zealand. This migratory circuit ranges from the Sub-Tropical Convergence (30°S) up to the Sub-Antarctic Convergence (48°–50°S). In central Chile, horse mackerel is the main off-shore fishery resource, being targeted by an important industrial fleet of purse seiners.

Hoki has a more restricted geographical distribution than horse mackerel: from central Chile (33°S) up to austral Chile, reaching the Atlantic off southern Argentina (37°S; Arana, 1970). Although hoki also reaches deeper waters than horse mackerel (200 to 300 m; Aguayo and Gili, 1984), in central Chile these two species are targeted by the same fleet.

Large pelagic fish: swordfish

This category is represented by the swordfish (*Xiphias gladius*). This is a highly migratory and cosmopolitan species distributed in all oceans in the globe, with preference for waters with temperature higher than 13°C (Barbieri *et al.*, 1998). Swordfish is a carnivorous species that prey mainly on fish and cephalopod species. This allows us to characterize this species as a top predator in the system. However, other life history parameters of swordfish are scarce off central Chile. Therefore, we used mainly input parameters informed for the same or similar species in other ecosystems.

Mesopelagic fish

Although no direct estimates of the abundance of this group have been conducted off central Chile, mesopelagic fishes are thought to be very abundant, with myctophiids representing the bulk of the biomass of mesopelagic fish (Siefeld *et al.*, 1995). Mesopelagic fishes are important consumers of zooplankton (copepods and euphausiids) and important prey of a wide diversity of predators, especially fish such as horse mackerel and hoki. Therefore, mesopelagic fishes represent an important trophic link between meso- and macrozooplankton and predators located in higher trophic levels (Acuña, 1986).

Demersal fish

Hake

Hake is a relatively large demersal fish that can reach over 80 cm in length. This species is distributed from 23°S to 47°S on the shallow continental shelf to the upper continental slope (Aguayo, 1995). In central Chile hake is an opportunistic predator that migrates vertically to mid-waters at night. Hake diet is based on galatheid crustaceans (such as squat lobster), small pelagics (such as anchovy and common sardine), euphausiids and cannibalism (Arancibia *et al.*, 1998; Cubillos *et al.*, 2003). Small squat lobsters constitute most of the diet of young hake (<36 cm LT), while small pelagics are more important in the diet of adult hakes (>36 cm LT) (Arancibia *et al.*, 1998). The fishery targeting Chilean hake is one of the most important fisheries in Chile. The fleet (both industrial and small scale) operates over the continental shelf between 31°S and 41°S.

Big-eye flounder

Big-eye flounder (*Hippoglossina macrops* Steindachner, 1876) is a demersal fish with a geographic distribution that ranges from central to southern Chile. It is mainly associated with sandy and muddy bottoms in depths of 50 to 120 m (Arancibia, 1989). Big-eye flounder co-occurs in the demersal fish assemblages dominated by Chilean hake, and it is normally found in the by-catch of the fishery targeting hake (Arancibia 1989; 1992).

Black conger-eel

Black conger-eel (*Genypterus maculatus* Shneider, 1848) is a demersal species in the industrial and small-scale trawl fisheries (hake, red squat lobster and pink shrimp). This species inhabits coastal waters from northern Chile (18°25'S) up to southern Chile (47°75'S), in depths between 20 and 150 m. Black conger-eel is also a co-occurring species in the demersal fish assemblages dominated by hake, and it is normally found in the by-catch of the fishery targeting hake (Arancibia 1989; 1992).

Cardinal fish

Off central Chile, Cardinal fish (*Epigonus crassicaudus*) is distributed in depths between 100 and 500 m over the continental shelf and break. This species co-occurs in the demersal fish assemblages dominated by Chilean hake, being normally found as by-catch during summer in the fishery targeting hake (Arancibia 1989; 1992).

Pacific sand perch

Pacific sand perch (*Prolatilus jugularis*) is normally associated with rocky and sandy substrata, between 5 and 250 m. Pacific sand perch is also a co-occurring species in the demersal fish assemblages dominated by Chilean hake, and it is normally found in the by-catch of the fishery targeting hake (Arancibia 1989; 1992).

Rattail fishes

Rattail fishes (*Coelorhyncus spp.*) inhabit depths between 70 m and 400 m. This group is distributed from northern to austral Chile. Rattail fishes co-occur in the demersal fish assemblages dominated by Chilean hake, and are normally found in the by-catch of the fishery targeting hake (Arancibia 1989; 1992)

Small chondrichthyans

This group is represented mostly by skates of the Family Rajiidae. In general, chondrichthyans are important due to conservation objectives. Skates are distributed from northern to southern Chile, with *Dipterus chilensis* being a representative species of the group. Skates are incidentally caught as a by-catch species by the industrial trawlers targeting hake.

C. Mollusks

In this category we identify Cephalopoda as the main group to be included in the model, since other families such as Bivalvia and Gastropoda are more restricted to sandy and rocky shores. Among cephalopods, squids are largely the most important compared to *Octopus* spp., which also inhabit rocky shores. We consider small squids and large squids as independent functional groups since they play different roles in the system. Small squids (Loliginidae) are important as prey of several predators (including top predators), while large squids (Omastrephidae) are important predators of fish species (including target species).

Small squids

Small squids are represented by common squid (*Loligo gahi* Orbigny), which is an important prey for several predators in the system. Because trophic/population parameters for this groups are not available locally, we use parameters estimated for similar groups in comparable ecosystems.

Large squids

Large squids are represented by jumbo squid. This is a fast-growing nictimeral species that is distributed along the coast of the Eastern Pacific Ocean (Rodhouse and Nigmatulin, 1996). Trophic studies indicate that this is a voracious and opportunistic predator with a diet based mostly on plankton crustaceans, mollusks (including other cephalopods) and fish. Mesopelagic fish species are the most important prey in jumbo squid diet, with pelagic species such as sardines (*Sardinops* sp.), anchovies (*Engraulis* sp.) and mackerel (*Scomber japonicus*) occupying a secondary position (Rodhouse and Nigmatulin, 1996; Nigmatulin, *et al.*, 2001; Markaida and Sosa-Nishizaki, 2003). Moderate to high cannibalism is common in jumbo squid, but it can account up to 70% of the diet in conditions of scarcity of other prey items (Arancibia *et al.*, 2007).

D. Benthic crustaceans

Benthic crustaceans are important in the study area (especially in the demersal realm) since they are normal prey of several demersal fish species (Arancibia, 1989). In addition, some species support important fisheries.

Red squat lobster

The red squat lobster is an important fishing resource in the study area. However, its biomass decreased significantly in the last decade, down by about 90% with respect to the early 1990s (Canales and Espejo, 2002). Consequently, the fishery has been closed since 2000, without evidence of recovery.

Yellow squat lobster

Yellow squat lobster is a secondary fishing resource in the study area. Its biomass is relatively low. Because yellow squat lobster is by-catch in the fishery targeting red squat lobster, its fishery is also closed since 2002.

Pink shrimp

Pink shrimp is also a secondary fishing resource in the study area. Its biomass is relatively low, but it supports a small-scale fishery in central Chile.

E. Anelida – Polychaeta

Available information indicates that the metazoan component of the benthos off central Chile (Concepción Bay) is dominated, both in number and weight, by Polychaeta. Other groups such as Molluska (Bivalvia and Gastropoda), Crustacea (Amphipoda and Brachyura), and Anthozoa seem to present low abundance in the system (Gallardo, 1979).

Polychaetes

The polychaete *Parapionospio pinnata* (Ehlers, 1901) is the dominant species in this functional group. *P. pinnata* presents euribathic distribution, typically in muddy, lime or sandy substrata (Gallardo, 1979; Carrasco and Arcos, 1980).

F. Plankton

Copepods

The zooplankton community off central Chile is dominated by copepods (in number), which reach higher abundance in coastal areas (<20 nautical miles). The copepod assemblage in the study area is composed of 42 taxa, with the following species dominating: *Calanoides patagoniensis*, *Calanus chilensis*, *Paracalanus parvus*, *Acartia tonsa*, *Centropages brachiatus*, *Oithona* sp. and *Oncaea* sp. (Núñez, 1995).

Euphausiids

Euphausiids constitute the main fraction (in weight) of the macro-zooplankton biomass in the study area. They are also a key prey for pelagic (*i.e.* horse mackerel) and demersal (*i.e.* hake) fish species. *Euphausia mucronata* is an endemic krill species in the Humboldt Current system.

Phytoplankton

The phytoplankton box includes all photosynthetic microorganisms, mainly micro-algae, inhabiting the study area. The phytoplankton box represents the primary producers or first level of the traditional food chain. Off central Chile most of the information about phytoplankton biomass (*Chlorophyll-a* concentration) show high values (>2 ug L^{-1}; 50 mg m^{-2}) out to 50 km from the coast (Montecino *et al.*, 1998). The primary production off central Chile has been estimated as 19.9 g C m^{-2} d^{-1} (Daneri *et al.*, 2000).

G. Non-living group

Detritus

Every Ecopath model requires at least one detritus group. We consider only one detritus box in our model representing both particulate and dissolved organic matter. This box is the sink for residual mortality for all other functional groups in the model. Since the detritus box corresponds to a ‘dead’ group, no input parameters are entered.

Age structure

The model includes age structure in groups where enough data is available to split the group into juvenile and adult stages. According to Arancibia (1987), in Chilean hake, the juvenile group corresponds to age 0 to 3 years old, while the adult group corresponds to ages 4+ years old. In common sardine, anchovy and red squat lobster, we considered that the juvenile and adult groups are individuals of the age group 0–1 year old (recruits) and 1+ years old, respectively.

The Ecopath model

The Ecopath model is fully described in many publications (Christensen and Pauly, 1992; Christensen and Walters, 2004; Christensen *et al.*, 2005), and due to space limitations we do not describe the full model in detail. We just present the two master equations in order to help the reader to understand the input parameters needed to run the model. In this application, we used the EwE software version 5.1. The mathematical structure of EwE is based in two master equations:

The first master equation describes the mass balance for each group in the model:

$$Q = P + R + U \qquad \textbf{Eq. 1}$$

where Q is prey consumption, both inside and outside the system (imports); P is production (which must be consumed by predators, exported from the system or contributed to detritus); R is respiration; and U is unassimilated food by predators.

The second master equation describes the fate of the production of each group (i) in the model:

production = catches + predation mortality + biomass accumulation + net migration + other mortality

or, more formally,

$$Pi = Yi + Bi * M2 + Ei + BAi + Pi * (1\text{-}EE) \qquad \textbf{Eq. 2}$$

where *i* is a model group; P_i is the total production rate of (i); Y_i is total fishery catch rate of (i); M2i is the total predation rate for the group (i); B_i the biomass of the group; E_i the net migration rate (emigration - immigration); BA_i is the biomass accumulation rate for (i); $M0_i = P_i (1\text{-}EE_i)$ is the other mortality rate for (i); and EE_i is the ecotrophic efficiency of (i), which represents the total fraction of the production of i that is either eaten by predators or exported from the system.

These lead to the following linear equation:

$$B_i * P/B_i + EE_i - \sum_j (B_j * Q/B_j * DC_{ij}) - EX_i = 0 \qquad \textbf{Eq. 3}$$

where *j* indicates any of the predators of (i); P/B_i is the production of (i) per biomass unit (equivalent to total mortality *Z* under steady-state conditions, *sensu* Allen, 1971); Q/B_i is the consumption by (i) per biomass unit; DC_{ij} is the fraction of (i) in the diet of (j) (in mass units); and EX_i are the exports of *i* (by emigration or yields).

This structure defines the input parameters needed to complete the model. Each group requires estimates of B, P/B and Q/B ratios, DC_{ij}, EX_i, assimilation and EE_i. Nevertheless, one of the parameters (B, P/B, Q/B or EE) can remain unknown for each group, since it can be estimated (together with respiration) from the solutions of the system of linear equations. Values of the gross efficiency of food conversion (GE), which corresponds to the production/consumption ratio (P/Q), can be used as alternative inputs to Q/B. For the phytoplankton group it is not necessary to enter Q/B or P/Q values, since this is an autotrophic group. Data sources and estimation methods used to estimate input parameters are presented in Table 1. In absence of further information, we assumed steady state conditions for each group (i) in 2000, i.e. $BA_i=0$ and $Ei=0$.

Annual B_i in big-eye flounder, black conger-eel, Pacific sand, perch cardinal fish, rattail fish and skates, which are by-catch species in the hake fishery, was estimated as follows:

$$B_i = B_{hake} * \left(\frac{C_i}{C_{hake}} \right) \qquad \textbf{Eq. 4}$$

where B_{hake} is the biomass of hake (Payá *et al.*, 2001); C_i is the yield of the species *i* during a research cruise carried out to estimate the hake biomass in 2000; C_{hake} is the yield of hake during the same cruise. We assumed that all species had the same response to the Chilean hake trawling fishing gear.

Annual Y_i for the same groups, were estimated as follows:

$$Y_i = Y_{hake} * \left(\frac{C_i}{C_{hake}} \right) \qquad \textbf{Eq. 5}$$

where Y_{hake} is the annual landing of hake obtained from the National Fishery Service (SERNAPesca, 2001).

Main assumptions when running the model

When running the EwE model, B, P/B, Q/B or EE can be unknown for any group *i*, since if the other three parameters are entered, EwE will estimate the unknown parameter when solving the system of equations that define the model. We use this model capability to estimate Bi in those groups where no data was available (see Table 1).

In small squids, mesopelagic fish, red squat lobster (j), euphausiids and copepods, B was estimated by EwE under the assumption that EE=0.999 for all these groups. This value of EE implies that EwE calculates the minimum biomass required to sustain predators of these groups (including the fishery). The biomass of large squids was calculated assuming EE=0.5. Following Jarre-Teichmann *et al.* (1998), B in gelatinous zooplankton was estimated assuming that EE=0.15. In phytoplankton, B was estimated assuming EE=0.8 in order to restrict the values of P obtained by EwE in the range of values informed for the marine system off central Chile (Daneri *et al.,* 2000).

Considering that for central Chile no B values have been estimated for cetaceans or marine birds and that EwE cannot estimate biomass in top predators, we assumed that the B of cetaceans and marine birds in the upwelling system off central Chile are similar to those calculated in other upwelling systems (Jarre *et al.*, 1989; Jarre-Teichmann *et al.*, 1998).

Balancing the model

The model was balanced by checking the values of EE_i and GE_i. Obviously, EE_i must be between 0 and 1, while GE_i must lie between 0.1 and 0.35 (Christensen and Pauly, 1992). When inconsistent values of either EE_i or GE_i were found, then we perform changes in the input parameters (i.e., B_i, P_i/B_i o DC_{ij}) following criteria presented by Christensen *et al.* (2005) until we obtained acceptable outputs, *i.e.* $EE<1$ and $0.1<GE<0.35$ for each group *i.*

Table 2 presents input and output parameters of the balanced Ecopath model representing the upwelling system of central Chile, year 2000. Table 3 presents the diet composition of predators in the same model.

Table 1. Functional groups considered in the modelling of the marine system off central Chile, year 2000 and the data used to parameterize the model. Key: (j)=juveniles; (a)=adults; (EC1)= equation 1, see text; (EC2) equation 2, see text; (SA)=Stock assessment; (OR)=Official Report from National Fisheries Service Statistic Yearbooks; (SCA)=Stomach content analysis; (GKS)=General knowledge of the same species/gender/group.

Group/Parameter	B_i $t{\cdot}km^{-2}$	P_i/B_i $year^{-1}$	Q_i/B_i $year^{-1}$	Y_i $t{\cdot}km^{-2}{\cdot}year^{-1}$	DC	EE_i	GE_i
1. cetaceans	20 and 21	21; 26	7; 26	-	24; 26		
2. sea lions	15	21	20	-	CGE based on 15		
3. marine birds	20 and 21	20	20	-	20; 21		
4. hake (j)	SA; 27	2	2	27	SCA; 3		
5. hake (a)	SA; 22 and 27	2	2	OR; 29	SCA; 3		
6. common sardine (j)	SA; 28	Cubillos, *pers. com**		OR; 29	SCA; 4		18
7. common sardine (a)	SA; 28	Cubillos, *pers. com**		OR; 29	SCA; 4		18
8. anchovy (j)	SA; 28	Cubillos, *pers. com**		OR; 29	SCA; 4		18
9. anchovy (a)	SA; 28	Cubillos, *pers. com**		OR; 29	SCA; 4		18
10. small squids		21		OR; 29	23; 31	0.999	30
11. large squids		21	13	OR; 29	13	0.500	
12. mesopelagic fish		18	21	-	1	0.999	
13. red squat lobster (j)		GKS based on 31	31	-	GKS based on 31	0.999	
14. red squat lobster (a)	SA; 10	31	31	OR; 29	GKS based on 31		
15. yellow squat lobster	SA; 17	31	31	OR; 29	GKS based on 31		
16. pink shrimp	SA; 9	31	31	OR; 29	GKS based on 31		
17. horse mackerel	SA; 11	Cubillos, *pers. com**	20	Cubillos, *pers. com**.	SCA; 3		
18. hoki	SA; 28	21		OR; 29	SCA; 12		
19. swordfish		21		OR; 29	SCA; 6		21
20. black conger-eel	Eq. 5	3; 25	3; 25	Eq. 6	3; 25		
21. rattail fish	Eq. 5	3; 25	3; 25	Eq. 6	3; 25		
22. big-eye flounder	Eq. 5	3; 25	3; 25	Eq. 6	3; 25		
23. cardinal fish	Eq. 5	3; 25	3; 25	Eq. 6	3; 25		
24. Pacific sand perch	Eq. 5	3; 25	3; 25	Eq. 6	3; 25		
25. small chondrichthyans	Eq. 5	3; 25	3; 25	Eq. 6	3; 25		
26. polychaetes	8	8	5	-	GKS based on 8		
27. gelatinous zooplankton		21	21	-	21	0.150	
28. copepods		16		-	19	0.999	19
29. euphausiids		19		-	19	0.999	19
30. phytoplankton		14	-	-	-	0.800	
31. detritus	-	-	-	-	-	-	-

1=Amstrong *et al.* (1991); 2=Arancibia *et al.* (1998); 3=Arancibia *et al.*, (2002); 4=Arrizaga *et al.* (1993); 5=Arreguin-Sánchez *et al.* (1993); 6=Barbieri *et al.* (1998); 7=Browder (1993); 8=Carrasco and Arcos (1980); 9=Canales (2002); 10=Canales and Espejo (2002); 11=Córdova et al. (2000); 12=Cubillos *et al.* (1998); 13=Cubillos *et al.* (2004); 14=Daneri *et al.*, 2000; 15=Doppler Ltda. (1997); 16=Escribano and McLaren (1999); 17=Espejo and Canales (2002); 18=Hewitson and Crushak (1993); 19=Hutchings et al. (1991); 20=Jarre *et al.* (1989); 21=Jarre-Teichmann *et al.* (1998); 22=Lillo *et al.* (2001); 23=Lipinski (1992); 24=Majluf and Reyes (1989); 25=Neira *et al.* (2004); 26=Pauly *et al.* (1998b); 27=Payá *et al.* (2001); 28=Quiñones *et al.* (2002); 29=SERNAPesca (2001); 30=Shannon and Jarre-Teichmann (1999); 31=Wolf (1994).

* Luis Cubillos (Universidad de Concepción, P.O. Box 160-C, Concepción, Chile; Email: lucubillos@udec.cl)

Table 2. Input and output (**bold**) parameters of the balanced Ecopath model representing the upwelling system off central Chile, year 2000. TL=trophic level; B=biomass; P/B=production:biomass ratio; Q/B=consumption:biomass ratio; Y=landings; EE=ecotrophic efficiency; GE=gross efficiency; F=fishing mortality; M2=predation mortality; M0=other mortalities; j=juveniles; a=adults.

Group/Parameter	TL	B ton·km^{-2}	P/B year^{-1}	Q/B year^{-1}	Y ton·km^{-2}·year^{-1}	EE	GE	F year^{-1}	M2 year^{-1}	M0 year^{-1}
1. cetaceans	**4.41**	0.0070	0.600	10.000	0.000	**0.167**	**0.060**	**0.000**	**0.100**	**0.500**
2. sea lion	**3.93**	0.0720	0.250	20.000	0.000	**0.381**	**0.013**	**0.000**	**0.095**	**0.155**
3. marine birds	**3.58**	0.0650	0.500	20.000	0.000	0.000	0.025	**0.000**	**0.000**	**0.500**
4. hake (j)	**3.35**	**7.755**	2.500	8.323	0.064	0.990	**0.300**	**0.008**	**2.467**	**0.025**
5. hake (a)	**3.92**	12.189	0.456	5.159	2.143	**0.668**	**0.088**	**0.176**	**0.129**	**0.151**
6. common sardine (j)	**2.03**	41.355	1.453	**14.530**	8.510	**0.309**	0.100	**0.206**	**0.243**	**1.005**
7. common sardine (a)	**2.03**	14.600	1.875	**18.750**	4.594	**0.275**	0.100	**0.315**	**0.201**	**1.359**
8. anchovy (j)	**2.03**	23.971	0.703	**7.030**	3.650	**0.613**	0.100	**0.152**	**0.279**	**0.272**
9. anchovy (a)	**2.03**	14.631	2.120	**21.200**	4.520	**0.240**	0.100	**0.309**	**0.201**	**1.611**
10. small squids	**3.73**	**3.362**	3.500	**10.606**	0.000	0.999	0.330	**0.000**	**3.497**	**0.003**
11. large squids	**4.48**	**6.413**	1.750	**5.303**	0.000	0.500	0.330	**0.000**	**0.875**	**0.875**
12. mesopelagic fish	**3.40**	**50.299**	1.200	12.000	0.000	0.999	**0.100**	**0.000**	**1.199**	**0.001**
13. red squat lobster (j)	**2.00**	**0.230**	5.900	18.000	0.000	0.999	**0.328**	**0.000**	**5.894**	**0.006**
14. red squat lobster (a)	**2.00**	**0.558**	3.569	12.500	0.080	0.999	**0.286**	**0.143**	**3.422**	**0.004**
15. yellow squat lobster	**2.00**	0.077	3.569	11.600	0.059	0.782	0.308	**0.766**	**2.023**	**0.780**
16. pink shrimp	**2.00**	0.400	2.500	12.000	0.089	**0.466**	**0.208**	**0.223**	**0.942**	**1.335**
17. horse mackerel	**3.52**	23.980	0.564	14.200	3.163	**0.359**	**0.040**	**0.132**	**0.070**	**0.362**
18. hoki	**3.77**	21.900	0.528	**5.280**	1.509	**0.705**	0.100	**0.069**	**0.303**	**0.156**
19. sword fish	**4.66**	**0.640**	0.500	**5.000**	0.240	0.750	0.100	**0.375**	**0.000**	**0.125**
20. black conger eel	**3.53**	0.300	0.700	**3.500**	0.068	**0.351**	0.200	**0.227**	**0.019**	**0.454**
21. rattail fish	**3.00**	**2.282**	0.700	**3.500**	0.001	0.999	0.200	**0.000**	**0.699**	**0.001**
22. big-eye flounder	**3.00**	0.200	0.700	**3.500**	0.002	**0.014**	0.200	**0.010**	**0.000**	**0.690**
23. cardinal fish	**3.50**	**6.830**	0.700	**3.500**	0.115	0.999	0.200	**0.017**	**0.682**	**0.001**
24. Pacific sand perch	**3.57**	0.045	0.700	**3.500**	0.003	**0.095**	0.200	**0.067**	**0.000**	**0.633**
25. skates	**3.00**	0.253	0.362	**2.413**	0.012	**0.131**	0.150	**0.047**	**0.000**	**0.315**
26. polychaetes	**2.00**	1.886	2.410	15.900	0.000	**0.000**	**0.152**	**0.000**	**0.000**	**2.410**
27. gelatinous zooplankton	**2.63**	**7.774**	0.584	1.420	0.000	0.150	**0.411**	**0.000**	**0.088**	**0.496**
28. copepods	**2.25**	**80.383**	45.000	154.519	0.000	0.999	**0.291**	**0.000**	**44.955**	**0.045**
29. euphausiids	**2.50**	**66.159**	13.000	**31.707**	0.000	0.999	0.410	**0.000**	**12.987**	**0.013**
30. phytoplankton	**1.00**	**347.971**	120.000	-	0.000	0.300	-	**0.000**	**36.000**	**84.000**
31. detritus	**1.00**	1000	-	-	0.000	**0.001**	-	**-**	**-**	**-**

Table 3. Diet composition of predators in the balanced Ecopath model representing the upwelling system off central Chile, year 2000.

	Predator																												
Prey	1. cetaceans	2. sea lion	3. marine birds	4. hake (j)	5. hake (a)	6. common sardine (j)	7. common sardine (a)	8. anchovy (j)	9. anchovy (a)	10. small squids	11. large squids	12. mesopelagic fish	13. red squat lobster (j)	14. red squat lobster (a)	15. yellow squat lobster	16. pink shrimp	17. horse mackerel	18. hoki	19. sword fish	20. black conger eel	21. rattail fish	22. big-eye flounder	23. cardinal fish	24. Pacific sand perch	25. skates	26. polychaetes	27. gel. zooplankton	28. copepods	29. euphausiids
1 cetaceans	0.01																												
2 sea lion	0.1																												
3 marine birds																													
4 hake (j)	0.06	0.250	0.100	0.040	0.170					0.050	0.088									0.013				0.065					
5 hake (a)	0.07	0.200	0.050								0.029									0.036									
6 com sardine (j)	0.1	0.180	0.284	0.118						0.050																			
7 com sardine (a)	0.03	0.065	0.100	0.042																									
8 anchovy (j)	0.06	0.110	0.165	0.070						0.050																			
9 anchovy (a)	0.04	0.062	0.101	0.042																									
10 small squids	0.15		0.040		0.002					0.210								0.035	0.010										
11 large squids	0.15		0.040		0.002						0.198							0.035	0.010										
12 mesopel. fish	0.1		0.120		0.300					0.100	0.206						0.025	0.180											
13 red s. lobst. (j)				0.015	0.002															0.004	0.030	0.020			0.002				
14 red s lobst. (a)				0.008	0.001															0.107	0.110	0.300			0.210				
15 yellow s. lobst.					0.002															0.002		0.020			0.023				
16 pink shrimp					0.006																								
17 h. mackerel	0.1	0.100																	0.480										
18 hoki											0.124								0.500										
19 sword fish																													
20 bl. conger eel		0.004																											
21 rattail fish					0.002						0.036																		
22 big-eye flound.																													
23 cardinal fish		0.030									0.113																		
24 P. sand perch																													
25 skates																													
26 polychaetes																													
27 gel. zooplankt.																	0.002												
28 copepods						0.02	0.02	0.02	0.02	0.44		0.4					0.002										0.5	0.2	0.4
29 euphausiids				0.500	0.505					0.10		0.6					0.971	0.750					0.5	0.679					
30 phytoplankt.						0.98	0.98	0.98	0.98																		0.5	0.8	0.6
31 detritus													1	1	1	1										1			
Imports	0.04			0.165	0.008						0.206									0.838	0.860	0.660	0.5	0.256	0.765				
Sum	1.00	1.000	1.000	1.000	1.000	1.00	1.00	1.00	1.00	1.00	1.000	1.0	1	1	1	1	1.000	1.000	1.000	1.000	1.000	1.000	1.0	1.000	1.000	1	1.0	1.0	1.0

REFERENCES

Acuña, E. 1986. El recurso mictófidos (Pisces, Myctophidae): antecedentes en aguas chilenas y marco de referencia para su investigación. *In:* La Pesca en Chile. P. Arana (Ed.) Valparaíso, Chile, pp. 315-339.

Aguayo-Lobo, A., Torres Navarro, D. and Acevedo Ramírez, J. 1998. Los mamíferos de Chile: I. Cetácea. Serie Científica INACH, 48: 19-159.

Aguayo, M. and Gili, R. 1984. Estudio de la edad y el crecimiento de la merluza de cola (*Macruronus magellanicus*, Lönnberg) (Gadiformes–Gadidae). Investigaciones Pesqueras (Chile), 31: 47–57.

Aguayo, M. 1995. Biology and fisheries of Chilean hakes (*M. gayi* and *M. australis*). *In:* Hakes, biology fisheries and markets. J. Alheit, T. Pitcher (eds). Chapman and Hall, UK, pp. 305-338.

Allen, K. R. 1971. Relation between production and biomass. Journal of Fisheries Research Board of Canada, 28: 1573-1581.

Amstrong, M.J., James, A.G. and Valdés Szeinfeld, S. 1991. Estimates of annual consumption of food by anchovy and other pelagic fish species off South Africa during the period 1984-1998. South African Journal of marine Science, 11: 251-266.

Arana, P. 1970. Nota sobre la presencia de ejemplares de merluza de cola (*Macruronus magellanicus*, Lönnberg) frente a la costa de Valparaíso. Investigaciones Marinas (Chile), 1(3): 55-68.

Arancibia, H. 1992. Distribution patterns of the demersal fish assemblage off Central Chile. Biología Pesquera (Chile), 21: 43-53.

Arancibia, H. 1989. Distribution patterns, trophic relationships and stock interactions in the demersal fish assemblage off Central Chile. Dr. Rer. Nat. Thesis, University of Bremen, RFA, 221 pp.

Arancibia, H. 1987. On the application of multivariate analysis in the determination of "ontogenetic trophic units" in the Chilean hake, *Merluccius gayi* (Guichenot, 1848). ICES Demersal Fish Committee, Ref. Statistics Committee, C.M. 1987/G:6.

Arancibia, H. and Neira, S. 2003. Simulación de cambios en la biomasa de los principales recursos pesqueros de Chile central (V – IX región) bajo el marco de la ley de pesca N° 19.713 y sus posteriores modificaciones. Informe Final. Universidad de Concepción, 53 pp.

Arancibia, H., Barros, M., Neira, S., Markaida, U., Yamashiro, C., Icochea, L., Salinas, C., Cubillos, L., Ibáñez, Ch., León, R., Pedraza, M., Acuña, E., Cortés, A., and Kesternich, V. 2007. Informe Final Proyecto FIP 2005-38. Análisis del impacto de la jibia en las pesquerías de peces demersales. Universidad de Concepción / Universidad Católica del Norte, 299 p. + Anexos.

Arancibia, H., Neira, S., Christensen, V., Olson, R., Cubillos, L., Quiñones, R., Gatica, C., and Medina, M. 2002. Enfoque metodológico para el análisis ecosistémico en la administración de pesquerías de la zona central de Chile. Pre-informe Final Proyecto FIP-2001-29. Universidad de Concepción, 266 pp.

Arancibia, H., Catrilao, M. and Farías, B. 1998. Evaluación de la demanda de alimento en merluza común y análisis de su impacto en pre-reclutas. Informe Final Proyecto FIP 95-17. Universidad de Concepción, 98 pp.

Arreguín-Sánchez, F., Seijo, J.C. and Valero-Pacheco, E. 1993. An application of Ecopath to the Continental Shelf ecosystem of Yucatan, Mexico. *In:* Trophic models of acuatic ecosystems. Christensen, V. and D. Pauly. (Eds.). ICLARM Conference Proceedings, Nº 26, pp. 269-278.

Arrizaga, A., Fuentealba, M., Espinoza, C., Chong, J. and Oyarzún, C. 1993. Hábitos tróficos de dos especies de peces pelágicos: *Strangomera bentincki* (Norman, 1936) y *Engraulis ringens* Jenyns, 1842 en el litoral de la Región del Bio-Bio, Chile. Boletín de la Sociedad de Biología de Concepción (Chile), 6-4: 27-35.

Avaria, S. and Muñoz, P. 1982. Producción actual, biomasas y composición específica del fitoplancton de la bahía de Valparaíso en 1979. Revista de Biología Marina de Valparaíso, 18: 129-157.

Barbieri, M.A., Canales, C., Correa, V., Donoso, M., González, A., Leiva, B., Montiel, A., and Yáñez, E. 1998. Development and present State of the Sword fish, Xiphias Gladius, fishery in Chile. pp. 1-10. In: Biology and Fisheries of sword fish, *Xiphias gladius*. Barret, I., O. Sosa-Nishizaki and N. Bartoo (Eds). Papers from the International Symposium on Pacific sword fish, Ensenada, Mexico 11-14 December 1994.

Bax, N. J. 1991. A comparison of the fish biomass flow to fish, fisheries, and marine mammals in six marine ecosystems. ICES Mar. Sci. Symp., 193: 217–224.

Bax, N. J. 1998. The significance and prediction of predation in marine fisheries. ICES Journal of Marine Science, 55(6): 997-1030.

Botsford, L., Castilla, J.C. and Peterson, C.H. 1997. The management of fisheries and marine ecosystems. Science, 277: 509-515.

Browder, J.A. 1993. A pilot model of the Gulf of Mexico Continental Shelf. *In:* Trophic models of aquatic ecosystems, Christensen, V. and D. Pauly. (Eds.), ICLARM Conference Proceedings, Nº 26, pp. 279-284.

Camus, P. 2001. Biogeografía marina de Chile continental. Revista Chilena de Historia Natural, 74: 587-617.

Canales, C. 2002. Informe de avance Proyecto "Investigación CTP camarón nailon 2002" Diagnóstico actualizado del estado de situación del recurso camarón nailon 2001. 32 pp. + 3 Anexos.

Canales, C. and Espejo, B. 2002. Informe de avance Proyecto "Investigación CTP Langostino colorado 2002" Diagnóstico actualizado del estado de situación del recurso langostino colorado. 27 pp. + 6 Anexos.

Carrasco F. and Arcos, D. 1980. Estimación de la producción secundaria de *Parapionospio pinnata* (Spionidea, Polychaeta) frente a Bahía de Concepción, Chile. Boletín del Instituto Oceanográfico de Sao Paulo, 29 (2): 79-82.

Christensen, V. and Pauly, D. 1992. ECOPATH II. A software for balancing steady state ecosystem models and calculating network characteristics. Ecological Modelling, 61: 169-185.

Christensen, V. and Walters, C.J. 2004. Ecopath with Ecosim: methods, capabilities and limitations. Ecological Modelling, 172: 109-139.

Christensen, V. and McLean, J.L. 2004. Placing Fisheries in their ecosystem context. Conference Proceedings. Ecological Modelling, 172 (2-4): 103-440.

Christensen, V. and Pauly, D. 1993. Trophic models of aquatic ecosystems. ICLARM Conference Proceedings, Nº 26, 390 pp.

Christensen V., Walters, C.J. and Pauly, D. 2005. Ecopath with Ecosim: a User's guide. Fisheries Centre, University of British Columbia, Vancouver. November 2005 edition, 154 p.

Córdova, J., Barbieri, Mª A., Miranda, H., Espejo, M., Rojas, M., Núñez, S., Ortiz, J., Catasti, V., Valenzuela, V., Braun, M., Miranda, L., Cuevas, C., Rebolledo, H. and Galindo, G. 2000. Evaluación hidroacústica del recurso jurel en la zona económica de Chile. Pre-Informe Final Proyecto FIP Nº 2000-03, 110 pp.

Cubillos, L., Hernández, A., Vilugrón, L., Miranda, L., Alarcón, R., Pino, C., Sepúlveda, A. and Vásquez, G. 1998. Estudio Biológico pesquero de merluza de cola en el área de distribución de la pesquería pelágica centro-sur. Informe Final Proyecto FIP Nº 96-19. 158 pp.

Cubillos, L., Rebolledo, H. and Hernández, A. 2003. Prey composition and estimation of Q/B for the Chilean hake, *Merluccius gayi* (Gadiformes-Merluccidae), in the central-south area off Chile (34º-40ºS). Arch. Fish. Mar. Res. 50, 271-286.

Cubillos, L.C., Ibáñez, C., González, C. and Sepúlveda, A. 2004. Pesca de Investigación: Pesca de jibia (*Dosidicus gigas*) con red de cerco entre la V a X Regiones, 2003. Instituto de Investigación Pesquera, 48 pp.

Cushing, D.H. 1982. Climate and Fisheries. Academic, London/New York.

Daneri, G., Dellarossa, V., Quiñones, R., Jacob, B., Montero, P. and Ulloa, O. 2000. Primary production and community respiration in the Humboldt Current System off Chile and associated oceanic areas. Marine Ecology Progress Series, 197: 41-49.

Doppler, Ltda. 1997. Censo poblacional del lobo marino común en el litoral de la V a IX Regiones. Informe final Proyecto FIP-IT/96-51, 218 pp.

Elton, C. S. 1927. Animal ecology. Sidgwick & Jackson, London.

Escribano, R. and McLaren, I. 1999. Production of *Calanus chilensis* in the upwelling area of Antofagasta, northern Chile. Marine Ecology Progress Series, 177: 147-156.

Escribano, E., Fernández, M. and Aranís, A. 2003. Physical-chemical processes and patterns of biodiversity of the Chilean eastern boundary pelagic and benthic marine ecosystems: an overview. Gayana, 67(2):190-205.

Espejo, V. and Canales, C. 2002. Informe de avance Proyecto "Investigación CTP Langostino amarillo 2002" Diagnóstico actualizado del estado de situación del recurso langostino amarillo, 26 pp. + 4 Anexos.

FAO 2003. The ecosystem approach to fisheries. FAO Technical Guidelines for Responsible Fisheries. No. 4, Suppl. 2. Rome, FAO. 2003. 112 p.

Frank, K. T., Choi, J.S., Petrie, B. and Leggett, W.C. 2005. Trophic cascades in a formerly cod dominated ecosystem. Science, 308: 1621-1623.

Gallardo, V.A. 1979. El bacterioplancton de la plataforma continental de la costa sur-occidental de Sudamérica: un reciente descubrimiento. En. Memorias del Seminario sobre ecología bentónica y sedimentación de la Plataforma Continental del Atlántico Sur. UNESCO, Montevideo: 259-267.

Hewitson, J. and Crushak, R.A. 1993. Production and consumption by planktivores fish in the northern Benguela ecosystem in the 1980s. South African Journal of marine Science, 13:1031-1050.

Hutchings, L., Pillar, S.C. and Verheye, H. 1991. Estimates of standing stock, production and consumption of meso- and macrozooplankton in the Benguela ecosystem. South African Journal of marine Science, 11: 499-512.

Jarre, A, Muck, P. and Pauly, D. 1989. Interactions between fish stocks in the Peruvian upwelling ecosystem. ICES Marine Science Symposium, Paper Nº 27, ICLARM Contribution Nº 563, 23 pp.

Jarre-Teichmann, A., Shannon, L., Moloney, C. and Wickens, P. 1998. Comparing trophic flows in the Southern Benguela to those in other upwelling ecosystems. *In:* Pillar, S., Moloney, C., Payne, A., Shillington (Eds.). Benguela Dynamics. South African Journal of marine Science, 19: 391-414.

Lillo, S., Ojeda, V., Olivares, J., Tascheri, R., Braun, M., Núñez, S., Ortiz, J. and Torres, P. 2001. Evaluación acústica de merluza común en la zona centro sur, año 2000. Informe final Proyecto FIP Nº 2000-04. 126 p. +29 tablas, 57 figs.+ 2 anexos.

Lindeman, R. 1942. The trophic-dynamic aspect of ecology. Ecology, 23: 399-418.

Link, J.S. 2002a. What does ecosystem-based fisheries management mean?. Fisheries, 27 (4): 21.

Link, J.S. 2002b. Ecological considerations in fisheries management: What does it matter?. Fisheries, 27 (4): 10-17.

Lipinski, M.R. 1992. Cephalopods and the Benguela ecosystem; trophic relationships and impact. In: Benguela trophic functioning, Payne, A.J.L., Brink, K.H., Mann, K.H. and R. Hilborn (Eds.), South African Journal of Marine Science, 12: 791-802.

MacPhaden, M. 1999. Genesis and evolution of the 1997-1998 El Niño. Science, 283:950-954.

Majluf, P. and Reyes, J. 1989. The marine mammals of Peru: a review. 344-363. En: D. Pauly, P. Muck, J. Mendo and I. Tsukayama (Eds).

The Peruvian upwelling ecosystem: dynamics and Interactions. ICLARM conference Proceedings 18, 483 pp.

Markaida, U. and Sosa-Nishizaki, O. 2003. Food and feeding habits of jumbo squid *Dosidicus gigas* (Cephalopoda: Ommastrephidae) from the Gulf of California, Mexico. J. Mar. Biol. Assoc. U.K., 83 (2003), pp. 507–522.

Meléndez, R. 1984. Alimentación de *Merluccius gayi* (Guichenot) frente a Chile central (32°05'S-36°50'S). Bol. Mus. Nac. Hist. Nat. Chile, 54 p.

Miranda, L., Hernández, A., Sepúlveda, A. and Landaeta, M. 1998. Alimentación de jurel y análisis de la selectividad en la zona centro-sur de Chile. In: Arcos, D. (Ed.), Biología y Ecología del Jurel en Aguas Chilenas. Instituto de Investigación Pesquera, Talcahuano-Chile, pp. 173– 187.

Montecino, V., Paysant, L., Barría, I., and Sepúlveda, A. 1998. Space scales of variability of chlorophyll-a off central Chile (between 33ºS-40ºS): ground truth of April-May 1984 coastal zone color scanner (CZCS) images. Ocean Optics XIV Kaiua Kona, Hawaii, USA: Extended abstract.

Montecinos, A., Purca, S. and Pizarrro, O. 2003. Interannual-to-interdecadal sea surface temperature variability along the western coast of South America. Gophisical Research Letters, 30(11): 1570-1573.

Neira, S. and Arancibia, H. 2004. Trophic interactions and community structure in the Central Chile marine ecosystem (33ºS-39ºS). Journal of Experimental Marine Biology and Ecology, 312: 349-366.

Neira, S., Arancibia, H. and Cubillos, L. 2004. Comparative analysis of trophic structure of commercial fishery species off Central Chile in 1992 and 1998. Ecological Modelling, 172 (2-4): 233-248.

Nigmatulin, Ch.M., Nesis, K.N. and Arkhipkin, A.I. 2001. A review of the biology of jumbo squid *Dosidicus gigas* (Cephalopoda: Omastrephidae). Fisheries Research, 54: 9-19.

Núñez, S. 1995. Variaciones temporales y espaciales sen la asociación de copépodos del sistema de surgencia de Talcahuano (Chile). Tesis de Magister, Universidad de Concepción. 162 pp. + 10 anexos.

Osgood, W.H. 1943. The Mammals of Chile. Field Museum of Natural History, Chicago. Zoological Series Vol. 30. 268 pp.

Palma, S. and Rosales, S. 1995. Composición, distribución y abundancia estacional del macroplancton de la bahía de Valparaíso. Investigaciones Marinas 23: 49-66.

Pauly, D. and Christensen, V. 1995. Primary production required to sustain global fisheries. Nature, 374: 255-257.

Pauly, D., Christensen, V., Dalsgaard, J.P.T., Froese, R. and Torres, F. 1998a. Fishing down the marine food webs. Science, 279: 860-863.

Pauly, D., Trites, A.W., Capuli, E. and Christensen, V. 1998b. Diet composition and trophic levels of marine mammals. ICES Journal of Marine Science, 55:467-481.

Pauly, D., Christensen, V. and Walters, C. 2000. Ecopath, Ecosim, and Ecospace as tools for evaluating ecosystem impacts of fisheries. ICES Journal of Marine Science, 57: 697-706.

Pauly, D., Alder, J., Bennett, E., Christensen, V., Tyedmers, P. and Watson, R. 2003. The future of world fisheries. Science 302, 1359-1361.

Payá, I., Tascheri, R., Montenegro, C. and Bravo, C. 2001. Investigación CTP Merluza común 2002. Primer Informe de Avance. IFOP, 43 pp. + figuras y anexos.

Pikitch, E.K., Santora, C., Babcock, E.A., Bakun, A., Bonfil, R., Conover, D.O., Dayton, P., Doukakis, P., Fluharty, D., Heneman, B., Houde, E.D., Link, J., Livingston, P.A., Mangel, M., McAllister, M.K., Pope, J. and Sainsbury, K.J. 2004. Ecosystem-based fisheries management. Science, 305: 346-347.

Quinoñes, R., Aliaga, B., Arancibia, H., Navarrete, I., Barriga, O., Henríquez, G., Palma, C., Dresdner, J., Chávez, C. and Salgado, H. 2002. Proyecto análisis biológico, económico y social de las pesquerías de la VIII Región. Informe de avance proyecto FNDR código BIP N° 20183334-0.181 pp. + 8 Anexos.

Rodhouse, P.G. and Nigmatulin, Ch.M. 1996. Role as consumers. Philosophical Transactions. Biological Sciences, Vol. 351, No. 1343, The role of cephalopds in the World's Oceans. Pp. 1003-1022.

SERNAPesca. 2001. Anuario Estadístico de Pesca 2000. Departamento de Información y Estadística Pesquera. Ministerio de Economía, Fomento y Reconstrucción, Chile. 283 pp.

Shannon, L.J. and Jarre-Teichmann, A. 1999. A model of trophic flows in the Benguela Upwelling System during the 1980s. South African Journal of Marine Science, 21: 349-366.

Siefeld, W., Vargas, M. and Fuenzalida, R. 1995. Peces mesopelágicos frente a la costa norte de Chile (18º25'-21º47'S). Investigaciones Marinas Valparaíso (Chile), 23: 83-97.

Siefeld, W. 1999. Estado del conocimiento sobre conservación y preservación de *Otaria flavescens* (Shaw, 1800) y *Arctocephalus autralis* (Zimmermann, 1783) en las costas de Chile. Estudios en Oceanologia (Chile), 18: 81-96.

Sinclair, M., O'Boyle, R., Burke, D.L. and Peacock, G. 1997. Why do some fisheries survive and other collapse?. *In:* D. A. Hancock, D. C. Smith, A. Grant, and J. P. Beumer (Eds.). Developing and Sustaining World Fisheries Resources: The State of Science and Management. Second World Fisheries Congress, Brisbane 1996. CSIRO publishing, Melbourne, pp. 23-35.

Strub, P., Mesías, J.M., Montecino, V., Ruttlant, J. and Salinas, S. 1998. Coastal ocean circulation off western South America. *In:* The Sea 11. Brink K.H. and A.R. Robinson (eds). Wiley and Sons, Inc., New York, USA, pp. 273-313.

Walters, C., Christensen, V. and Pauly, D. 1997. Structuring dynamic models of exploited ecosystems from trophic mass-balance assessments. Reviews in Fish Biology and Fisheries, 7: 139-172.

Walters, C.J. and Martell, S.J.D. 2004. Fisheries Ecology and Management. Princeton University Press. Princeton, New Jersey, USA.

Wolff, M. 1994. A trophic model for Tongoy Bay. A system exposed to suspended scallop culture (Northern Chile). Journal of Experimental Marine Biology and Ecology, 182: 149-168.

Worm, B., Barbier, E.B., Beaumont, N., Duffy, J.E., Folke, C., Halpern, B.S., Jackson, J.B.C., Lotze, H.K., Micheli, F., Palumbi, S.R., Sala, E., Selkoe, K.A., Stachowicz, J.J. and Watson, R. 2006. Impacts of biodiversity loss on ocean ecosystem services. Science, 787-790.

SPATIAL RESOURCES AND FISHERY MANAGEMENT FRAMEWORK IN THE EAST CHINA SEA[1]

He-Qin Cheng[a,e], Hong Jiang[a], Hai-Gen Xu[b], Jun Wu[b], Hui Ding[b], Will Le Quesne[c], and Francisco Arreguín-Sánchez[d]
[a] - State Key Laboratory of Estuarine & Coastal Research,
East China Normal University, 200062, Shanghai, China;
[b] - Nanjing Institute of Environmental Sciences, State Environmental
Protection Administration of China, 210042, Nanjing, China;
[c] - School of Marine Science and Technology, University of Newcastle,
Ridley Building, Newcastle upon Tyne NE1 7RU, UK;
[d] - Centro Interdisciplinario de Ciencias Marinas del IPN, Apdo. Postal 592,
La Paz, 23000, Baja California Sur, México
[e] - Email: hqch@sklec.ecnu.edu.cn

ABSTRACT

A unique combination of environmental factors including primary productivity, water currents, water masses, temperature, salinity and nutrient level in the East China Sea (ECS) has supported a highly productive fishery and rich biodiversity. Since the 1950s, the government of the People's Republic of China has introduced a range of spatial management measures including marine protected areas (MPAs), fishery protected areas (FPAs) and large-scale seasonal spatial fishing closures to protect the ECS marine resources. Based on the constructed ECS Ecopath and Ecosim model, this study focuses on the spatial model (Ecospace) description. The main spatial information consisting of environmental factors in the ECS are briefly reviewed, and basic data input to the ECS Ecospace model, such as habitat, location of MPAs, allocation of fleets and main scenarios are introduced.

INTRODUCTION

The East China Sea (ECS) is a typical epicontinental sea and part of the western Pacific Ocean bordered by China, South Korea and Japan (Figure 1). It covers an area of 770,000 km^2 (Zheng *et al.*, 2003), of which 65% has a water depth less than 200 m. The ECS deepens eastward and southward to a maximum depth of 2,300 m in the Okinawa Trough. Large quantities of land-based nutrients and pollutants flow into the ECS along with large fresh water inputs, mainly from the Changjiang (Yangtze) riverine system. The confluences of the alongshore current, the Yellow Sea cold water mass and the Kuroshio Current provide good fishing grounds in the ECS. The superior geography of the ECS has supported a highly productive fishery and rich biodiversity.

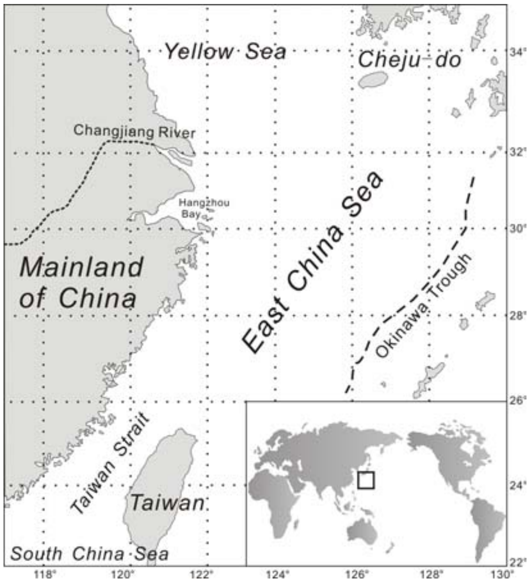


Figure 1. Study area of the East China Sea

Economic development and population growth in China and neighboring countries over the last several decades have led to intensified anthropogenic impacts on fishing stocks and biodiversity in the East China Sea. In recent

---

[1] Cite as: Cheng, H.Q., Jiang, H., Xu, H.G., Wu, J., Ding, H., Le Quesne, W. and Arreguín-Sánchez, F. 2007. Spatial resources and fishery management framework in the East China Sea, p. 87–99. *In*: Le Quesne, W.J.F., Arreguín-Sánchez, F. and Heymans, S.J.J. (eds.) INCOFISH ecosystem models: transiting from Ecopath to Ecospace. Fisheries Centre Research Reports 15(6). Fisheries Centre, University of British Columbia [ISSN 1198-6727].

years, species outbreaks (such as large jellyfish) in the ECS have been thought to be related to ecosystem and fishery resources deterioration. In response, the Chinese government has introduced a range of spatial management measures including large-scale seasonal spatial closures, offshore fishery boxes and coastal biodiversity protected areas.

Based on a previously constructed ECS Ecopath and Ecosim model (Jiang *et al,* 2006), this report describes the development and parameterization of the present of the ECS Ecospace model. The sources and information used to construct the ECS Ecospace model are presented.

SPATIAL CHARACTERISTICS OF THE ECS ECOSYSTEM

The ECS is a vast, semi-enclosed marginal sea. The water depth of most of the ECS continental shelf ranges from 60 to 140 m with an average depth of 72 m. The depth contours of the ECS are almost parallel to the coastline. Many harbors and islands are located to the west of the ECS shelf where the water depth is less than 30 m. Primary productivity, water current, water mass, temperature, salinity and nutrient level of the ECS have important effects on the distribution and productivity of the fishery resources, which can be considered environmental resources.

Primary productivity

There is seasonal variation and a bimodal character to the monthly distribution of primary productivity in the ECS. The monthly distribution of primary productivity is at its lowest level in the winter and rises rapidly to its peak in spring. It goes down a little in summer, with a slight increase in autumn (Table 1, Li *et al.*, 2003). The spatial distribution shows that the primary productivity decreases from the near-shore zone toward the open sea (Figure 2). Primary productivity estimated by SeaWiFS is less than 200 g·m^{-2}·yr^{-1} (wet weight) southeast of the line from Taiwan northeast to Kyushu Island, is about 200 to 250 g·m^{-2}·yr^{-1} in the middle part of the ECS and is higher than 250 g·m^{-2}·yr^{-1} in near-shore waters. The peak values are higher than 400 g·m^{-2}·yr^{-1} in the Changjiang River estuary and Hangzhou Bay, where the important Zhoushan Fishing Ground is located.

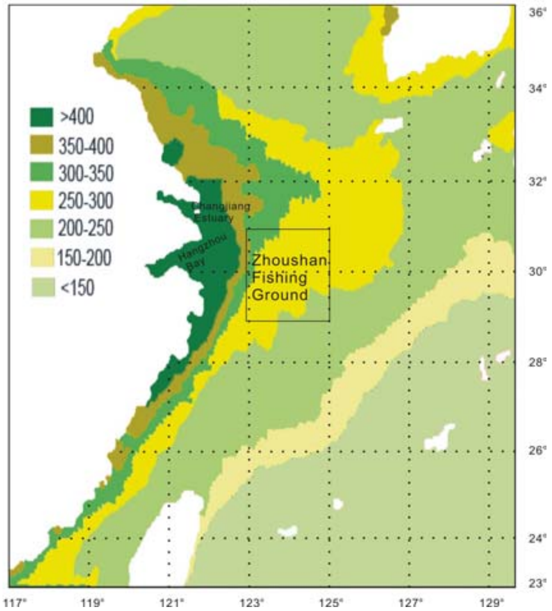


Figure 2. Distribution of total primary productivity in the ECS for the year 1998 (g·m^{-2}·yr^{-1}).

Table 1. Monthly variation of primary productivity in g·m^{-2}·yr^{-1} in the ECS in 1998 (Li *et al.*, 2003).

Time	Jan.	Feb.	Mar.	April	May	June	July	Aug.	Sep.	Oct.	Nov.	Dec.
g·m^{-2}·yr^{-1}	440.1	519.3	538.9	610.5	681.8	696.1	607.6	534.6	516.0	543.3	522.5	464.7

Hydrodynamic regime

Water currents

Water currents in the East China Sea are dominated by the Coastal Current and the Kuroshio Current. In the western part, the ECS Coastal Current (ECSCC) flows southward in fall and winter and northward in summer (Su, 2001) (Figure 3). To the east of the ECSCC, the broad shelf is dominated by the Taiwan Warm Current (TWC), which starts from the Taiwan Strait and penetrates into the Yellow Sea and/or flows toward the Tsushima Strait (Su, 2001; Liu *et al.*, 2003) (Figure 3). Year-round northward expansion of the TWC has been observed by hydrological investigations (Su, 2001). The TWC is constrained within a water depth of 50–100 m near the west coast.

On the eastern boundary, the Kuroshio Current moves northward, separating the ECS from the open ocean (Figure 3), and its branches intrude into the ECS, forming upwelling water due to topographic deflection (Tang *et al.*, 2000; Liu *et al.*, 2000). This circulation pattern greatly influences the dispersal of sediment and fresh water. During fall and winter, the Changjiang plume is constrained by an intensified coastal current flowing in a narrow band southwards along the coast (Liu *et al.*, 2003) and prohibited by the TWC from further eastward expansion to the shelf (Su, 2001). In the flood season (i.e., summer), Changjiang-diluted water may extend northeastward to Cheju Island (Liu *et al.*, 2003).

Water masses

Kuroshio warm water mixes with the low-salinity coastal water when it rushes onto the continental shelf of the ECS. This mixing produces three main water masses in the ECS: Kuroshio water, mixed modified water and coastal water (Liu *et al.*, 1993). The surface and bottom water masses in the ECS during February and August are given in Figure 4.

The Kuroshio Current includes two parts, the Kuroshio Surface Water Mass (K) and the Kuroshio Subsurface Water Mass (KC) on the ECS continental shelf. The K is characterized by high temperature (mean annual temperature 18.0–29.0°C) and high salinity (mean annual salinity 34.2–34.9 ppt). The K is distributed mainly in the south of the ECS and covers an area ¼ the size of the whole ECS; thus its fluctuation and change controls the hydrodynamic condition of the ECS directly. The KC with medium temperature (mean annual temperature 14.4–20.5°C) and high salinity (mean annual salinity 34.4–34.9 ppt) is under the water layer of the K. The KC occurs widely across the ECS continental shelf from May to November.

The mixed modified water masses can be divided into 9 parts, according to geographical location and degree modified: E, EC, T, TC, YE, Y, YC, C and M (Figure 4). The main features of the mixed modified water masses are the great changes in their seasonal distribution and medium temperature and salinity between the Kuroshio and coastal water.

Diluted water from the Changjiang and Qiantang Rivers is the main source of the ECS coastal water mass (C) that is characterized by low salinity (lower than 31 ppt). Land-air temperature and river runoff have a significant influence on the temperature of the coastal water masses (mean annual temperature 4.0–28.0°C) and on their salinity. The ECS coastal water occurs as a narrow belt along the coast in autumn and winter, but a finger-like projection expands northeast from the Changjiang estuary across the ECS continental shelf from spring to summer.

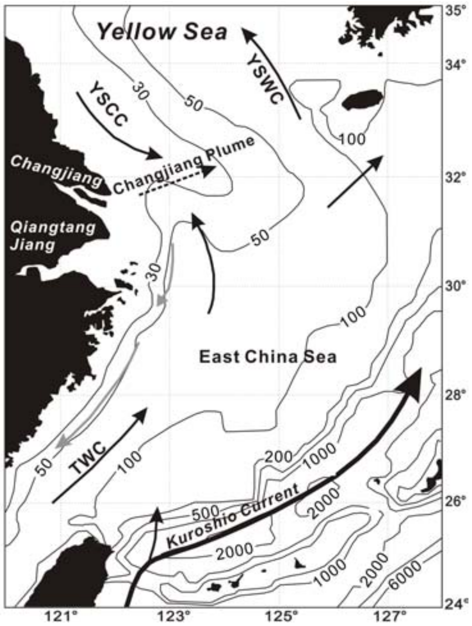


Figure 3. Morphology and current patterns in the ECS. ECSCC - ECS Coastal Current; TWC - Taiwan Warm Current; YSCC - Yellow Sea Coastal Current; YSWC - Yellow Sea Warm Current. Solid black lines indicate year-round current; solid gray lines indicate winter currents; dashed black lines indicate summer currents (from Deng *et al.*, 2006).

As the main component of the water column over the ECS continental shelf, ECS surface water (E) features significant seasonal fluctuation of temperature and salinity. It is affected by strong vertical mixing, with a range of temperature of 13.0–19.0°C and salinity of 33.75–34.75 ppt, bordered by a strong front with the low temperature and low salinity of the coastal water mass (C) in the southwest part of the ECS in winter. The E occurs in the southeast of the ECS in spring, but in the fall it occurs back on the main parts of the ECS continental shelf with a temperature range of 19.0–25.0°C and salinity larger than 33.75 ppt. The ECS bottom cold water mass (EC) occurs in the southeast of the ECS continental shelf due to the rushing of the KC in summer.

Separated from the K, the Taiwan Strait surface water mass (T) is limited by the submarine bathymetry; it shows obvious seasonal changes of temperature and salinity. It is distributed on the narrow part of the southwest ECS, with temperature of 17.9–19.6°C and salinity of 31.0–34.0 ppt in winter, 28.0–29.0°C and 33.1–34.2 ppt in summer. The Taiwan Strait bottom water mass (TC) occurs in a high salinity (>34 ppt) area generated from the KC in summer.

The Yellow Sea surface cold water mass (Y), characterized by low temperature and medium salinity, is distributed in the northwest of this study area. It is mixed vertically during winter at low temperatures (<12.0°C) and higher salinity (31.5–33.0 ppt). The Y expands eastward and also, in part, deeper to the ECS bottom, with a temperature of 22.0°C and a salinity of less than 32.0 ppt during summer. Part of the northwest ECS bottom is covered by Yellow Sea bottom cold water mass (YC) with temperature of 7.0–14.0°C and salinity of 32.5–34.0 ppt in summer, which strongly impacts the ECS fishery.

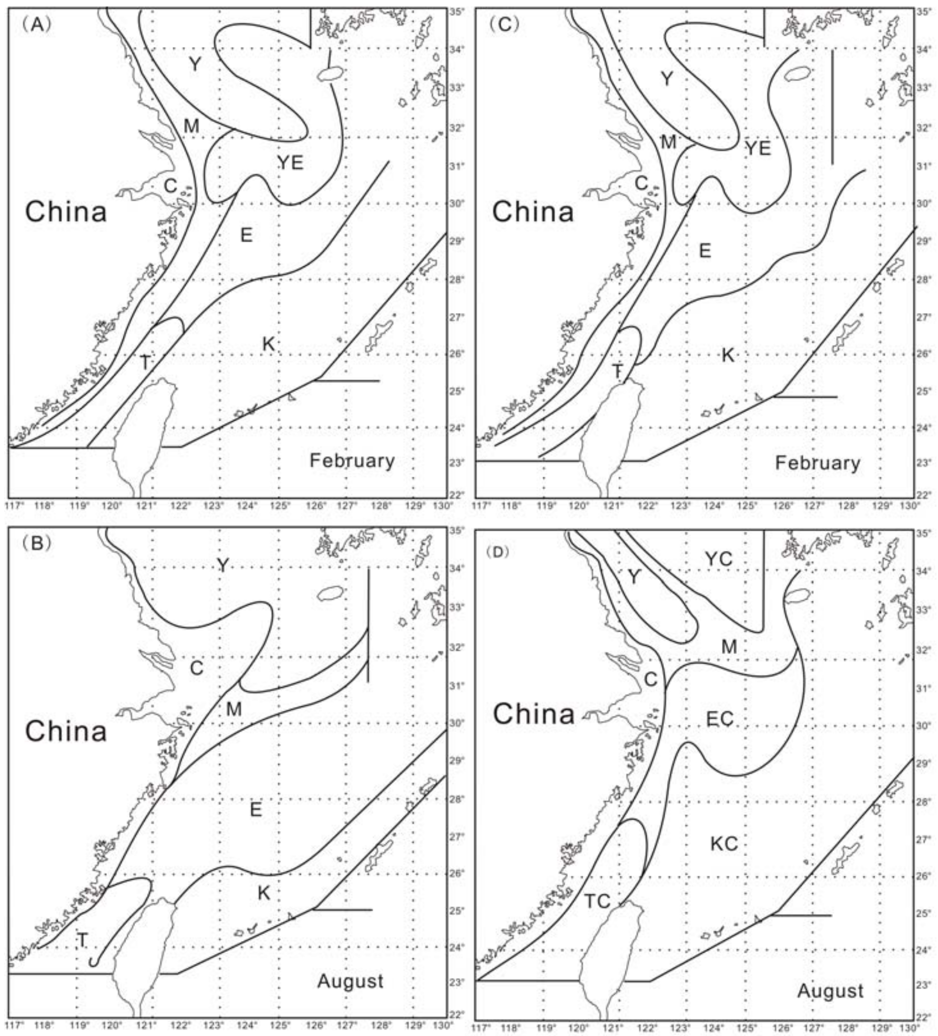


Figure 4. Distribution of water masses in bottom (A & B) and surface (C & D) layers in the ECS.
K - Kuroshio surface water; KC - Kuroshio subsurface water; E - ECS surface water; EC - ECS bottom cold water; T - Taiwan Strait surface water; TC - Taiwan Strait bottom water; YE - Yellow Sea and ECS mixed water; Y - Yellow Sea surface cold water mass; YC - Yellow Sea bottom cold water mass; C - ECS coastal water mass; M – mixed and transitional water (Yang *et al*., 2001; Zheng *et al*., 2003; Hong and Yang, 2005)

The Yellow Sea and ECS mixed water (YE) is variable, distributed in the northeast part of the ECS in winter. It features strong vertical mixing in temperatures of 8.5–15.0°C and salinity of 32.5–34.0 ppt. Mixed and transitional water (M) normally occurs between the mixed modified water or coastal water mass (C).

Sea Surface Temperature

The spatial distribution of mean sea surface temperature (SST) in the ECS shows a decrease from southeast to northwest, which indicates the influence of the Kuroshio (Zeng *et al.*, 2006). The seasonal variation of SST is distinctive, as the ECS is located in subtropical and temperate climate zones, but annual variation is small due to the continual influence of the Kuroshio warm water current. The distribution of yearly variation in SST in the ECS shows the same trend as SST (Figure 5). Specifically, the yearly variation in the main part of the Kuroshio is the smallest (within 8°C); in the Taiwan warm current and Tsushima warm current zones it is slightly larger (8–14°C); in the Yellow Sea warm current zone and Taiwan Strait variation is 14–17°C and 11–17°C, respectively; and the maximum seasonal variation in SST in the Changjiang Estuary and along the northeastern coast of the ECS is 20–26.1°C.

Sediment types

Surface sediments of the East China Sea continental shelf fall into 9 categories (Figure 6): fine medium sand, medium fine sand, fine sand, silty fine sand, muddy silt, fine sandy silt, mud-silt-sand, muddy silt and silty mud, which are divided by the 50–60 m depth contour line into two east and west belts.

In the western belt, sediments are predominantly fine ooze and silt coming from the Yangtze River, Qiantang River and Oujiang River. Mud and sand coming from the Yellow Sea form sediments in the vicinity of the Yangtze River estuary and in the northeast part of the East China Sea. Sediments in the east belt consist primarily of fine sand originating from the shallow waters. Surface sediments on the continental shelf range from medium fine sands to silty mud. Sediments in the Okinawa Trough are primarily ooze.

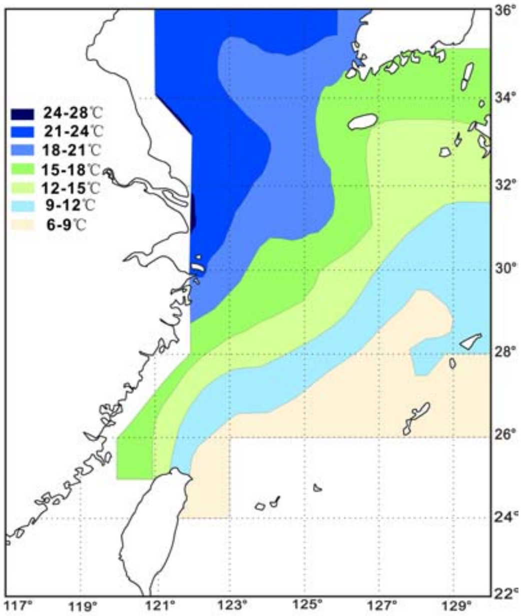


Figure 5. Yearly variation in SST in the ECS and Yellow Sea in 2005 (Shen *et al.*, 2006)

Nutrient levels

Marine nutrient levels (including inorganic nitrogen, phosphate and silicate) are closely related to primary productivity (Ning *et al.*, 1985). Recently, eutrophication has been increasing in parts of the ECS, and red tides are increasingly frequent. This has resulted in destroyed habitats and damaged fishery resources in the ECS (Zou *et al.*, 1983). The nutrient levels and changes in the ECS are affected by river runoff in coastal geo- and bio-chemical processes (Gu, 1991).

The inorganic nitrogen (IN) and nutrient level E (E = COD×IN×IP/4500, μmol/dm^3) distribution in the middle part of the ECS are given in Figure 7, where COD is chemical oxygen demand and IP is inorganic phosphorus. Values of E in the ECS are between 0.01 and 2.62 with an average of 0.28, which indicates that most of the ECS is still oligotrophic.

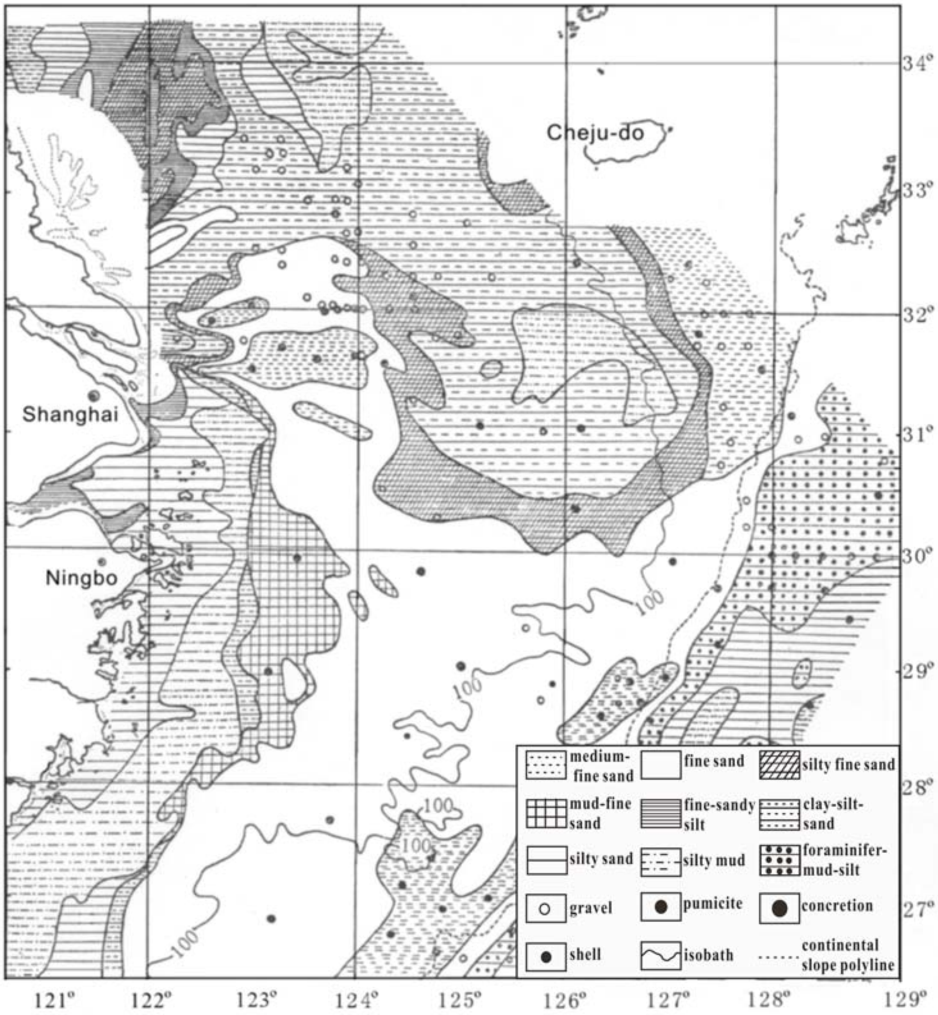


Figure 6. Sediment composition of the East China Sea

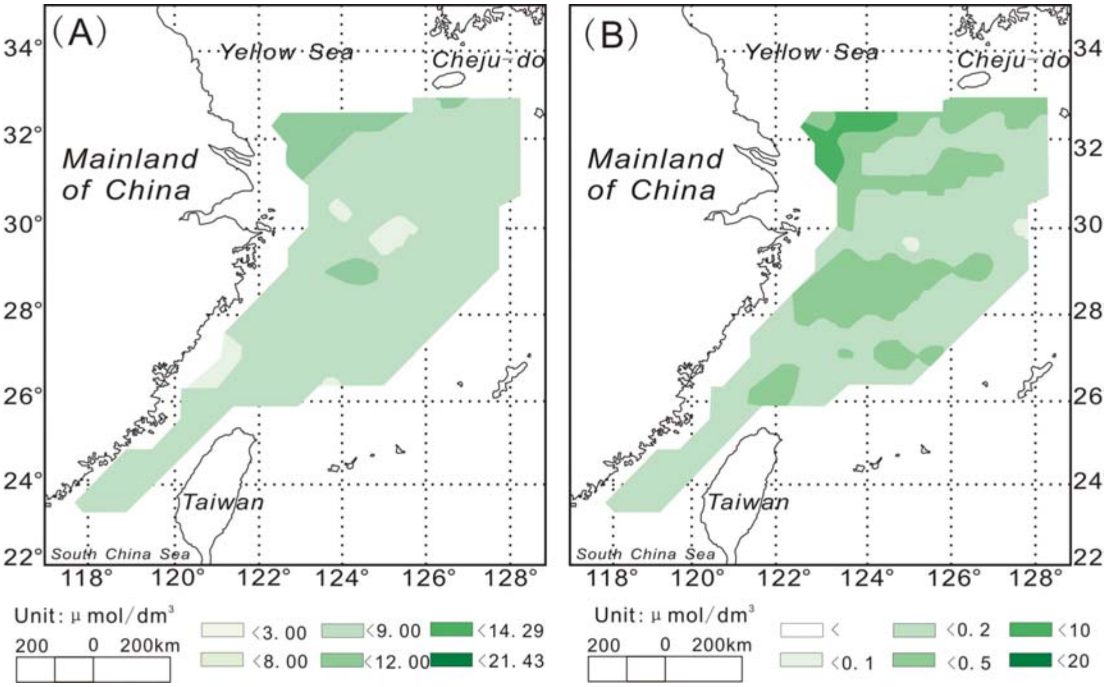


Figure 7. The inorganic nitrogen (A) and nutrient level E (B) distribution in the ECS (Zheng *et al.*, 2003)

SPATIAL MODELLING OF FISHERY MANAGEMENT SCENARIOS IN THE ECS

The ECS supports a highly productive fishery and is rich in biodiversity. In 2002 landings from the Chinese ECS accounted for over 7% of reported global landings. Economic development and population growth in China over the last four decades have led to intensified anthropogenic impacts on the ECS, including impact on fishing stocks and biodiversity. In response, the government of the People's Republic of China has introduced a range of spatial management measures including marine protected areas (MPAs), fishery protected areas (FPAs) and large-scale seasonal spatial fishing closures.

In order to examine optimal management with sustainable development and spatial fishery management, a spatial ecosystem model (Ecospace) of the ECS was developed to examine the effects of the current management framework. Ecospace is a dynamic and spatial ecosystem modeling tool that is especially effective for fishery and MPA management exploration (Christensen *et al.*, 2005). Spatial information on environmental factors and resources are integrated into Ecospace in order to develop a non-spatial Ecopath and Ecosim model into a spatially explicit ecosystem simulation. This model is developed to simulate the large-scale spatial closures and offshore fishery boxes in the ECS.

Base map

The base map is set up as a grid with 48 columns and 38 rows. The length of each cell is 25.8 km. The northwestern corner of the base map is located at 33°N and 117°W.

Habitat definition

Five habitats (Figure 8) have been defined based on the distribution of water mass, water depth, bed sediment, water temperature, salinity and nutrient level. These are:

H1: Alongshore current (C): The habitat C covers the alongshore currents and is also characterized by low salinity of 28.4 ppt in summer to 30.4 ppt in winter, remarkable inter-annual variation of water temperature from 11.59°C in winter to 24.5°C in summer, with high turbidity and nutrient levels over the sediments, which are composed of mud, silts and fine sands.

The alongshore current area on the continental shelf of the ECS provides spawning grounds for many species with high economical value, such as hairtail (*Trichiurus lepturus*) and large yellow croaker (*Larimichtys crocea*). There are 17 national nature reserves and 5 special marine protected areas in this habitat. Since 1955, China established a prohibited fishing line along the 50 m water depth contour, inside which trawl fishing is prohibited and other fishing activities are limited, in order to protect the coastal fishery resources and spawning ground environment. The waters west of the prohibited fishing line are used here as habitat C, the alongshore current area.

H2: Mixed Yellow Sea and East China Sea (YE): Mixed water masses are formed in the northwestern area of the ECS continental shelf where the cold water from the Yellow Sea mixes with high salinity water from offshore in the ECS. This water mass features low temperatures ranging from 9.8°C in winter to 28.3°C in summer, high salinity ranging from 30.1 ppt in summer to 32.0 ppt in winter and sediments composed of mud and silts. The juvenile hairtail reserve that is closed to the trawl fleets during August, September and October is situated in this habitat.

H3: Warm water on the main continental shelf of the East China Sea (E): Warm water is pushed onto the main continental shelf of the ECS by the Kuroshio Current from the south. The temperature ranges from 13°C in winter to 29°C in summer, salinity ranges from 33 ppt in summer to 32.0 ppt in winter and sediments are composed of fine sands and silts. This habitat was assigned to most of the fish functional groups. The reserve for spawning hairtail, which is closed to trawl fishing during May and June, is located in this habitat.

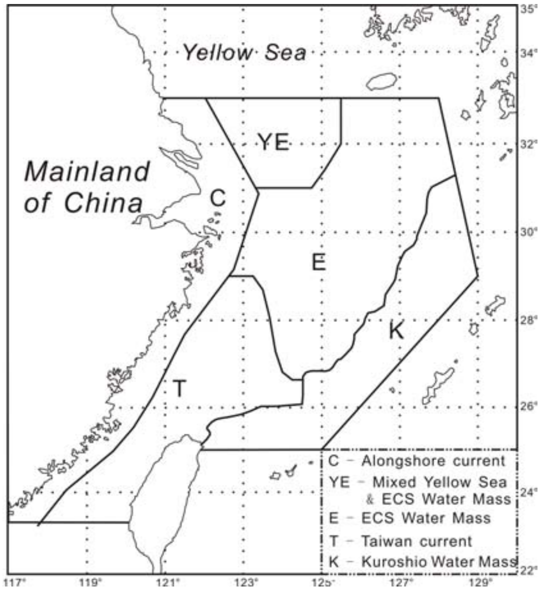


Figure 8. Habitats defined in the ECS Ecospace model

H4: Taiwan warm water (T): The Taiwan warm current is characterized by high salinity and temperature and the high transparency of its water. The inter-annual variation of temperature and salinity of the Taiwan current is smaller than in the alongshore current. The temperature ranges from 17.9 to 19.6°C in winter to 28–29°C in summer, salinity ranges from 31.0 to 34 ppt in winter to 33.1–34.2 ppt in summer, and sediments are composed of fine sandy silts and silty fine sand.

H5: Kuroshio current (K): The 200 m depth contour defines the shelf break of the ECS. The Kuroshio mainly influences the water east of the shelf break line. The Kuroshio is characterized by high but steady salinity and temperature. The temperature ranges from 20°C in winter to 29–30°C in summer, salinity ranges from 34.5 ppt in winter to 34 ppt in summer and sediments are composed of muddy silt sands and silty mud, shells, and silty sand.

Habitat assignment

The habitats of the 40 functional groups are based on the biomass distribution map of the fishery survey data from 1997 to 2000 (Zheng *et al.*, 2003). The habitats of the remaining 5 groups, the sea birds, sea turtles, marine mammals, *Seriola lalandi* and *Acipenser sinensis,* were based on the records of fisheries and surveys (Table 2) in ships' logs and other media sources, including newspapers and the internet.

Base dispersal rate, migration and advection

Due to the lack of specific information on dispersal, the base dispersal rates have been set according to the general scheme used by Zeller and Reinert (2004). Therein, the dispersal rates of functional groups are set according to their general type: marine mammals, 300 km·yr^{-1}; sea birds, 300 km·yr^{-1}; pelagic fish, 300 km·yr^{-1}; demersal fish, 30 km·yr^{-1}; benthic invertebrates, 3 km·yr^{-1}; plankton, 300 km·yr^{-1}; detritus, 3 km·yr^{-1}; turtles, 300 km·yr^{-1}; and pelagic invertebrates, 300 km·yr^{-1} (Table 2).

The only modification to this scheme is for *Coilia*, one of the main target small pelagic fishes of the Yangtze River estuary. Its distribution is limited to nearshore and coastal waters, and they migrate to estuaries in the breeding season. The base dispersal rate of *Coilia* is set at the reduced level of 150 km·yr^{-1}.

Twenty-four of the groups undergo seasonal migrations (Table 2), which allows the groups to be subject to fitness-driven dispersal and also allows the definition of seasonal migration patterns in the base map to be applied. Twenty-one of the groups had seasonal dispersal patterns defined on the base map (Appendix A) according to the survey results (Zheng *et al.*, 2003).

The advection field (Figure 9) for the ECS Ecospace model has been set according to the ECS flow field distribution of average depth in summer under wind stress (Lin, 2004). Large jellyfish, zooplankton, heterotrophic bacteria, phytoplankton and detritus are set as advected groups.

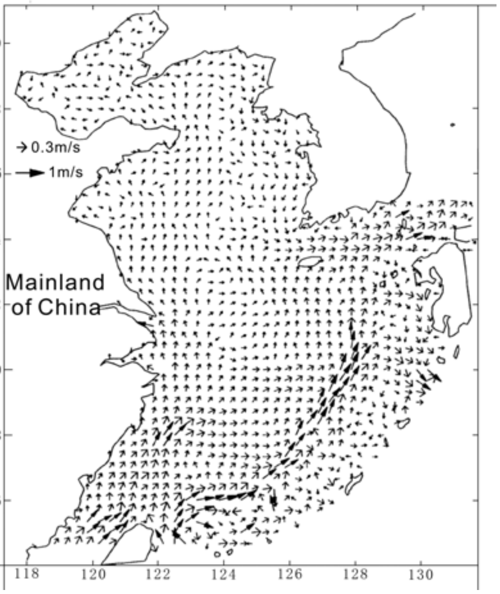


Figure 9. Advection field for the ECS Ecospace model based on Lin (2004).

Locations of MPAs, FPAs and seasonal spatial fishing closures

The government of China has established a range of spatial fishery management measures, which are outlined below, noted where they have been incorporated into the model.

Prohibited fishing line

The alongshore current area on the continental shelf of the ECS provides a natural spawning ground for many species of high economical value, such as hairtail and large yellow croaker. China set the prohibited fishing line along the 50 m depth contour in order to protect the coastal fishery resources and spawning ground environment (Figure 10). West of the line there is a permanent ban on fishing with trawls, light purse seine nets and entangling nets.

Marine protected areas (MPAs)

Seventeen national nature reserves and 5 special marine protected areas (Figure 10) have been established west of the prohibited fishing line. This excludes the nature reserves in the Taiwan district. These protected areas are not large enough to be represented on the Ecospace model base map, so they are not incorporated into this study.

Fishery protected areas (FPAs)

Three FPAs were created in the ECS by China during the 1980s (Figure 10). The first two FPAs were established in 1981 and are closed to trawl fishing from August to October every year to protect juveniles of large yellow croaker and hairtail. The third FPA was established in 1988 and is closed to trawling from May to June to protect spawning hairtail.

Summer closure area and duration

The summer closed fishing area in the ECS was established in 1995 and operates between 27°N and 35°N. In this area trawl and stow net fleets are prohibited from fishing between July 1st and August 31st each year. In 1998 the location was enlarged to 26°N–35°N, the prohibited fishing fleets were extended to include shrimp trawlers and the duration was prolonged from June 16th to September 16th.

The summer closed fishing area was also extended to the South China Sea, the Yellow Sea and the Bohai Sea. Details of the summer fishing closures in 2006 are shown in Table 3.

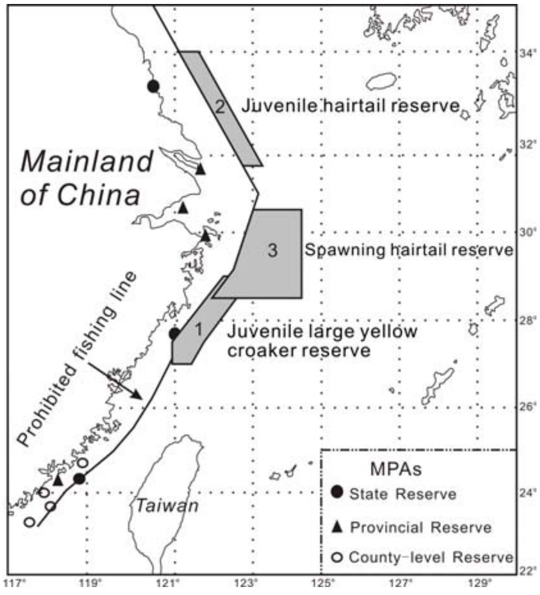


Figure 10. Prohibited fishing line, MPAs and 3 FPAs in the Chinese ECS

Table 2. Habitat assignment, base dispersal rates, advection and migration of the functional groups.

Group\Habitat	All	C	YE	E	T	K	Base dispersal rate (km·year^{-1})	Advected	Migrating
Marine mammals	+						300		+
Sharks and rays		+		+	+	+	300		+
Lophius litulon		+	+	+			30		
Sphyraena		+		+	+	+	300		
Seriola lalandi				+	+	+	300		+
Larimichthys crocea (2+)			+	+	+		30		+
Saurida		+		+	+	+	30		
Sea turtles	+						300		+
Branchiostegus			+	+	+	+	30		
Trichiurus lepturus (2+)	+						30		+
Scomberomorus niphonius				+			300		+
Nibea albiflora		+	+	+	+		30		+
Seabirds	+						300		
Acipenser sinensis		+	+	+	+		30		+
Thamnaconus				+	+	+	30		+
Harpadon nehereus		+	+	+			30		+
Pennahia argentata		+	+	+	+		30		+
Pleuronectiform				+	+	+	30		
Champsodon capensis	+						30		
Priacanthus macracanthus				+	+	+	30		
Sparidae				+	+	+	30		
Coilia		+	+				150		+
Large jellyfish		+	+				300	+	
Cephalopods	+						300		+
Larimichthys polyactis		+	+	+			30		+
Larimichthys crocea (1)			+				30		+
Argentinidae				+		+	300		
Shrimps	+						3		+
Small demersal fishes	+						30		
Stromateoidae		+	+	+			300		+
Crabs	+						3		
Engraulis japonicus	+						300		+
Scomber japonicus	+						300		+
Trachurus japonicus	+						300		+
Decapterus maruadsi	+						300		+
Small pelagic fishes	+						300		+
Setipinna taty		+	+				300		
Macrobenthic	+						3		
Sardinae		+		+	+		300		
Trichiurus lepturus (1)		+		+	+		30		+
Microbenthic	+						3		
Zooplankton	+						300	+	
Heterotrophic bacteria	+						300	+	
Phytoplankton	+						300	+	
Detritus	+						3	+	

Table 3. Summer fishing closures in the ECS in 2006

No.	Region	Closed seasons	Closed fleets
1	117°E–120°E; 22.5°N–23.5°N	June 1st to Aug. 1st	Trawl, Stow net & Purse seine
2	23.5°N–26.5°N	June 1st to Aug. 1st	Trawl & Stow net
3	26.5°N–35°N	June 16th to Aug. 16th	Shrimp trawl
4	26.5°N–35°N	June 16th to Sep. 16th	Trawl & Stow net

Allocation of fleets

Six fleets were included in the ECS Ecospace model and allocated to habitats as shown in Table 4.

Table 4. Allocation of 6 fleets in the ECS

Fleet/Habitat use:	C	YE	E	T	K	Fleet/Habitat use:	C	YE	E	T	K
Trawl		+	+	+	+	Purse seine			+		+
Stow net	+	+	+			Shrimp trawl		+	+	+	
Drift gill net	+	+		+		Taiwan and Japanese fleets			+	+	+

Scenarios

The ECS Ecospace model was developed to allow exploration of different future spatial management scenarios and examination of the potential impacts of present spatial management scenarios. Several scenarios based on the present arrangement of spatial management regulations will be run with and without specific regulations to try to establish the effects of the present spatial management regulations and from this elucidate the potential benefits of further future spatial management regulations.

ACKNOWLEDGEMENTS

We are grateful for financial support from the Sixth European Framework Program and the INCOFISH project (EC contract #003739), and management support by Dr. Froese Rainer, Dr. Silva Opitz, and Ms. Crispina Binohlan. We are also greatly thankful to Dr. Villy Christensen for technical support.

REFERENCES

Christensen, V.C., Walters, J. and Pauly, D. 2005. Ecopath with Ecosim: a User's Guide. Fisheries Centre, University of British Columbia, Vancouver. November 2005 edition, 154 p.

Deng, B., Zhang, J. and Wu, Y. 2006. Recent sediment accumulation and carbon burial in the East China Sea. Glob. Biogeochem. Cycl., 20(3), GB3014.

Gu, H.K. 1991. Marine chemistry of the Boihai Sea, Yellow Sea and East China Sea. Science Press, Beijing.

Hong, B. and Yang, H. 2005. The Application of Fisher's Stepwise Discriminant Analysis to the Water Mass in the East China Sea. Mar. Fish., 27(2): 143-149 (in Chinese, with English abstract).

Jiang, H., Cheng, H.Q., Shen, F., Xu, H.G., Arreguín-Sánchez, F. and Le Quesne, W.J.F. 2006. Preliminary study on fishery impact by trophic structure and flow analysis in the East China Sea. Proceedings of the second international conference on estuaries and coasts (ICEC-2006), 537-543.

Li, G.S., Wang, F., Liang, Q. and Li, J.L. 2003. Estimation of Ocean Primary Productivity by Remote Sensing and Introduction to Spatio-temporal Variation Mechanism for the East China Sea. Act. Geogr. Sin., 58(4): 483-493 (in Chinese, with English abstract).

Lin, J.G. 2004. Numerical simulation of three-dimensional current field and temperature field of the Bohai Sea, Yellow Sea and the East China Sea. Master degree thesis. Ocean University of China, Qingdao, China, pp. 20.

Liu, K.K., Pen, T.H., Shaw, P.T. and Shiah, F.K. 2003. Circulation and biogeochemical processes in the East China Sea and the vicinity of Taiwan: An overview and a brief synthesis. Deep Sea Res., Part II, 50, 1055-1064.

Liu, K.K., Tang, T.Y., Gong, G.C., Chen, L.Y. and Shiah, F.K. 2000. Cross-shelf and along-shelf nutrient fluxes derived from flow fields and chemical hydrography observed in the southern East China Sea off northern Taiwan, Cont. Shelf Res., 20, 493-523.

Liu, S.X., Shen, X.Q., Wang, Y.Q. and Han, S.X. 1993. Preliminary analysis of distribution and variation of perennial monthly mean water masses in the Bohai Sea, Yellow Sea and East China Sea. Act. Ocean. Sin., 15(4): 1-11 (in Chinese).

Ning, X.R., Liu, Z.L. and Hu, Q. X. 1985. The distribution of chlorophyll-a and primary productivity in the coastal upwelling zone of Zhejiang Province. Acta Oceanologica Sinica, 7(6): 751-762 (in Chinese, with English abstract).

Shen, J.H., Zhou, S.F. and Dong, Y.L. 2006. Analysis on SST structure of the East China Sea and Yellow Sea in 2005. Mar. Fish., 28(1): 30-36 (in Chinese, with English abstract).

Su, J.L. 2001. A review of circulation dynamics of the coastal oceans near China, Acta Oceanol. Sin., 23(4), 1-16.

Tang, T.Y., Tai, J.H. and Yang, Y.J. 2000. The flow pattern north of Taiwan and the migration of the Kuroshio, Cont. Shelf Res., 20, 349-371.

Yang, H., Zhang, S.Y., Dai, X.J., Jin, C.F., Wu, W.Z. and Sui, H.B. 2001. Characteristics of water masses and its influence on mackerel scad fishery in the East China Sea in summer. J Fish. China, 25(3): 209-214 (in Chinese, with English abstract).

Zeng, G.E., Lian, S.M., Cheng, X.H., Hua, Z.L. and Qi, Y.Q. 2006. EOF Analysis of Intra-seasonal Variabilities of SST in the East China Sea and Yellow Sea. Adv. Mar. Sci., 24(2): 146-155 (in Chinese, with English abstract).

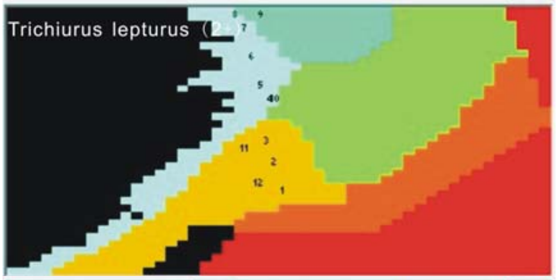
Zeller, D. and Reinert, J. 2004. Modelling spatial closures and fishing effort restrictions in the Faroe Islands marine ecosystem. Ecol. Mod. 172:403-420.

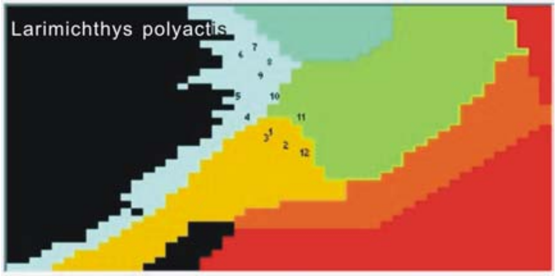
Zheng, Y.J., Chen, X.Z., Cheng, J.H., Wang, Y.L., Shen, X.Q., Chen, W.Z. and Li, C.S. 2003. Living Resources and Environments within the East China Sea. Shanghai Science and Technology Press, Shanghai, China, 852 pp. (in Chinese).

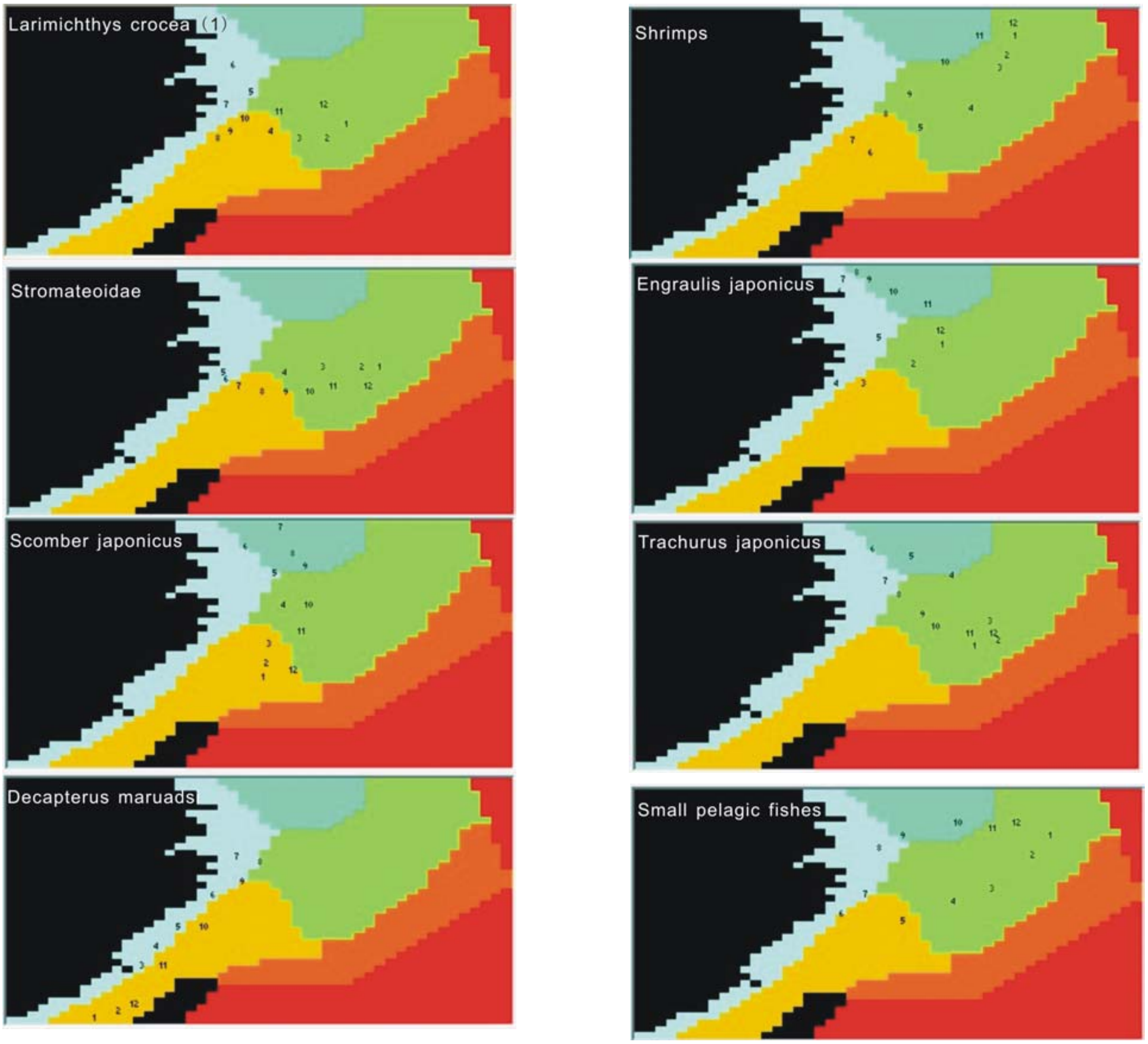
Zou, J.Z., Dong, L.P. and Qin, B.P. 1983. Primary discuss on the eutrophication and red-tide problems in Bohai bay. Mar. Env. Sci., 2(2): 41-54 (in Chinese, with English abstract).

Appendix A: Seasonal migration patterns

The figures below indicate the seasonal migration patterns defined for 21 functional groups that were set as undergoing seasonal migrations.






Larimichthys crocea (1)
Shrimps
Stromateoidae
Engraulis japonicus
Scomber japonicus
Trachurus japonicus
Decapterus maruads
Small pelagic fishes

AN ECOSYSTEM SIMULATION MODEL OF THE NORTHERN GULF OF CALIFORNIA[1]

Diego Lercari[a, b], Francisco Arreguín-Sánchez[a] and Will Le Quesne[c]
[a] - CICIMAR-IPN A.P. 592, La Paz 23000, Baja California Sur, Mexico
[b] - UNDECIMAR, Facultad de Ciencias. Iguá 4225, Montevideo 11400, Uruguay
[c] - School of Marine Science and Technology, University of Newcastle,
Ridley Building, Newcastle upon Tyne NE1 7RU, UK

ABSTRACT

The Northern Gulf of California is an important Mexican aquatic ecosystem both in terms of biodiversity and also in valuable fishing resources. Two highly endangered, endemic species inhabit the area and three Marine Protected Areas (MPAs) are already implemented. Some conflicts are evident between conservation and exploitation by multi-species and multi-sector fisheries. In this context, ecosystem trophic models coupled with temporal and spatial dynamics simulations are considered important tools to test temporal and spatial management alternatives in the fishing effort allocation.

In this report, we show several ecosystem model results and describe the construction of the spatial ecosystem model considering today's fishing spatial allocation. Ecopath results highlight the role of the endangered species, top predators and fleets on ecosystem components. Ecosim outcomes show the effects of temporal fishing effort increments and decrements on the two endangered species. The simulation of no fishing illustrates the recovery potential of these species while the simulation of doubling fishing points up the risk of an even more drastic decrease of the biomass of the endangered species. Finally, the implementation of the Ecospace model permits a satisfactory representation of the known spatial distribution of the model components. This allows the setting of possible MPA scenarios in order to test the ecological effects of diverse spatial fishing allocation designs.

INTRODUCTION

The Gulf of California is a long, narrow gulf (1,500 km long by 175 km wide) opening into the Pacific at its southern end. Physical and biological characteristics vary significantly along the Gulf; this study focuses particularly on the northern Gulf of California (NGC), an area of c.a. 36,000 km^2 partially isolated from the rest of the Gulf by the Angel de la Guarda and Tiburón islands, north of 29°N (Figure 1). It is characterized by a temperate climate and is nutrient enriched (Lluch-Cota, 2003). Upwelling occurs along the eastern coast of the northern Gulf of California in winter. This region shows the highest pigment concentrations of >10 mg·m^{-3} (Santamaría del Angel *et al.*, 1994) in the Gulf of California.

The northern Gulf of California is home to 2,257 invertebrate and 516 vertebrate species (including fishes, marine reptiles, marine mammals and seabirds). At least 138 of these species are endemic to the northern Gulf of California (Brusca *et al.*, 2004). A number of species are now comparatively rare, including the endangered *Totoaba macdonaldi*, the result of overfishing and habitat changes (Lercari and Chávez, 2007; Cisneros-Mata *et al.*, 1995), and the Gulf porpoise or vaquita (*Phocoena sinus*), the smallest of all cetaceans and among the most endangered species worldwide. Both species are listed as critically endangered in the IUCN Red List (IUCN, 2006). The vaquita's distribution is restricted to the northern Gulf of California and has a population of only around 600 individuals (Rojas Bracho and Jaramillo Legorreta, 2005). Only one pinniped species reproduces inside the northern Gulf (*Zalophus californianus*); other species are recorded but are infrequent visitors. Five endangered species of turtle frequent the Gulf. A number of waterbirds are in decline through the loss of habitat (Mellink *et al.*, 1997).

---

[1] Cite as: Lercari, D., Arreguín-Sánchez, F. and Le Quesne, W. 2007. An ecosystem simulation model of the northern Gulf of California, p. 100–113. *In*: Le Quesne, W.J.F., Arreguín-Sánchez, F. and Heymans, S.J.J. (eds.) INCOFISH ecosystem models: transiting from Ecopath to Ecospace. Fisheries Centre Research Reports 15(6). Fisheries Centre, University of British Columbia [ISSN 1198-6727].

Fishing in the northern Gulf of California is dominated in terms of both fleet size and catch by shrimp fisheries. Two main shrimp fleets operate in the NGC: the commercial shrimp trawl fishery and a small-scale artisanal fishery operating with fibreglass boats (pangas). The commercial shrimp fleet (approximately 100 boats) exploits blue and brown shrimp from depths of 10–80 m. The artisanal fleet is composed of approximately 800 boats (≤6 m long) that target both shrimps and fishes. Until recently, catch was comparable for both fleets; however, as of 2002 the contribution of the artisanal fleet to total catch has increased. Species that present a significant contribution to landings in the northern Gulf of California other than shrimp are *Cynoscion othonopterus* (golfina croaker), *Dasyatis brevis* (manta ray), *Paralichthys aestuarius* (flounder), *Mustelus lunulatus* and *Rhizoprionodon longurio* (sharks).

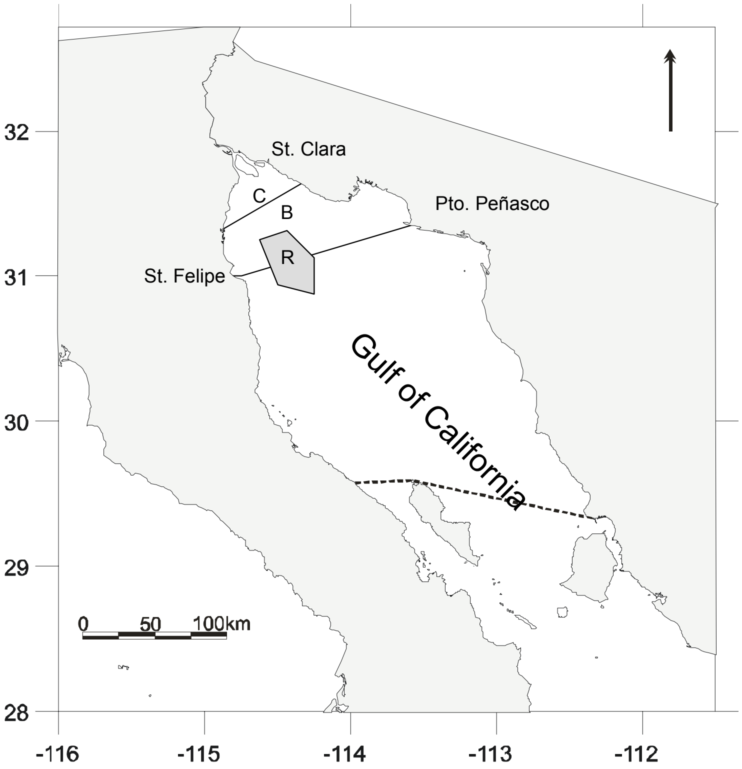


Figure 1. Map of the NGC showing the main fishing harbours and 3 MPAs (C - core zone of the UGCCRDBR; B - buffer zone of the UGCCRDBR; R - vaquita refuge).

Spatial restrictions on fishing have been used in the Gulf of California since 1970 to both enhance shrimp fishing and conserve biodiversity and/or particular species. Fishing-related MPAs (e.g., shrimp trawling exclusion coastal area) are managed by the Ministry of Agriculture, Ranching, Rural Development, Fisheries, and Food Supply (SAGARPA), while conservation-associated MPAs are managed by the Ministry of Environment and Natural Resources (SEMARNAT). Inside this Ministry, the CONANP (National Commission of Natural Protected Areas) regulates and manages most Mexican protected areas, including marine protected areas. Several protected areas exist in the Gulf of California, usually with both marine and terrestrial components, but none has been planned to explicitly consider spatial fisheries management.

The Upper Gulf of California and Colorado River Delta Biosphere Reserve (UGCCRDBR), established in 1993, is the biggest MPA in the NGC. Principal reasons for establishment for the marine portion of the UGCCRDBR were conservation of the vaquita, maintenance of biodiversity and fisheries management. The highly endangered Gulf of California porpoise (vaquita or *Phocoena sinus*) lives only in the northern-most reaches of the Upper Gulf of California, with a population size of only 567 individuals (Jaramillo Legorreta *et al.*, 1999) making it in the top 4 most endangered marine mammals. Morover, the UGCCRDBR region is an area of diverse flora and fauna inhabited by 1,048 species of invertebrates, 43 of which are endemic. In addition to a rich and diverse invertebrate fauna, the UGCCRDBR contains 15 species of marine mammals (43% of the entire Gulf marine mammal fauna) and 230 species of marine fishes, including the endangered totoaba and the currently over-fished Gulf corvina.

The constant entanglement of vaquitas and the non-reappearance of big totoabas suggest that the basic aims of the MPA have not been fulfilled. This realization has contributed to the expansion of the area protected to fishing to protect more the vaquita population (D'Agrossa, 1995; D'Agrossa *et al.*, 2000). The new refuge for the protection of the vaquita has been recently approved by law (DOF, 2005). The area of the Vaquita Conservation Refuge (VCR) includes 897.09 km^2 of the western portion of the UGCCRDBR buffer zone, near to the coast of the State of Baja California and extends out beyond the reserve boundary a further 366.76 km^2 (Anónimo, 2002). The vaquita distribution extends beyond the UGCCRDBR, but it was considered necessary to establish additional protection of this aquatic species (Jaramillo Legorreta *et al.*, 1999).

There are serious conservation concerns in the NGC, and simultaneously, there are important fisheries. Yet, no formal studies have been conducted using spatial models of the interaction between conservation and exploitation. Given these circumstances, the application of spatial ecosystem modelling methods and dynamic simulations in the NGC can contribute to the analysis of the ecological consequences of the spatial fishing restrictions. In particular, some basic questions could be explored using trophic models as analytical tools. For example: Are the MPAs in the NGC effective in enhancing the vaquita and totoaba populations? Which MPA designs could optimize the vaquita and totoaba conservation? How could the potential enhancement impact the catch and value obtained by the different fleets?

The main aim of this work is to explicitly account for the spatial distribution of the present-day NGC ecosystem components and to perform simulations, considering diverse scenarios of alternative configurations of the MPA of the region. To do this, we start with a previously constructed Ecopath trophic model and a validated Ecosim scenario (Morales-Zarate *et al.*, 2004; Lercari, 2006). In this work, we review some Ecopath and Ecosim results; particularly, we describe the development of an Ecospace scenario representing the current MPAs and fisheries operation in the NGC.

DESCRIPTION OF MODEL COMPONENTS: ECOPATH

Input data

The mass-balanced model of the NGC ecosystem considers 37 functional groups: 4 marine mammals, 2 birds, 18 fishes, 9 invertebrates, 1 zooplankton, 1 phytoplankton, 1 macroalgae and 1 detritus. These groups represent the most abundant species in the NGC as well as groups composed of only one important species. This approach allows us to focus on modelling groups with economic, social or ecological value: *Totoaba macdonaldi, Phocoena sinus*, *Zalophus californianus* and the shrimps (*Farfantepenaeus californiensis* and *Lytopenaeus stylirostris*). In addition, juvenile stages were added as distinct functional groups for *Totoaba macdonaldi, Farfantepenaeus californiensis* and *Litopenaeus stylirostris,* and thus consider trophic ontogenic changes in these valuable species. Eight fleets were included in the model (Table 1) considering the catch and the bycatch of 3 different gears in 3 ports: the industrial trawl, the small-scale shrimp fishery and the small-scale finfish gillnet gear.

Extensive details of Ecopath input data can be found in the literature (Morales-Zarate *et al.*, 2004; Lercari, 2006; Lercari and Arreguín-Sánchez, *in prep* (submitted to AQMFE)).

Table 1. Fleets and gears operating in the NGC included in the Ecospace model.

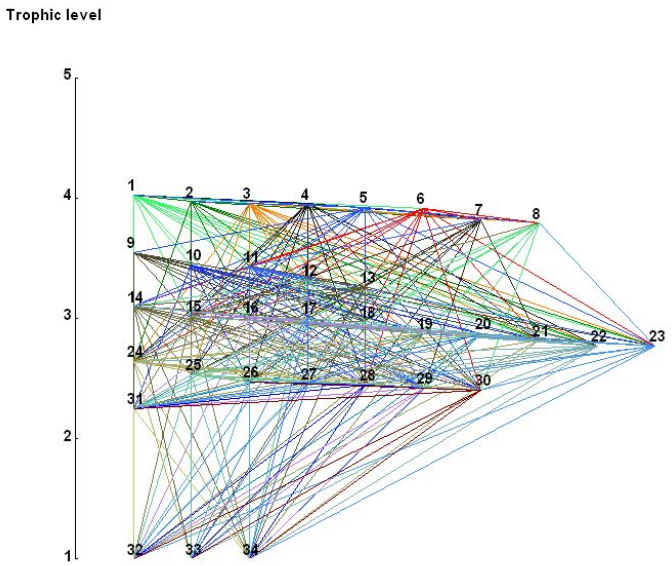
Model Fleet #	Gear	Port
1	Shrimp trawl	Puerto Peñasco
2	Shrimp artisanal	Puerto Peñasco
3	Gillnets artisanal	Puerto Peñasco
4	Shrimp trawl	San Felipe
5	Shrimp artisanal	San Felipe
6	Gillnets artisanal	San Felipe
7	Shrimp artisanal	Santa Clara
8	Gillnets artisanal	Santa Clara

Model balancing

The constructed model represents the ecosystem state for the decade 1990–2000, as the majority of data were obtained in this decade. Once the input information was collected, mass balance was obtained by slightly adjusting input data (mainly DC_i) to obtain $EE_i<1$ for all functional groups. After balancing the model, the Ecoranger routine was applied (Christensen and Pauly, 1992) to incorporate uncertainty in the data. Model resampling was conducted using 10% variability on all the input data and a normal probabilistic density distribution. Mass balance and physiological constraints (e.g., $0<EE<1$), were used to test for model consistency, and the most suitable run (among 3000) was chosen using a least square criterion with all the input values. Physiological restrictions were also checked to be fulfilled. The information quality index (i.e., data pedigree *sensu* Funtowicz and Ravetz, 1990) obtained for the ecosystem model of the NGC was 0.51.

Ecosystemic description

Basic model parameterization results were shown in Lercari (2006) and Lercari and Arreguín (*in prep*). This report focuses the Ecopath results on the role and interaction of the model components (highlighting the endangered species) using the connectance estimation by group and fisheries. We show 4 examples of the Mixed Trophic Impacts analysis to stress the importance of top predators and different fishing fleets on all the modelled groups. Connectance diagrams for the complete ecosystem model are in Figure 2.

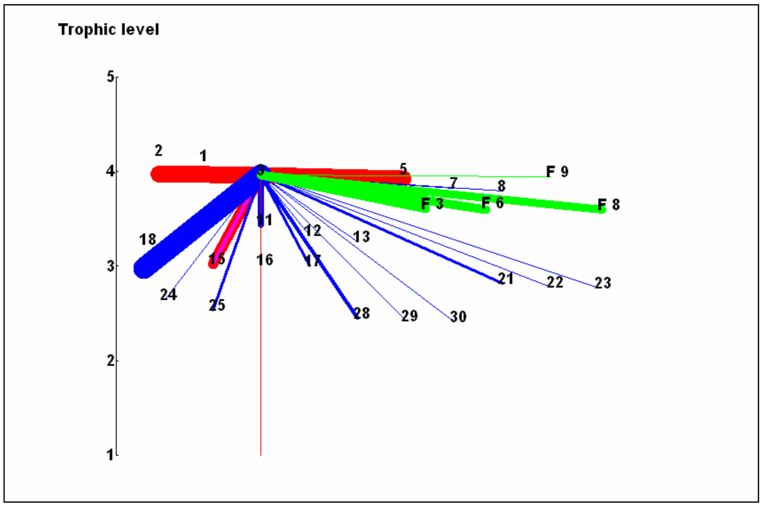


FUNCTIONAL GROUP	
1	Elasmobranchi (SHARKS)
2	*Zalophus californianus*
3	*Totoaba macdonaldi* (ADULTS)
4	Marine birds
5	Odontoceti
6	*Phocoena sinus*
7	*Totoaba macdonaldi* (JUVENILES)
8	Merluccidae
9	Mysticeti
10	Coastal birds
11	Sciaenidae
12	Rhinobatidae
13	Serranidae
14	Elasmobranchi (RAYS)
15	Other fishes
16	Haemulidae
17	*Sicyonia penicillata*
18	Small pelagics
19	*Farfantepenaeus californiensis* (JUVENILES)
20	*Litopenaeus stylirostris* (JUVENILES)
21	Cephalopoda
22	Flat fishes
23	Myctophidae
24	Mojarras
25	*Callinectes sp.*
26	Polychaeta
27	Stomatopoda
28	*Litopenaeus stylirostris* (ADULTS)
29	Benthic invertebrates
30	*Farfantepenaeus californiensis* (ADULTS)
31	Zooplankton
32	Phytoplankton
33	Macrophites
34	Detritus

Figure 2. Connectance diagram obtained for the Northern Gulf of California ecosystem. All the modelled groups are included.

Connectance (scaled by predation strength) of endangered groups is shown in Figure 3 for *Totoaba macdonaldi* and in Figure 4 for *Phocoena sinus*. Note the important predation produced by sharks, sea lions and dolphins on totoaba, while the predation strength of totoaba is mainly directed towards small pelagics and shrimps. Gillnets also have a large impact on this group.

In the case of vaquita, note the important predation produced almost exclusively by sharks. The predation strength of vaquita is directed towards various groups (small pelagics, serranidae, shrimps). Again gillnets have a large impact on this group.



Fleets	
F1	Peñasco Shrimp Trawl
F2	Peñasco Shrimp Artisanal
F3	Peñasco Gillnet
F4	St. Felipe Shrimp Trawl
F5	St. Felipe Shrimp Artisanal
F6	St. Felipe Gillnet
F7	St. Clara Shrimp Artisanal
F8	St. Clara Gillnet

Figure 3. Connectance diagram obtained for *Totoaba macdonaldi in* the Northern Gulf of California ecosystem. Connectance is scaled by predation strength (red = predators and blue = prey). Fisheries are represented by green lines. Functional groups are the same as in Figure 2.

Selected results of mixed trophic impact are shown for sharks and dolphins (Figure 5). The analysis shows a possible trophic cascade effect produced by these predators.

Sharks produce a negative impact on other top predators, which in turn results in a benefit for intermediate trophic level groups. On the other hand, dolphins produce a negative impact on sharks, which in turn benefits the other top predators of this system.

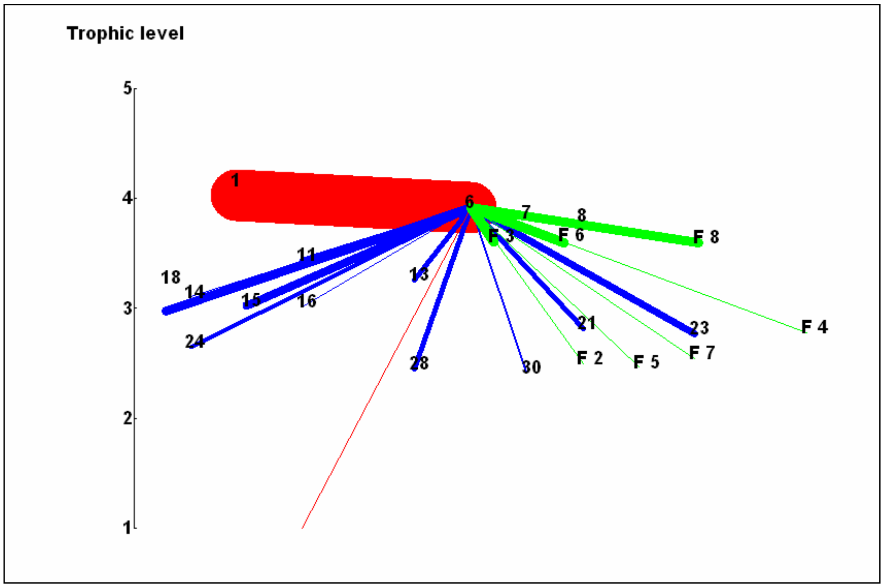


Figure 4. Connectance diagram obtained for *Phocoena sinus in* the Northern Gulf of California ecosystem. Connectance is scaled by predation strength (red = predators and blue = prey). Fisheries are represented by green lines. Functional groups are the same as in Figure 2; fleets are the same as in Figure 3.

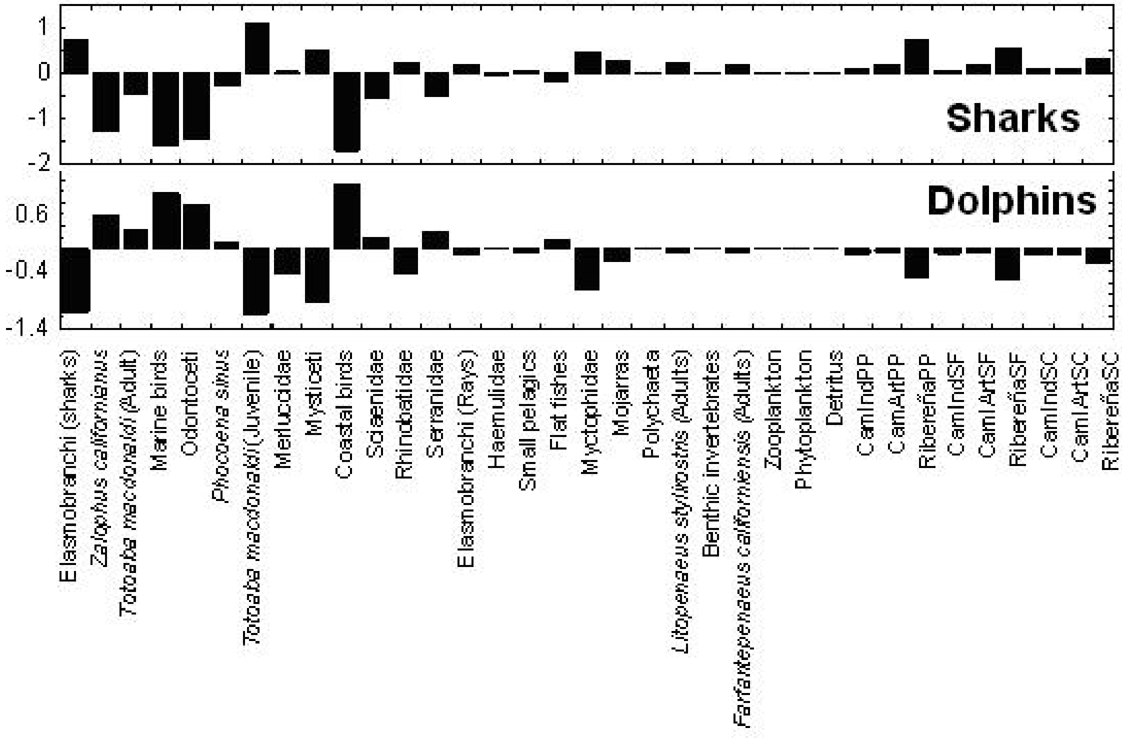


Figure 5. Examples of the Mixed Trophic Impacts analysis for the Northern Gulf of California model, showing the direct and indirect impacts produced by two top predator groups.

Selected results of mixed trophic impact are shown for an artisanal and an industrial fishing fleet (Figure 6). The analysis shows that the impact of the gillnets mostly affects the top predators while the shrimp trawl mainly affects the intermediate trophic levels. The impacts that the fleets (right side) produce on other fleets illustrates the conflict between different fishing activities in the Northern Gulf of California.

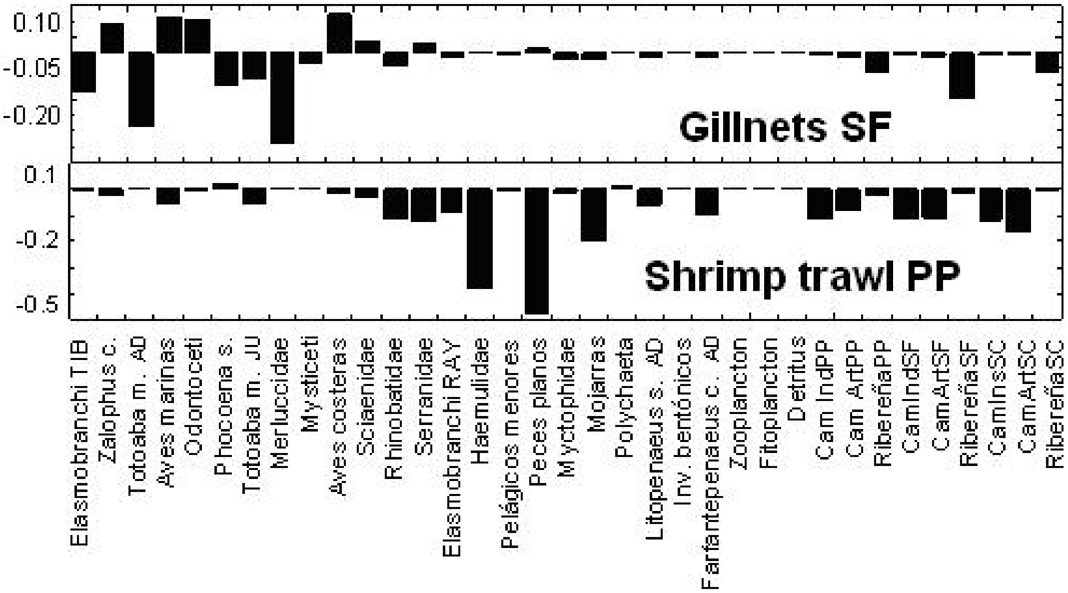


Figure 6. Examples of the Mixed Trophic Impacts analysis for the Northern Gulf of California model, showing the direct and indirect impacts produced by two fleets.

DESCRIPTION OF MODEL COMPONENTS: ECOSIM

Model independent data were used to fit the Ecosim vulnerability parameters through a least square algorithm. Time series of biomass, fishing effort and forcing factors were used as reference data to obtain a reasonable calibration of model backward predictions. This procedure provides a model validation, useful prior to the application of time dynamic simulations (Christensen and Walters, 2004).

We used 6 independent biomass time series for model prediction comparisons, i.e., historic totoaba CPUE from 1940 to 1975 (Ortiz, 2002), 2 shrimp CPUE from 1963 to 2004 (Calderon-Aguilera, *pers. com.*), and Californian sea lion biomass from 1979 to 2002 (Aurioles-Gamboa, *pers. com.)*. The Colorado River discharge time series and the Pacific Decadal Oscillation Index (PDOI) (Mantua *et al.*, 1997) were used as model forcing functions. These variables correlate with shrimp (Aragón-Noriega *et al.*, 1999) and totoaba biomass (Lercari and Chávez, 2007; Flanagan and Hendrickson, 1976), and with significant ecosystem changes (Lavin *et al.*, 1998; Rodríguez *et al.*, 2001).

Basic dynamic simulations

Two 20-year basic scenarios were simulated to assess the fisheries' effects on the endangered species. We simulated both the doubling of total fishing effort and the total cessation of fishing during the simulation period. Each scenario was tested assuming 4 ecosystem control settings (i.e., vulnerabilities configurations): top down (v = 4); bottom-up (v = 1); mixed default (v=2) and mixed by calibration (different v by groups).

Figure 7 shows the temporal biomass trajectories of totoaba adults (A), totoaba juveniles (B) and vaquita (C) resulting after 20 years of double fishing effort. In every case, the model predicts that the endangered species decreased, and in the extreme top-down controls, this species essentially disappeared. On the other hand, simulating a decrease of fishing effort showed that both endangered species have an important recovery potential, despite the strong differences between the vulnerability settings (Figure 8).

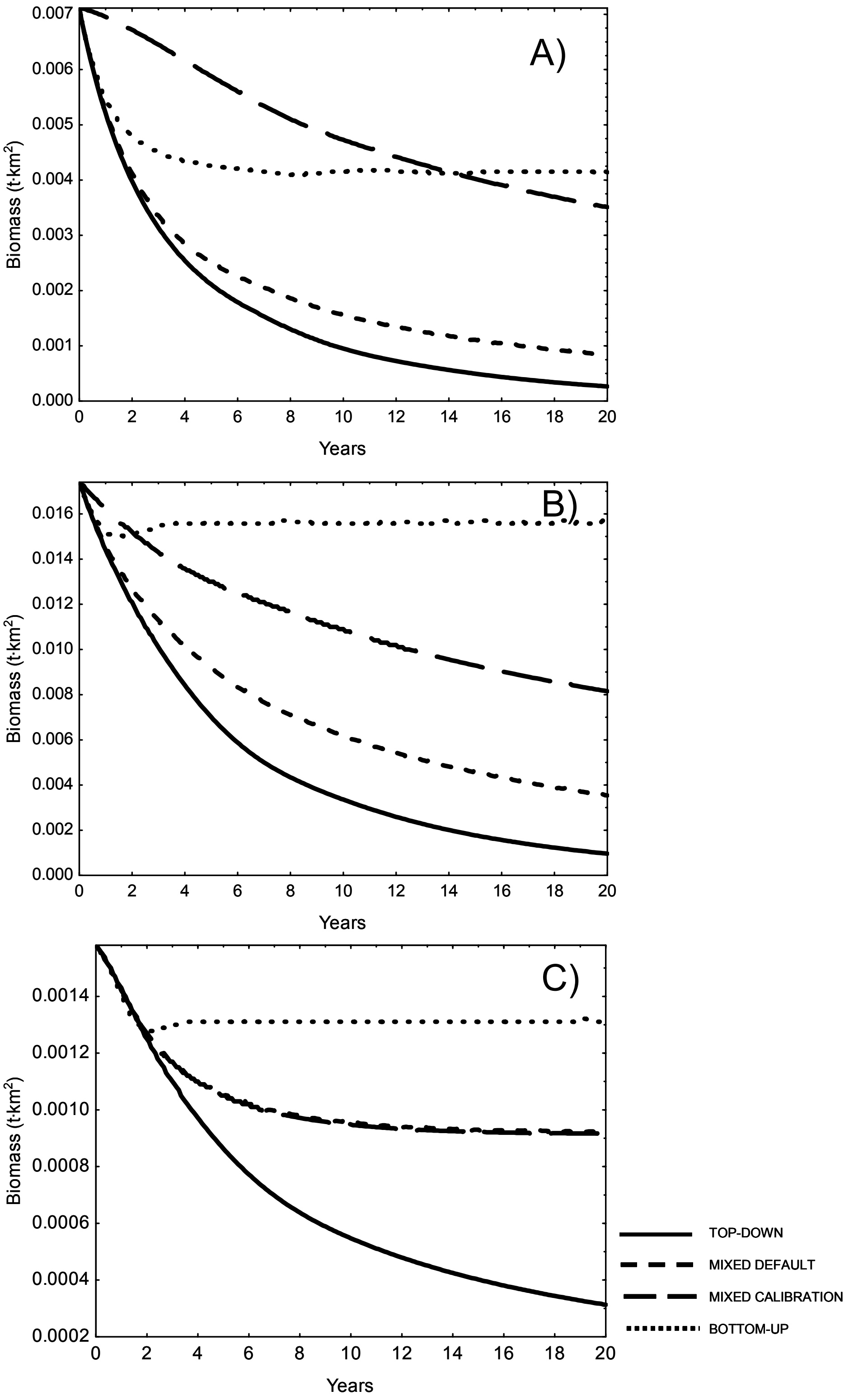


Figure 7. Biomass trajectories obtained after a simulated two-fold increase in total fishing effort. A) Totoaba adults; B) Totoaba juveniles; C) *Phocoena sinus*

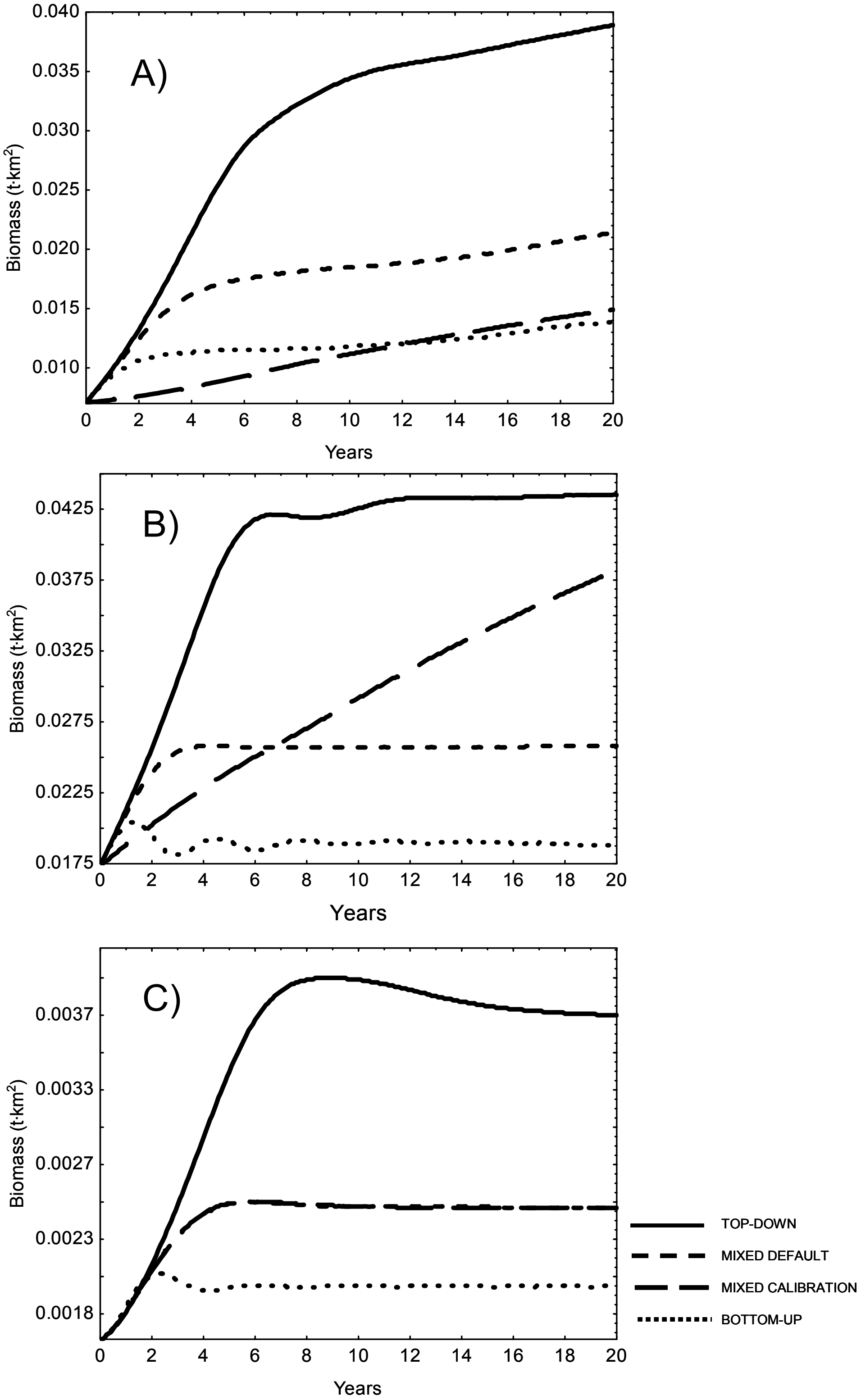


Figure 8. Biomass trajectories obtained after a simulated total cessation of total fishing effort. A) Totoaba adults; B) Totoaba juveniles; C) *Phocoena sinus*

DESCRIPTION OF MODEL COMPONENTS: ECOSPACE

The first step for the model construction was the drawing of the base map and the habitat definition. These tasks were achieved with the help of a GIS. The base map is a 40 by 40 grid using a cell length of 10 km.

Definition of habitats

Seven different habitats (Table 2; Figure 9) were included in the Ecospace base map, considering depth, bottom type and other special habitats. Additionally, we define areas with different relative PP, using Seawifs annual composite data.

Table 2. Definition of habitat for the NGC Ecospace model.

Habitat #	Habitat name	% of total area	Habitat description
1	>200 m	19.3	Deepest areas
2	<100 m	21.5	Shallower areas
3	100–200m	40.4	Intermediate depth area
4	Colorado River Delta	1.0	Highly productive area, nursery ground
5	Rocky bottom	4.5	–
6	Bays and marsh	5.8	Highly productive area, nursery ground
7	Vaquita area	7.6	*Phocoena sinus* distribution area

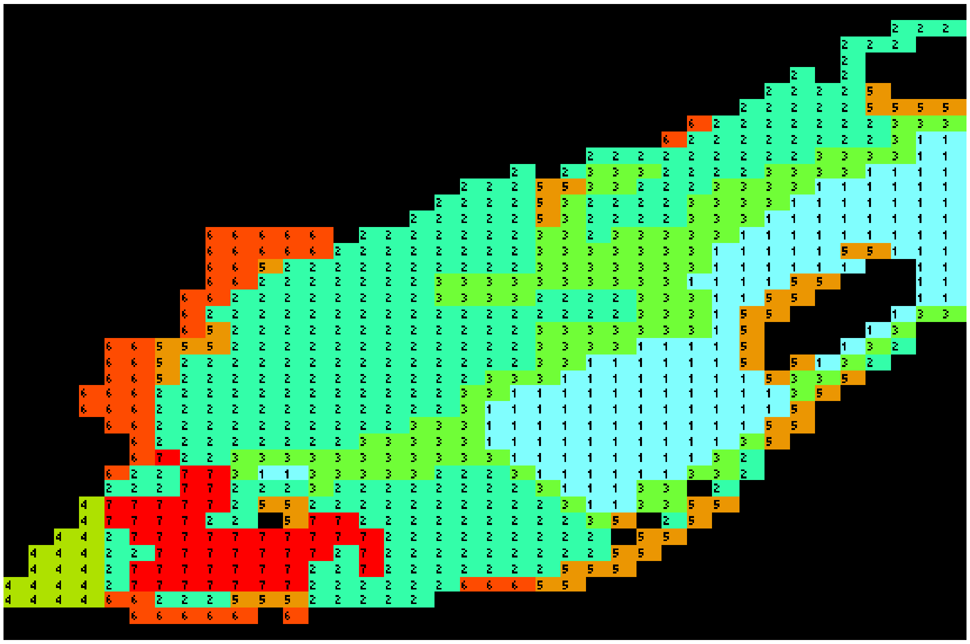


Figure 9. Ecospace basemap of the NGC showing the 7 habitats defined.

Definition of MPAs

Four MPAs were defined, considering the current fishing effort spatial allocation (Table 3; Figure 10).

Table 3. Description of MPAs operational in the NGC.

MPA #	MPA name	MPA description
1	Core zone Biosphere Reserve	Corresponds to the Colorado River Delta. Fishing activities mostly banned. Only artisanal fleets form Santa Clara allowed to fish.
2	Buffer zone Biosphere Reserve	No shrimp trawling allowed
3	Vaquita refuge	All fishing totally banned inside
4	Bays and shallowest areas	No shrimp trawling allowed

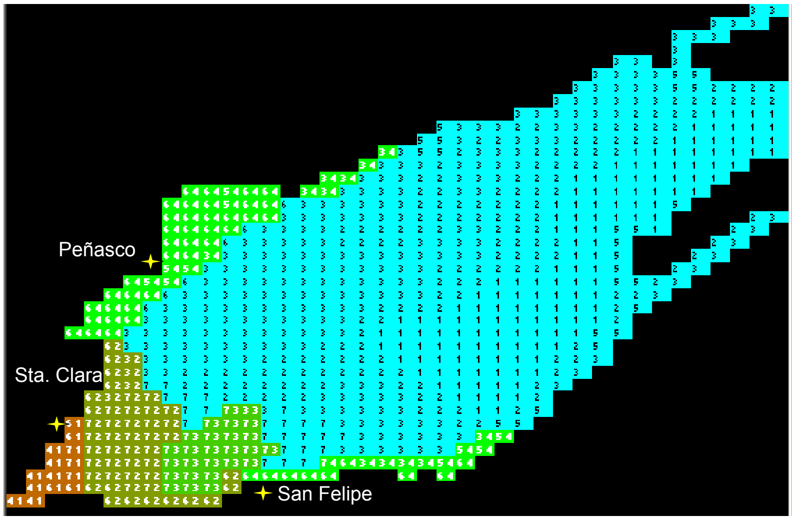


Figure 10. Ecospace location map of the MPAs in the NGC and main landing ports.

Movement of functional groups (Table 4) was included, considering the random dispersal rate (km·year^{-1}) as well as advection in the advected groups and migration where the information was available.

Table 4. Functional groups movement settings for the Ecospace model of the NGC.

Functional group	Base dispersal rate (km·year^{-1})	Advection	Migration
Elasmobranchi (sharks)	300		
Zalophus californianus	300		
Totoaba macdonaldi (adults)	300		yes
Marine birds	300		
Odontoceti	300		
Phocoena sinus	100		yes
Totoaba macdonaldi (juveniles)	300		
Merluccidae	300		
Mysticeti	300		
Coastal birds	300		
Sciaenidae	1000		
Rhinobatidae	30		
Serranidae	300		
Elasmobranchi (RAYS)	30		
Other fishes	300		
Haemulidae	300		
Sicyonia penicillata	3		
Small pelagics	1000		
Farfantepenaeus californiensis (juveniles)	10	yes	
Litopenaeus stylirostris (juveniles)	10	yes	
Cephalopoda	30		
Flat fishes	30		
Myctophidae	300		
Mojarras	300		
Callinectes sp	30		
Polychaeta	3		
Stomatopoda	3		
Litopenaeus stylirostris (adults)	500		
Benthic inv.	50		
Farfantepenaeus californiensis (adults)	500		
Zooplankton	300	yes	
Phytoplankton	300	yes	
Macrophytes	300		
Detritus	10		

Fishing allocation

Spatial distributions of fishing were assigned using the actual regulations of the fisheries as well as a published map of fishing areas in the NGC (Cudney Bueno and Turk Boyer, 1998). Fishing activities were restricted to those regions assigning high fishing cost in Ecospace. The fleet allocation maps obtained are shown in Figure 11.

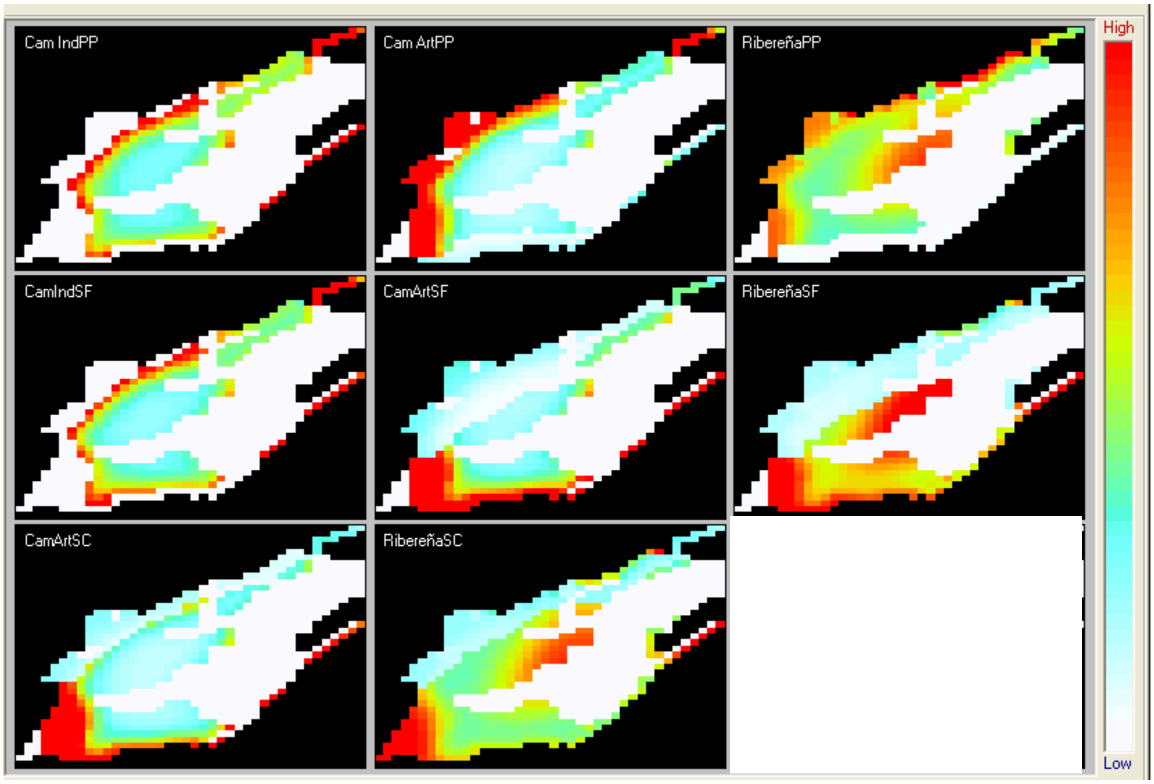


Figure 11. Spatial distribution of relative fishing effort obtained using Ecospace.

Advection fields and migration patterns

To adequately simulate known spatial distribution patterns in the NGC, an advection field was included, which follows the general circulation patterns (Figure 12) in the NGC and affects the spatial distribution of the lower trophic levels (i.e., phytoplankton and detritus). Moreover, in some functional groups (e.g., adult totoaba), rough migration patterns were considered, as delineated by Cisneros Mata *et al.* (1995).

Output maps and interpretations

Figure 13 shows the biomass distribution maps generated by Ecospace considering the actual fishing situation in the NGC. The distribution patterns obtained agree in general terms with previously reported distributions of every group considered.

The first inconvenience detected consists of the decreasing trend during the simulation of the

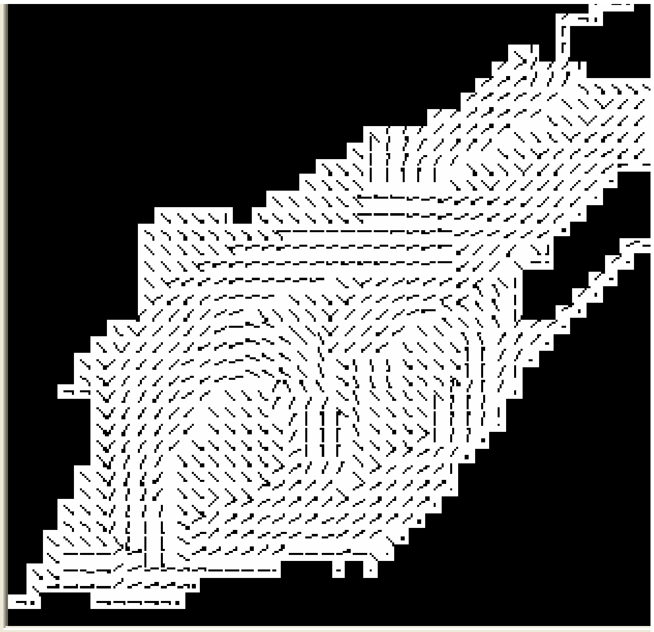


Figure 12. Advection field obtained using Ecospace, representing the general circulation patterns for the NGC.

vaquita biomass. This could be due to the differential habitat assignment between predators and prey. The situation was improved by correcting the habitat assignment of the small pelagics and myctophids, the main group predated by the vaquita. However, in general, the biomass trajectories were improved by initializing the Ecospace runs using the Ecopath base biomass rather the habitat adjusted biomass Ecospace default setting.

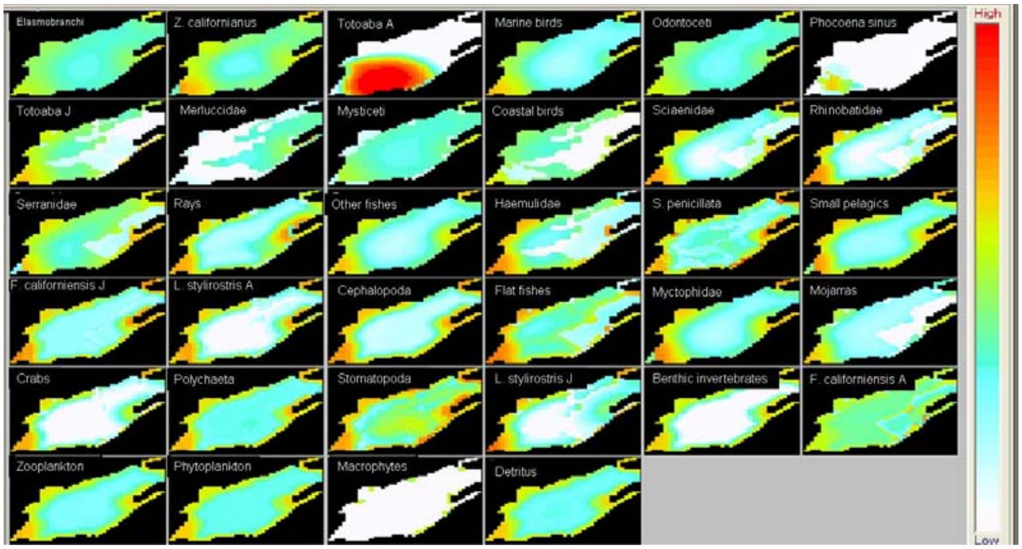


Figure 13. Simulated distribution patterns of relative biomass of every group modelled for the NGC in Ecospace.

The Ecospace output map shows the spatial distribution of relative biomasses using the Ecopath biomass input data as reference. In order to obtain a map showing the simulated spatial distribution in absolute biomass ($t\cdot km^{-2}\cdot year^{-1}$), we extract the grid data results (shown in absolute biomass) to a coordinates 3-column format (xyz) saved to a .dat file. This file was used as input to an interpolation routine to obtain a smoothed distribution map (Figure 14).

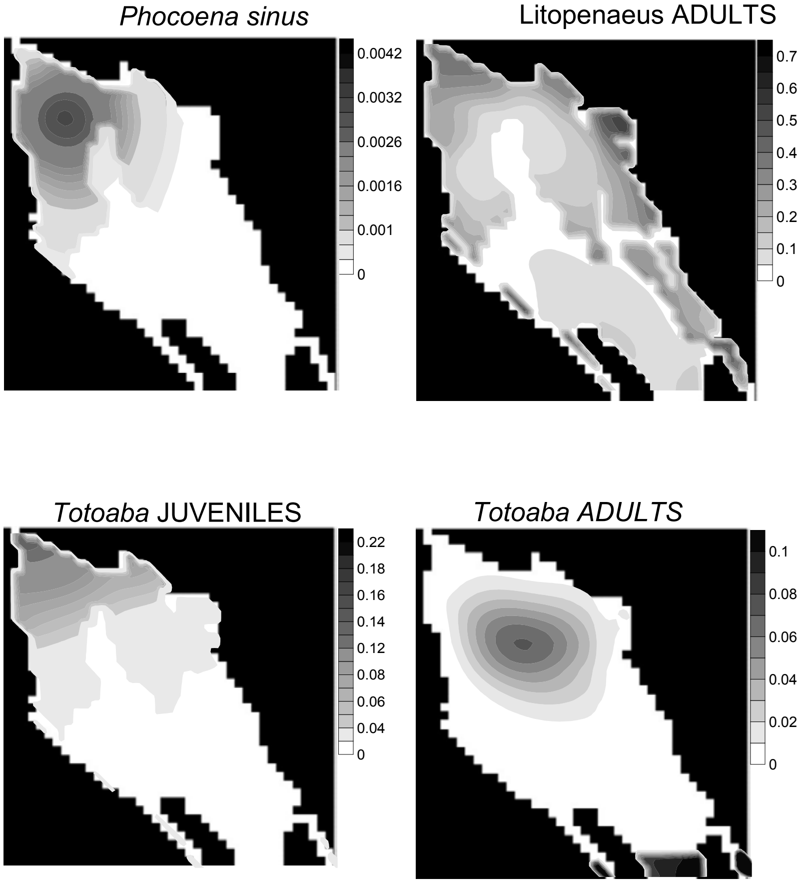


Figure 14. Absolute biomass simulated distribution predicted by Ecospace model of the NGC, for four selected groups modelled for the NGC after polynomial interpolation.

CONCLUSIONS

Ecopath results permit identification of the trophic role of endangered species, top predators and fleets on ecosystem components, as relevant information to estimate potential direct or indirect relationships and impact. This is of relevance considering the existing conflicts between conservation and exploitation.

Ecosim outcomes show the effects of temporal changes in fishing patterns on the two endangered species. Simulation of no fishing illustrates the recovery potential of these species while the simulation of doubling fishing shows the risk of an even more drastic decrease of the biomass of the endangered species. Such simulations confirm the idea that conservation and fishing could be compatible under a good management scheme, which in terms of the simulations means control of fishing.

Previous studies based on Ecosim suggested a high risk for endangered species due to fishing (Arreguín-Sánchez, 2005); however, those simulations only consider a general artisanal fleet and an industrial fleet. The disaggregation of fleets permitted a best representation of the fishing impact possible and provided a proper framework in which conservation and fishing could realistically interact.

The implementation of the Ecospace model permits a satisfactory representation of the known spatial distribution of the model components. This allows the setting of possible MPA scenarios in order to test the ecological effects of diverse spatial fishing allocation designs. Our next steps will be the identification of spatial allocation of fleets in combination with Ecosim outputs. In general terms, our results suggest that a model developed may be a useful tool for representing management scenarios.

REFERENCES

Anónimo. 2002. Programa de Manejo Reserva de la Biosfera Alto Golfo de California y Delta del Río Colorado. CONANP. 134pp

Aragón-Noriega, E.A., Cervantes Valle, C., Garcıá Juárez, A.R. and Calderon-Aguilera, L.E. 1999. Evaluación del stock desovante de camarones peneidos del norte del Golfo de California. Revista Ciencia y Marina 9, 37–48.

Arreguín-Sánchez, F. 2005. The role of scientific advice in the management of benthic fisheries in Mexico: present status and perspectives. 59 – 71 pp. In: Barnes, P.W. and J.P. Thomas (editors). Benthic habitats and the effects of fishing. American Fisheries Society Symposium 41, Bethesda, Maryland, USA

Brusca, R.C., Findley, L.T., Hastings, P.A., Hendrickx, M.E., Torre Cosio, J. and van der Heiden, A.M. 2004. Macrofaunal Biodiversity in the Gulf of California. In: Cartron, J.L.E., Ceballos, G., Felger, R. (Eds.), Biodiversity, Ecosystems, and Conservation in Northern Mexico. Oxford University Press, New York, pp. 179–203.

Christensen, V. and Pauly, D. 1992. Ecopath II: a software for balancing steady-state ecosystem models and calculating network characteristics. Ecological Modelling 61, 169-185.

Christensen, V. and Walters, C.J. 2004. Trade-offs in ecosystem-scale optimization of fisheries management policies. Bulletin of Marine Science 74(3), 549-562.

Cisneros-Mata, M.A., Montemayor-López, G. and Roman-Rodriguez, M.J. 1995. Life history and conservation of *Totoaba macdonaldi*. Conservation Biology 9, 806-814.

Cudney-Bueno, R. and Turk-Boyer, P. 1998. Pescando entre mareas del Alto Golfo de California. Centro Intercultural de Estudios de Desiertos y Océanos, Puerto Peñasco, México. México. 166 p.

D'Agrosa, S., Lennert-Cody, C. and Vidal, O. 2000. Vaquita bycatch in Mexico's artisanal gillnets fisheries: driving a small population to extinction. Conservation Biology 14, 110-119

D'Agrosa, C.O., Vidal, O. and Graham, W.C. 1995. Mortality of the vaquita (*Phocoena sinus*) in gillnet fisheries during 1993-1994. Report of the International Whaling Commission Special Issue 16, 283-291.

DOF (Diario Oficial de la Federación) 2005. Programa de protección de la vaquita dentro del área de Refugio ubicada en la costa occidental del Alto Golfo de California. 29 de diciembre de 2005.

Flanagan, C.A. and Hendrickson, R. 1976. Observations on the commercial fishery and reproductive biology of the totoaba, *Cynoscion macdonaldi*, in the northern Gulf of California. Fisheries Bulletin 74, 531-544.

Funtowicz, S.O. and Ravetz, J.R. 1990. Uncertainty and Quality in Science for Policy. Kluwer, Dortrecht.

IUCN Red List of Threatened Species reveals ongoing decline of the status of plants and animals. http://www.iucn.org/themes/ssc/redlist2006/redlist2006.htm.

Jaramillo Legorreta, A.M., Rojas Bracho, L. and Gerrodette, T. 1999. A new abundance estimate for vaquitas: First step for recovery. Marine Mammal Science 15, 957-973.

Lavin, M., Godíinez, V.M. and Alvarez, L.G. 1998. Inverse-estuarine features of the Upper Gulf of California. Estuarine, Coastal and Shelf Science 47, 769-795.

Lercari, D. 2006. Manejo de los recursos del ecosistema del norte del Golfo de California: integrando explotación y conservación. Doctoral Thesis CICIMAR-IPN, Mexico. 173pp.

Lercari, D. and Chávez, E. 2007. Possible causes related to historic stock depletion of the Totoaba: *Totoaba macdonaldi*, (Perciformes: Sciaenidae) endemic to the Gulf of California. In press: Fisheries Research doi:10.1016/j.fishres.2007.05.010

Lercari, D. and Arreguín-Sánchez, F. 2007. An ecosystem modelling approach to deriving viable harvest strategies for multispecies management of the northern Gulf of California. Submitted to: Aquatic Conservation Marine and Freshwater Ecosystems.

Lluch-Cota, S.E. 2003. Gulf of California: North Pacific Ecosystem Status Report. PICES Special Publication Number, www.pices.int/publications/special_publications/NPESR/2005/npesr_2005.aspx.

Mantua, N.J., Hare, SR., Zhang, Y. Wallace, JM. and Francis, RC. 1997. A Pacific interdecadal climate oscillation with impacts on salmon production. Bulletin American Meteorological Society 78, 1069-1079.

Mellink, E., Palacios, E. and González, S. 1997. Non-breeding waterbirds of the delta of the Rio Colorado, México. Journal of Field Ornithology 68, 113-123.

Morales-Zárate, M.V., Arreguín-Sánchez, F., López-Martínez, J. and Lluch-Cota, S.E. 2004. Ecosystem trophic structure and energy flux in the Northern Gulf of California, Mexico. Ecological Modelling 174: 331-345.

Ortiz, I. 2002. Impacts of fishing and habitat alteration on the population dynamics of the vaquita, (*Phocoena sinus*). MSc Thesis, University of Washington, Seattle, USA. 72pp.

Rodríguez, C.A., Flessa, K.W. and Dettman, D.L. 2001. Effects of upstream diversion of Colorado River water on the estuarine bivalve Mollusk *Mulina coloradoensis*. Conservation Biology 15, 249-258.

Rojas Bracho, L. and Jaramillo Legorreta, A. 2005. Todo lo que quería saber de la vaquita y no había a quién preguntarle. Instituto Nacional de Ecología, 15 pp., www.ine.gob.mx/dgoece/con_eco/vaquita.html.

Santamaría del Angel, E., Alvarez Borrego, S. and Müller Karger, F., 1994. Gulf of California biogeographic regions based on coastal zone color scanner imagery. Journal Geophysical Research 99, 7411-7422.

MARINE ECOSYSTEM ANALYSES IN THE GULF OF ULLOA, MEXICO: BAC MEETS ECOPATH[1]

Pablo del Monte-Luna, Francisco Arreguín-Sánchez and Daniel Lluch-Belda
Departamento de Pesquerías y Biología Marina, Centro Interdisciplinario de Ciencias Marinas.
Instituto Politécnico Nacional. Av. Instituto Politécnico Nacional s/n;
Col. Playa Palo de Santa Rita, PO Box 592, CP 23096,
La Paz, Baja California Sur, Mexico;
Email: pdelmontel@ipn.mx

ABSTRACT

The Ecopath modelling package (EwE) satisfies some of the international guidelines for promoting an ecosystem-based fisheries management; however, proper definition of ecological management units has not been fully accomplished. The Biological Action Centre (BAC) concept may address this problem. BACs are small, highly productive coastal areas whose productivity is almost constant throughout the year when compared to adjacent zones; thus these areas may sustain large amounts of exploitable biomass. By using EwE it was possible to characterize the Gulf of Ulloa, Mexico, as a BAC, since it shows high absolute and instantaneous productivity rates, despite sharing certain ecological attributes with upwelling zones.

Using temporal (Ecosim) and spatial (Ecospace) dynamic versions of the model, we simulated abundance and distribution patterns of the main fishery resources and key ecological groups in the area. For the blue abalone CPUE time series, the best fitting resulted from the addition of annual sea level anomalies as a forcing factor. Dynamic simulation of biomass time series of the Pacific sardine showed a relatively poor fit, even after introducing forcing factors whose influence on this stock is well documented. The low sensitivity of Ecosim was possibly due to the model's underlying assumption of the existence of a linear relationship among forcing factors and between forcing factors and sardine stock dynamics. Simulations of geographical distribution patterns of phytoplankton and zooplankton and the estimation of exported biomass from this BAC to adjacent systems using the Ecospace model were very similar to those estimated with alternative methods and data. Whilst EwE was shown to be useful to analyze key functional, organizational and structural aspects of highly productive marine ecological systems such as the BACs, the model must take into account at least causal nonlinear relationships between forcing factors and stock dynamics in order to derive more relevant information to fisheries management.

INTRODUCTION

The effect that fishing activities exert upon a variety of interacting species propagates throughout the food web and eventually may alter the organization, structure and functioning of marine ecosystems. This situation has created a pressing national and international need for adopting an ecosystem-based fisheries management (EBF). This concept, of course, does not imply the manipulation of ecological systems as a whole, but the development of fishing regimes in accordance with the sustainable use of ecosystem goods and services. In this sense, the Ecopath mass balance approach has been a useful tool, for it addresses questions related to past and future ecosystem impacts of fishing and environmental disturbances by means of spatio-temporal dynamic modelling.

However, one of the problems inherent to the EBF is the definition of management units. If ecological management units are too large, there will never be enough human and economic resources to properly investigate them. Alternatively, if they are too small, they may not be representative of ecological processes that are taking place within larger areas, and thus fail to lead to coherent generalizations. The Biological

---

[1] Cite as: del Monte-Luna, P., Arreguín-Sánchez, F. and Lluch-Belda, D. 2007. Marine ecosystem analyses in the Gulf of Ulloa, Mexico: BAC meets Ecopath, p. 114–133. *In*: Le Quesne, W.J.F., Arreguín-Sánchez, F. and Heymans, S.J.J. (eds.) INCOFISH ecosystem models: transiting from Ecopath to Ecospace. Fisheries Centre Research Reports 15(6). Fisheries Centre, University of British Columbia [ISSN 1198-6727].

Action Centre (BAC) concept (Lluch-Belda, 1998) might be valuable for defining such units: i.e., small, geographically fixed, coastal areas that exhibit high and relatively constant productivity throughout the year when compared to adjacent systems; this productivity not only supports large quantities of marine living resources, but presumably contributes to adjacent systems via the food web. In the present contribution, we test the use of ecosystem management units (BAC) by using a mass balance ecosystem approach (Ecopath).

Mass balance ecosystem approach: Ecopath

Polovina (1984) originally developed the Ecopath approach for application to the coral reefs of the French Frigate Shoals. Ecopath models are food web models that describe the state of biotic flows in an ecosystem. The most typical currency used is biomass wet weight, and the models include all biotic components of an ecosystem.

Ecopath has been under continuous development since 1990 (Christensen and Pauly, 1992), with Ecosim emerging in 1995 (Walters *et al.*, 1997; 2000) and Ecospace in 1998 (Walters *et al.*, 1999), leading to an integrated software package, 'Ecopath with Ecosim' (EwE). Since its creation, EwE has been widely accepted for aquatic and even terrestrial ecosystem modelling (Krebs *et al.*, 2003). In 2004 there were 2,400 users from 120 countries and EwE has been the base of at least 150 international publications. EwE has proved a useful methodological platform for evaluating fishery resources and exploring management policies in a more integrative context than that offered by mono-specific methods.

Biological Action Centres

Some areas of the world oceans are recognized as highly productive, as compared to the vast majority of the seas. Neritic areas are far more productive than the open ocean, and among them, those with dynamic mixing of different water masses appear to be the richest ones. Coastal upwelling regions, such as the eastern boundary currents (Humboldt, California, Canaries, Benguela) temperate-polar mixing areas (Japan, Labrador), tidal front areas (East Bering Sea, North Sea) and others contribute a large proportion of the world's landings of fishing products.

Within those productive regions (for instance, the California Current or the Bering Sea) are certain areas that clearly hold larger biomasses than the ocean around them. Similarly, there are also zones in which biomasses are relatively large throughout the year, as opposed to areas surrounding them that only carry high abundance of individuals during part of the year (for example, during upwelling season). Such areas may be referred to as 'Biological Action Centres' (BAC; Lluch-Belda, 1998).

Some of these areas are evident because of their high biomasses; others become clear when finding poor productivity around them (Figure 1). These areas may be associated with either a particular tidal front, vertical mixing provoked by sea bottom topography and intense currents or perhaps to river discharges. Bakun (1996) has summarized the characteristics that marine areas should have to be highly productive—the equivalent to BACs—as the 'triad' of processes yielding favourable habitat for fish spawning: enrichment (upwelling, mixing), concentration (convergence, frontal formation, water column stability) and retention within or towards appropriate habitats.

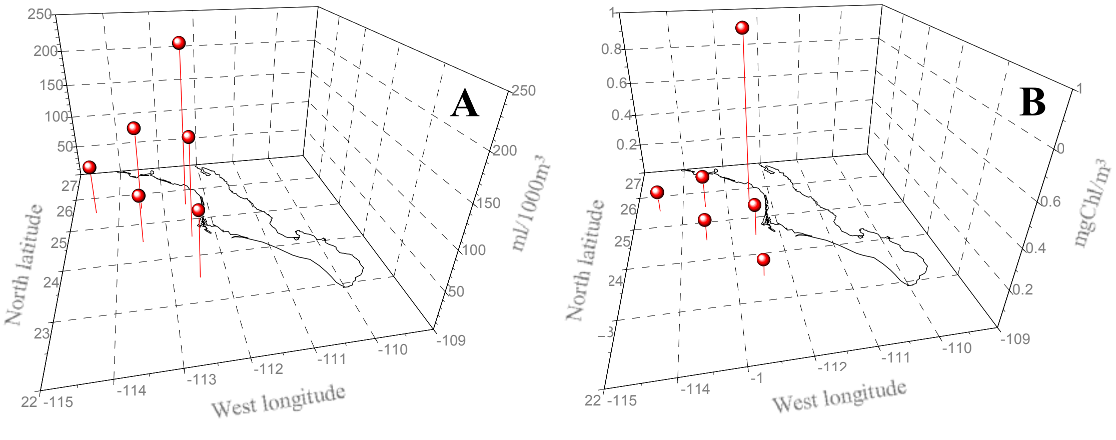


Figure 1. Comparison between zooplankton average annual abundance (A) and phytoplankton average annual pigment concentration in the Gulf of Ulloa (GU) Mexico, and adjacent areas. The Biological Action Center of the GU is the area of highest values of each variable.

These BACs are relatively small (up to about 100 km^2) and their contribution in terms of productivity (whatever the measure) to the global region must be comparatively high. Certain species (e.g., sardines) concentrate during the poor part of the year (for instance, the non-upwelling season) in the BACs (Lluch-Belda, 2000). The importance of these areas should be assessed not only by their share of productivity, but also as a key factor in the existence of certainly many species. Maximum population size of some of these species might be determined largely by the biological capacity and habitat suitability of the BACs supporting them during the poor season.

There are some clues that BACs might be strongly affected by interannual variability. The sardine populations in the California Peninsula might be largely dependent on the Bahía Magdalena and Punta Eugenia BACs. Spawning of this population has varied considerably in the past; perhaps there is interdecadal alternation of suitable/poor conditions for these populations to grow. What these conditions are has been a matter of speculation. As for interannual variability, ENSO events have a great effect on the abundance of *Macrocystis*, a key primary producer in some BACs (such as the Punta Eugenia and the GU) and of small pelagics such as the Pacific sardine, *Sardinops sagax*. Parallel to this change in kelp abundance and coverage, some bottom dwellers that represent a highly lucrative fishery, such as the blue abalone, *Haliotis fulgens*, also appear to become more or less abundant and subject to the effects of interannual climate variation (Lluch-Belda, 1998).

The existence of these areas has been related to the combination of certain oceanographic processes described by Bakun (1996) as 'The Triad'. Among the physical mechanisms involved in those processes are the wind-driven upwelling that enriches the system through the vertical transportation of nutrients from sub-surface waters; oceanic fronts, which tend to geographically concentrate this enriched water; and the formation of meso-scale eddies, that confine and retain it. All these processes (and probably others as well) may be observed at different locations along the coast of all oceans. At present, however, 11 BACs have been identified along the west coast of North America (Figure 2) of which 4 are located along the Peninsula of Baja California. One of these is located in the central part of the Gulf of California and the other 3 are on the western coast: Punta Baja, Vizcaino Bay and the Gulf of Ulloa, the subject of this study.

The BAC of the Gulf of Ulloa

The Gulf of Ulloa (GU; ±10,000 km^2) is in the austral edge of the California Current System (CCS) (Figure 3). The CCS transports sub-arctic water from the Pacific to the Equator, from around 48°N latitude to 25°N latitude, and presents a mixture of water from the central North Pacific which penetrates to the system from the west. A deep warm tropical counter-current, the Davidson current, enters from the southern border to the north during autumn and winter but is not present during the rest of the year. Seasonally, wind-driven upwellings incorporate into the surface nutrient-rich and cold subsurface waters and then are expelled offshore all along the coast.

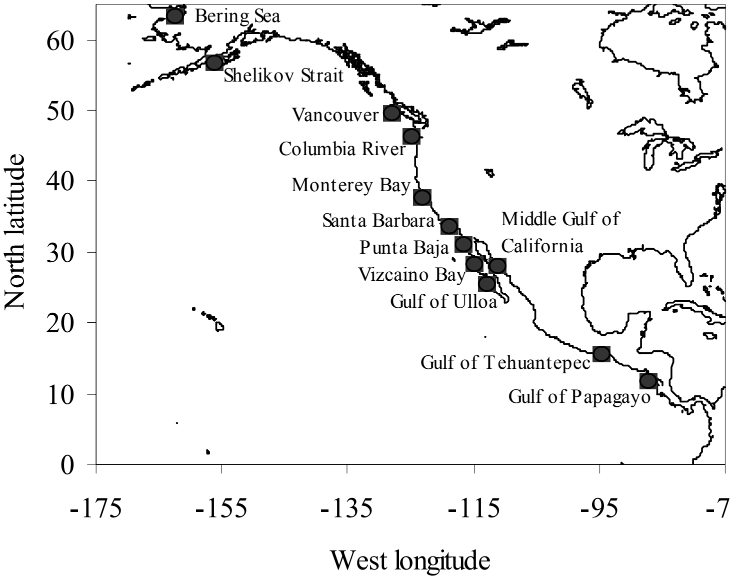


Figure 2. Location of Biological Action Centres identified by 1998.

Throughout the year, the CCS is subject to a considerable variability. In the coastal domain, for example, the 18°C isotherm moves from the Gulf of Ulloa (24°N) during May up to the Santa Barbara Basin, near 34°N, during August and September. In the Gulf of Ulloa, wind-driven upwelling, although permanent, is stronger at mid-year during April and May.

In the southern part of the CCS, there are two processes which are responsible for surface water enrichment: upwelling and advection. These factors are stronger during spring, coinciding with the minimum values of sea level height and with the maximum intensity of the CC. Although a series of phenomena occur simultaneously during this season, the relative contribution of the advection process is relatively small, and the primary and secondary productivity is more closely related to local coastal upwelling processes.

The GU shows important differences between the upwelling season and the rest of the year; for example, pigment concentration values during the upwelling season are as much as twice those of other upwelling areas along the peninsula. The overall biological productivity extends up to 80 km offshore but lasts 3 months, and it is closely related to upwelling intensification (Lluch-Belda, 1998).

In the GU, high macro-zooplankton abundances correspond geographically with the high pigment concentration areas, which suggest a quasi-immediate trophic transfer. On the other hand, areas of high larvae concentration are relatively near to the pigment concentration cores. This could be a result of retention and concentration processes. Considering the strong seasonal behaviour of biological and physical variables in the GU, such retention would happen during certain parts of the year (Lluch-Belda, 2000).

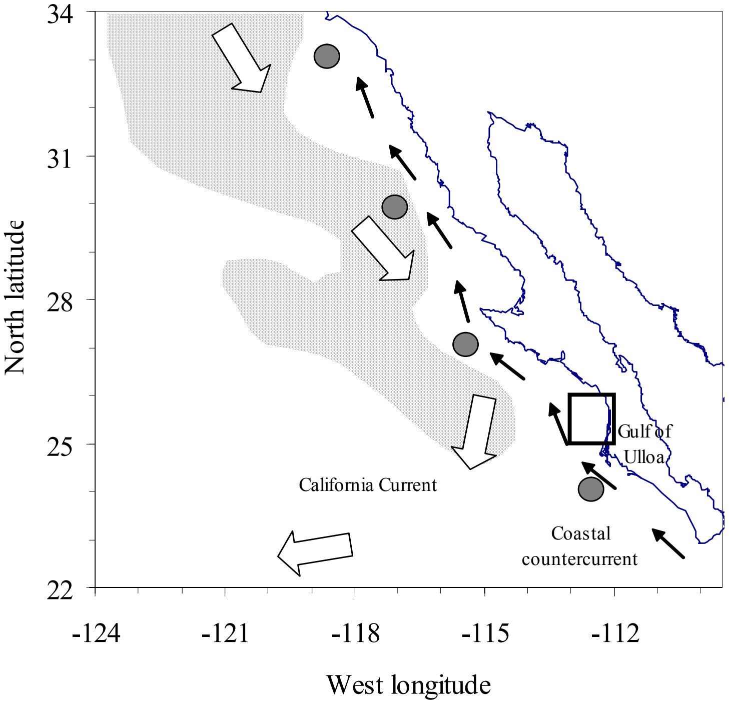


Figure 3. Study area (inner frame) showing the California Current System -CC- (large arrows), the coastal counter-current (dotted arrows), the area influenced by the advection of the CC (dotted area) and the standard positions for the calculation of the Bakun's upwelling Index (Bakun, 1973).

In the GU, the size of the continental shelf varies greatly. In the northern border it extends roughly 30 km, but it expands as the latitude decreases until it reaches 80 km in the middle part of the gulf. The region with the narrower shelf presents a rocky bottom with sandy patches; where the shelf is wider there is a typical sandy bottom with rocky patches along the coast, as a result of an intense sedimentation (Maeda-Martínez *et al.*, 1993).

Biological Action Centres as ecological management units

It is clear that BACs are relevant oceanic structures. In an ecological context, these areas pose important questions that must be tested and improved since they have substantial implications on many traditionally accepted concepts, for instance, the effects of climate change on an ecosystem's productivity. In a fishery context, on the other hand, a deeper knowledge of these areas may be critical to properly manage some fish resources that until now have been difficult to assess by means of traditional methods and techniques (Lluch-Belda, 1999).

It should be mentioned that BAC-oriented research will not substitute region-oriented research, but complement it. However, as knowledge is gained, some subjects, species or characteristics or a combination of these, may be evaluated faster and more cost effectively in a BAC than in the whole area. The infrastructure and instrumentation required are far more accessible than those needed to study deeper offshore areas. It should be easy, for instance, to study a population of moving fishes while the bulk of it is concentrated in a relatively small area than to study the same population distributed along thousands of square miles.

If BACs do contribute a sizeable part of the system's total productivity (1% of a whole coastal area –BACs display from 6 to 13 times more primary productivity than the rest), then it would also be faster and less costly to concentrate on a small area rather than the total. Even in the event that BACs would only parallel the total area processes but not meaningfully contribute to them, working in a restricted spot would permit deeper and more detailed research. What research has been done in merely average productive ocean spots could conceivably be more profitable in a highly productive one. Moreover, if the high concentration of primary producers and consumers rapidly dissipates from the BAC to the surrounding areas, then it would be reasonable to assume that a large part of the trophic flows are happening within the area, which fits quite well with the ecosystem definition proposed by Christensen and Pauly (1998).

Often underestimated, comparative studies generally yield higher-class information for integration and conceptualization. There are many good examples, such as the eastern boundary current comparative approach. Comparison between distant parallel phenomena has been used as a prime important research tool. BACs would be excellent comparative units: relatively small, biologically and socially relevant and most of all, diverse. Sharing fundamental properties (high and sustained biomasses), BACs are latitudinally separated and are likely influenced by different mechanisms, conditions and dynamics.

Finally, considering that the geographic resolution, ecological attributes and exploitation potential of these areas are coherent with the fundamental principles of the ecosystem-based management proposed by some organizations and authors (FAO, 2004; MFAC, 2003; Latour *et al.,* 2003), the BACs may represent suitable candidates to be regarded as ecological management units.

BAC meets Ecopath

In contrast to the BACs of California and Canada that have been intensively studied, information concerning the BACs in the Baja California peninsula is scarce and incomplete, and few efforts have been made to integrate them into holistic approaches.

In this sense, EwE has been a useful tool for exploring and characterizing other highly productive areas (Duarte and García, 2004). For instance, Jarre-Teichman and Pauly (1993) found that the circulating biomass in the food web of the Humboldt marine ecosystem is entirely determined by the seasonality of the upwelling process. Shannon *et al.* (2004), by using the Ecosim routine, were able to describe the alternation between stable states of the Benguela ecosystem as a function of the available phytoplankton and zooplankton biomass for the dominant species. Other upwelling systems from around the world (California, Peru, Benguela and Canarias) have also been compared in terms of different ecological attributes during different environmental regimes (Jarre-Teichman and Christensen, 1998).

The application of ecosystem models in analyzing BACs is concentrated in the North American and Canadian coasts, precisely where there is more information. The work of Olivieri *et al.* (1993) in Monterey Bay is a direct application. According to certain ecological indicators derived from Odum (1969) and Ulanowicz (1986), the distinctive features of BACs when compared to typical upwelling ecosystems are a high degree of stability and maturity, an efficient energy transfer throughout the food web and the proportion of the Primary Production Required to sustain regional fisheries is comparatively high (Pauly and Christensen, 1995).

In Mexico, the application of Ecopath models to the study of BACs is rather limited. Arreguín-Sánchez *et al.* (2002) analyzed the shrimp fishery in the benthic ecosystem of the central Gulf of California but did not characterize the BAC specifically. It is clear that more research efforts are needed in order to describe and model these systems. Presently, there are some incipient initiatives for studying Mexican BACs under holistic approaches (Francisco Arreguín-Sánchez CICIMAR-IPN *pers. comm.*). In the present contribution, by means of EwE, we will 1) describe the main ecological features of the Gulf of Ulloa; 2) estimate abundance trends of the most important fish resources in the area 3) improve previous estimates of phytoplankton and zooplankton distribution patterns; and 4) estimate exported biomass from the Gulf to adjacent systems and compare this to independent estimations.

INPUT DATA AND ECOSYSTEM CHARACTERIZATION

The Ecopath model for the Gulf of Ulloa comprises 26 functional groups: phytoplankton, phytobenthos, zooplankton, zoobenthos, lobster, red crab, abalone, shrimp, clams, ariidae, Carangidae, Gerreidae, Haemulidae, flat fish, Sciaenidae, Serranidae, sharks and rays, Triglidae, Merluccidae, Clupeidae, other fish, marine birds, dolphins, whales, sea lions and detritus. All units are expressed in tonnes per square kilometre ($t{\cdot}km^{-2}$). As much as was possible, the information of many functional groups was taken from the same source or from models of similar or nearby areas. For instance, P/B and Q/B ratios and diet composition for coastal and inner bay fish groups (Haemulidae, Gerreidae, Serranidae, sharks and rays, flat fish and 'other fish') were taken from an Ecopath model developed for Magdalena Bay (Chávez-Rosales, 2006) and for the rest of the ichthyofauna, from other upwelling zones within the California Current System, contained in FishBase (Froese and Pauly, 2001). Exportation values for phytoplankton and zooplankton were taken from del Monte-Luna (2004). Further details of sources of information and input data are shown in Tables 1 and 2, respectively.

For exploited species, the P/B ratio is equivalent to the sum of fishing mortality (Z) and natural mortality (M) and for non-exploited species, as F is negligible, is equal to M. These parameters were estimated from empirical relationships proposed by Pauly (1980). Comparisons between estimated and observed F values are discussed later. Q/B values for fish were taken from Jarre-Teichman and Christensen (1998); these calculations incorporate environmental temperature, weight, size and caudal fin morphology (indicating the degree of activity). This algorithm is available on FishBase. For invertebrates and marine amniotes, the Q/B ratio was taken from the literature; the diets for the later groups were obtained from Pauly *et al.* (1998). Equations are detailed in Table 1.

EwE was also applied to evaluate some ecological indices and holistic properties of the GU. These measures are basically derived from the information theory of Ulanowicz (1986). For the present study, we considered the following ecosystem attributes: PPR for sustaining regional fisheries; transfer efficiency between trophic levels (Christensen and Walters, 2004); ascendancy and overhead, denoting the system's degree of development (Ulanowicz, 1986) and stability, respectively; and the total amount of flows (Ulanowicz and Norden, 1990).

Balancing process

Ecopath equations must satisfy the equality between gains and losses: a mass balance for all functional groups. In order to achieve this, we assumed as a primary criterion that $0<EE\leq1$ (an $EE>1$ implies that biomass losses exceed production). The balancing process consisted in adjusting the diet matrix of those groups with an $EE>1$ by making small changes in the original diet values and running the balance process after each change, until all groups satisfied that criterion. We used this procedure because trophic spectra represent the main source of uncertainty in the model; changes in the diet proportions of individual groups, however, do not modify feeding preferences (items) of functional groups. For example, the original diet values of marine birds, which feed mainly on fish, were modified from 0.3 (Carangidae) to 0.063 without altering prey types and diet proportions are redistributed proportionally among the rest of the items. Model consistency was verified by comparing R/B (respiration-biomass ratio) values between groups, which is expected to be higher for fast-growing, short-lived species.

Once the model was consistent and properly balanced, residuals were minimized using Ecoranger routine (Pauly and Christensen, 1995). This procedure allows introducing a range of modal/average values of the original parameters (biomass, consumption and production rates, ecotrophic efficiency and all diet matrix elements). The routine generates a series of random variables with a user-defined frequency distribution; in this case we assumed a normal distribution with a 20% variation for all parameters. We used the average value for those parameters that showed a posterior uniform distribution, such as the EE, and the mode for the rest of the variables. Each model was evaluated through some thermodynamic criteria and restrictions to the Ecopath master equation (Christensen *et al.*, 2000). The process was repeated 10,000 times using the Monte Carlo simulation routine until we obtained 85% positive outcomes.

THE ECOSIM FOUNDATION

Ecosim provides a dynamic simulation capability at the ecosystem level, with key initial parameters inherited from the base Ecopath model. Ecosim uses a system of differential equations that express biomass flow rates among pools as a function of time varying biomass and harvest rates (for equations see Walters *et al.*, 1997; Walters *et al.*, 2000; Christensen and Walters, 2004). Predator-prey interactions are moderated by prey behavior to limit exposure to predation, such that biomass flow patterns can show either bottom-up or top-down (trophic cascade) control (Walters *et al.*, 2000). By doing repeated simulations, Ecosim allows for the fitting of predicted biomasses to time series data.

Table 1. Input data sources for the Ecopath model of the Gulf of Ulloa, Mexico.

Group	Biomass	P/B (Z)	Q/B	EE	Catch	Diet	Export
1 Phytoplankton	1	*	-	**	-	-	2
2 Phytobenthos	**	3	-	*	-	-	-
3 Zooplankton	4	5	6	**	-	7	2
4 Zoobenthos	**	8	6	*	-	7	-
5 Lobster	**	9	9	*	10	9	-
6 Red crab	11	**	12	*	-	11	-
7 Abalone	**	13	14	*	15	13	-
8 Shrimp	**	3	3	*	16	9	-
9 Clam	**	17	17	*	18	12	-
10 Ariidae	**	20	21	*	-	20	-
11 Carangidae	**	22	22	*	-	19	-
12 Gerreidae	**	19	19	*	-	19	-
13 Haemulidae	**	19	19	*	-	20	-
14 Lenguados ('soles')	**	19	19	*	-	20	-
15 Sciaenidae	**	23	23	*	-	19	-
16 Serranidae	**	19	5	*	-	19	-
17 Elasmobranches	**	23	23	*	-	19	-
18 Triglidae	**	23	23	*	-	23	-
19 Merluccidae	**	25	23	*	-	11	-
20 Sardine	26	**	23	*	26	7	-
21 Other fish	**	19	19	*	-	20	-
22 Birds	19	8	6	**	-	7	-
23 Dolphins	27	6	6	**	-	24	-
24 Whales	27	6	6	**	-	24	-
25 Sea lion	28	25	*	**	-	19	-

1: Behrenfeld and Falkowski (1997); 2: Derived from del Monte Luna (2004); 3: Morales-Zárate *et al.* (2004); 4: Hernández-Rivas (unpublished data); 5: Alvarez-Hernández (2003); 6: Aydin *et al.* (2003); 7: Olivieri *et al.* (1993); 8: Shannon *et al.*, (2003); 9: Arreguín-Sánchez *et al.* (1993); 10: Vega-Velázquez *et al.* (1996); 11: Aurioles-Gamboa and Balart (1995); 12: Jarre-Teichmann and Pauly (1993); 13: Guzmán del Proo (1994); 14: Machena *et al.* (1993); 15: León-Carballo and Muciño-Díaz (1996); 16: Sepúlveda-Medina (1999); 17: Trites *et al.* (1999); 18: Massó-Rojas (1996); 19: Chávez-Rosales (2006); 20: Cruz-Escalona (1998); 21: Zetina-Rejón *et al.* (2004); 22: Arreguín-Sánchez *et al.* (2002); 23: Froese and Pauly (2001); 24: Bundy *et al.* (2000); 25: Steven *et al.* (2002); 26: Félix-Uraga (2006); 27: Mangels and Gerrodette (1992); 28: Le Boeuf *et al.* (1983)
* approximated; ** Ecopath estimated value. Empirical equations for PB (=M; natural mortality for unfished groups) and QB are: $\log_{10}M = -0.0066 - 0.28 \log_{10} L + 0.654 \log_{10} K + 0.463 \log_{10} T$; $\ln(QB) = -0.178 - 0.202 \ln W + 0.612 \ln T + 0.516 \ln A + 1.26 F$; constants are defined according to reference number 23.

Forcing factors

When holistic models such as EwE are applied to analyze upwelling areas, the effects of environmental variability on the ecosystem, and thus on fishery resources, must be taken into account. The integration of climate indicators or 'forcing factors' to natural resources evaluation and management schemes has been considered critical. Some international organizations such as FAO and UNESCO have already incorporated this kind of consideration in their agendas (Medley, 2002; Barange, 2003). EwE allows us to explicitly include such information, particularly those variables that correlate with abundance changes of functional groups (commonly fish resources). Forcing factors directly affect the biomass expression in Ecopath's master equation and this effect transcends to other groups via the trophic web. In this contribution we used local sardine landings as an index of abundance (Schwartzlose *et al.*, 1999), fishing mortality for sardine (Morales-Bojórquez, 2004) and catch per unit of effort (CPUE) time series of blue abalone (Ponce-Díaz, 2004). We used a series of forcing factors whose influence on the GU has been well documented at the ecosystem and population levels (Lluch-Cota *et al.*, 2003; Lluch-Belda *et al.*, 2003): namely, the Decadal Oscillation Index (PDO; Mantua, 2000), Cabo San Lucas sea level anomalies (SLH, UHSLC, 2004), upwelling index from Bakun (1973) and sea surface temperature anomalies (SST; Lluch-Belda *et al.*, 2000).

Model performance

Since Ecosim time dynamic simulations are quite sensitive to changes in primary productivity (Steven *et al.*, 2002), several technical tools have been developed to counterbalance this effect by allowing a fitting-validating process between the model outputs and historical time series.

By using biomass, relative abundance indices and fishing mortality time series data of functional groups, Ecosim, in each numerical run, estimates the goodness of fit of estimated against observed data. This measure is expressed as the sum of squares (SS) of the logarithm of the observed and estimated biomass. Catch per unit of effort data (*v.g.* CPUE = y) are transformed to biomass units using a proportionality factor (q) and solving the equation y = q·B by the maximum likelihood method.

According to the length and completeness of historical information (Figure 4), we considered an 18-year period (1980–1997) for dynamic simulation of sardine and blue abalone abundance time series. Each simulation was iteratively evaluated by introducing (in that order) fishing mortality time series, forcing factors (one at a time) and then 'tuning' the vulnerability to predation. The search routines involved a minimization process of the SC based on Marquardt's algorithm. Basically, a change in the vulnerability parameter of Ecosim is analogous to the 'observation error' used in parameters estimation of single population models and has a similar effect to that of the catchability coefficient q.

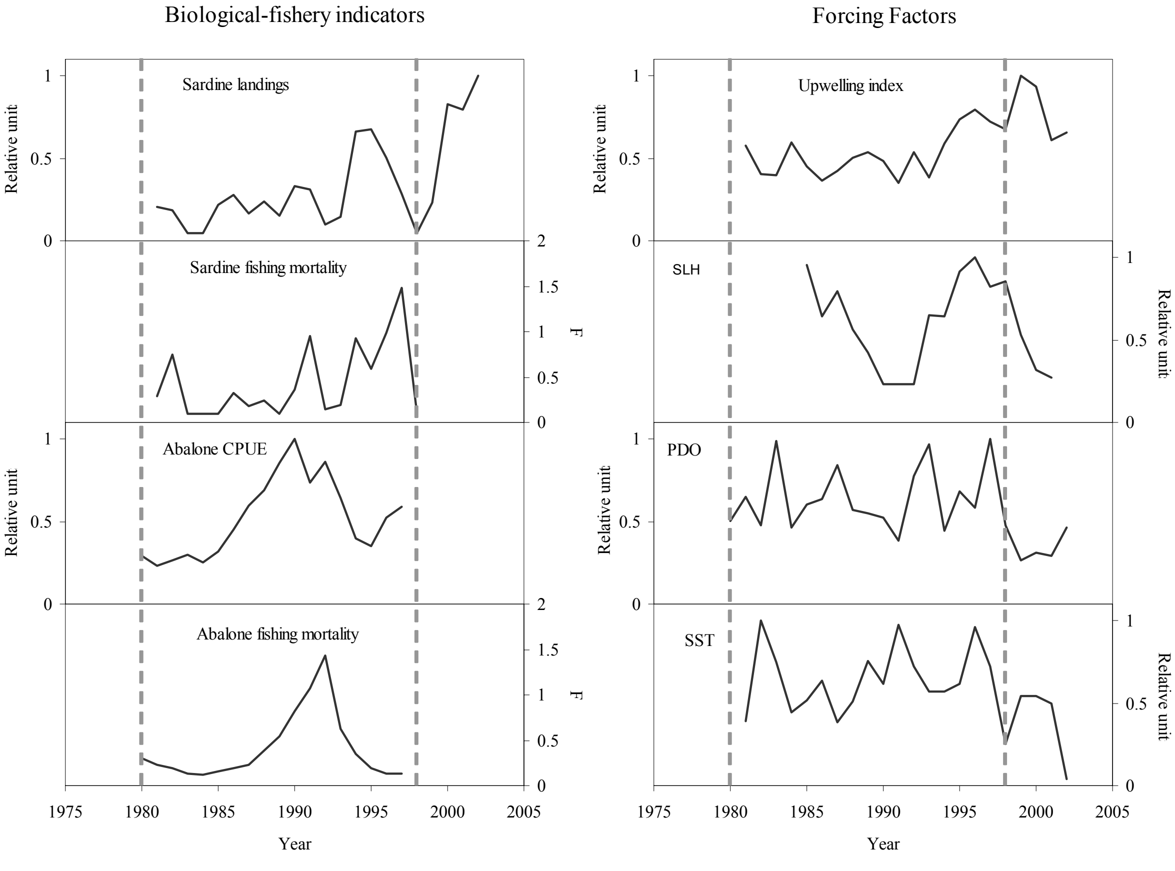


Figure 4. Time series of abundance and fishing mortality for sardine and abalone of the Gulf of Ulloa (GU). Time series of relevant environmental variables in the GU are also shown (right panels). From top to bottom: Bakun's Upwelling Index; SLH: mean sea level height of Cabo San Lucas; PDO: Pacific Oscillation Index; and SST: sea surface temperature. Dotted lines are the period considered for Ecosim time simulation (1980–1997).

THE ECOSPACE FOUNDATION

The major deficiency of the Ecopath/Ecosim approach is its assumption of homogenous spatial behavior. This has been remedied through the development of Ecospace (Walters *et al.*, 1997, 2000), a dynamic, spatial version of Ecopath, incorporating all key elements of Ecosim. While Ecospace has been used to explore the potential of Marine Protected Areas, there are few applications regarding the simulation of distribution patterns of key ecological groups, such as primary producers and consumers (Martell *et al.,* 2005).

In this section, we used the Ecosim model in order to represent the geographical distribution patterns of phytoplankton and zooplankton and to estimate the exported biomass from the GU to surrounding systems.

Advection in Ecospace

Currents deliver planktonic production to reef areas at much higher rates than would be predicted from simple turbulent mixing processes. Upwelling associated with movement of water away from coastlines delivers nutrients to surface waters, but the movement of nutrient-rich water away from upwelling locations means that production and biomass may be highest well away from the actual upwelling locations. Convergence (down-welling) zones represent places where planktonic production from surrounding areas is concentrated, creating special opportunities for production of higher trophic levels.

Ecospace provides a user interface for sketching general current patterns or wind/geostrophic forcing patterns for surface currents. Based on these patterns, Ecospace calculates equilibrium horizontal flow and upwelling/downwelling velocity fields that maintain continuity (water mass balance) and effects of Coriolis force. That is, the advection field is calculated by solving the linearized pressure field and velocity equations $dh/dt = 0$, $dV_u/dt = 0$, $dV_v/dt = 0$ across the faces of each Ecospace grid (u,v) cell, where h is sea surface anomaly, the V's are horizontal and velocity components (u, v directions) and the rate equations at each cell face satisfy:

$$\frac{dh}{dt} = \frac{V_{uh}}{u} + \frac{V_{vh}}{v} - D_h \tag*{Eq. 1}$$

$$\frac{dVu}{dt} = kW_u - kv_u - fv_v - \frac{gh}{u} \tag*{Eq. 2}$$

$$\frac{dv_v}{dt} = kW_v - kv_v - fv_u - \frac{gh}{v} \tag*{Eq. 3}$$

Here, the W's represent the user sketched forcing or general circulation field, h sea surface anomaly, k represents bottom friction force, f the Coriolis force, D represents downwelling/upwelling rate, and g acceleration due to sea surface slope (Christensen *et al.*, 2000).

Input data requirements for this field are surface current velocities and the Coriolis coefficient. Surface currents must be entered as separate velocity vectors, i.e., to the right (X) and from the top (Y). In this case, the net water transport resulting from the upwelling process is offshore; therefore the X vector is negative. Surface currents were obtained from a single resultant vector divided into the X and Y components (taken from Bakun and Nelson (1976). We used values of -150 km·year^{-1} for the X (longitudinal) component and 350 km·year^{-1} for the Y (latitudinal) component. The Coriolis parameter for 25°N latitude (at the GU) is roughly 0.00005 (Bakun, 1996). Transformed to the scale used in Ecospace (from -1 to 1), this value is equal to 0.5.

Habitat definition

Habitats, in Ecospace, are sets of (water) cells sharing certain features affecting the movements, feeding rate, and survival of the Ecopath model components occurring therein. Typically, the features defining habitats are distance from the coast (inshore, offshore) or depth (shallow, intermediate, deep) and/or bottom type (rocky, sandy, muddy). Habitats are thus as easy to define as it is to obtain rough bathymetric maps or maps indicating bottom types. Ideally, the habitats defined in Ecospace should correspond to 'subweb', i.e., to a set of primary producers, herbivores and other consumers occurring only over that habitat. In the present study, we considered regional environmental dynamics for defining distribution patterns of phytoplankton and zooplankton (Christensen *et al.*, 2000).

In the GU, enriched, upwelled water, along with planktonic organisms, is transported (advected) offshore, creating a longitudinal concentration gradient. We propose the existence of a 'theoretical coastal belt' from which, in a given time, the water is displaced away; this belt also represents the only real physical boundary of such gradient, coinciding with the 50 m depth isoline (the minimum depth to trigger the upwelling process). Phytoplankton and zooplankton functional groups were assigned to that habitat, as subjects of advection. The defined habitats (Figure 5) are: 1) Bay, 2) Upwelling belt, 3) Shelf and 4) Slope.

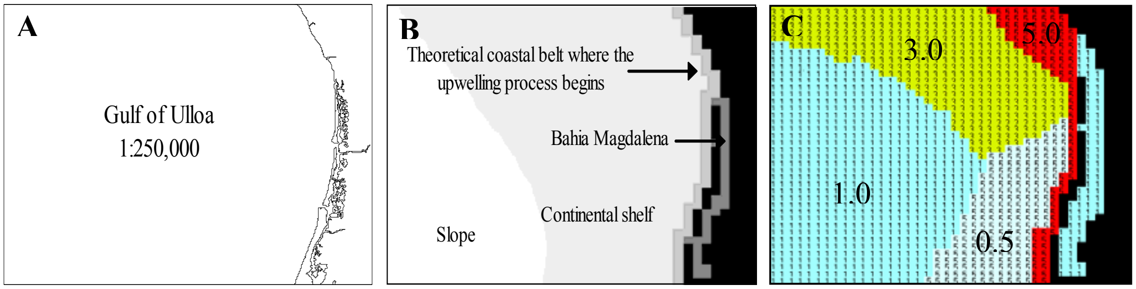


Figure 5. (A) Map of the Gulf of Ulloa (GU) 25°N/113°W-26°N/112°W); (B) GU as represented by the Ecospace model, showing four habitat types defined for this study: continental shelf (light grey), upwelling belt (grey area beside the coastline), inner Bay (dark grey) and the mainland (black); (C) Assumed distribution and assigned values for the distribution of the P/B ratio for primary producers in the GU.

Since primary production may vary in different areas of an ecosystem, e.g., due to terrigenous inflow of nutrients or processes that lead to mixing or upwelling of water masses, the Ecospace model allows sketching a multiplier of the baseline P/B for primary producers (PP-P/B) in the ecosystem map. This multiplier can be used to depict anything from areas with very low primary production rates to areas with very high rates compared to the underlying Ecopath model.

In order to force the phytoplankton and zooplankton biomass gradient, we assumed that the P/B ratio for primary producers is unevenly distributed in the area. As depicted in Figure 5, we sketched different PP-P/B zones assuming values of 5.0, 3.0, 1.0 and 0.5 according to observed zooplankton and phytoplankton concentration patches within the gulf (Funes-Rodríguez *et al.*, 2000).

RESULTS

Ecopath results

The diet matrix after balancing is shown in Table 2 and Ecopath output and estimated values (after balancing) are shown in Table 3; R/B ratio and fishing mortality estimates are also shown. The raw diet matrix, before the balancing process, is shown in Appendix A. Most trophic level values estimated with Ecopath for the GU are consistent with those of nearby systems and other upwelling areas within the California Current System.

Table 2. Ecopath predator-prey (diet) matrix for the Gulf of Ulloa (balanced).

	Prey/predator	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
1	Phytoplankton	0.84	0.05				0.15	0.05											0.84					
2	Phytobenthos	0.03	0.16	0.03		0.8		0.15			0.05							0.01		0.03				
3	Zooplankton	0.01	0.11		0.34					0.53	0.08		0.16	0.07				0.07	0.12	0.01	0.13			
4	Zoobenthos			0.32		0.2	0.35	0.1	0.69	0.13	0.87	1	0.33	0.23	0.56	0.15	1			0.78			0.62	
5	Lobster														0.02	0								0.01
6	Red crab			0.13									0.07			0.02		0.22	0.01				0.38	0.11
7	Abalone			0.03												0.09								0.06
8	Shrimp								0.2	0.04			0.16	0.2	0.12	0.25								0.09
9	Clam			0.09												0.25		0.22						0.17
10	Ariidae														0.01	0.02						0.02		
11	Carangidae															0.01					0.06	0		0.01
12	Gerreidae								0.03						0.03							0.21		
13	Haemulidae														0.08	0.06						0.04		
14	Lenguados			0.06											0.08			0.19				0.11		
15	Sciaenidae															0.02						0		
16	Serranidae			0.02					0.01													0.07		0.02
17	Elasmobranches																							0.01
18	Triglidae									0.01					0.01	0.01						0.01		
19	Merluccidae			0.06											0.01							0.07		0.23
20	Sardine	0.01							0.07	0.29				0.4	0.05	0.09		0.3	0.04	0.19	0.67	0.18		0.21
21	Other fish														0.01	0.02					0.13	0.3		0.1
22	Birds															0.01								
23	Dolphins																							
24	Whales																							
25	Sea lion															0.01								
26	Detritus	0.11	0.68	0.26	0.66		0.5	0.7					0.27	0.1										

Table 3. Output data of Ecopath model of the Gulf of Ulloa. Values in italics were estimated by Ecopath.

Group	TL	B ($t{\cdot}km^{-2}$)	P/B ($year^{-1}$)	Q/B ($year^{-1}$)	EE	Y ($t{\cdot}km^{-2}$)	F	EX	R/B ($year^{-1}$)
1 Phytoplankton	1.0	4000	17	-	*0.09*	-	-	1300	
2 Phytobenthos	1.0	*48.76*	1.83	-	0.95	-	-	-	
3 Zooplankton	2.0	12	55.20	225.08	*0.27*	-	-	7	*124.8*
4 Zoobenthos	2.1	*0.35*	5.08	21.52	0.95	-	-	-	*12.14*
5 Lobster	2.3	*0.068*	0.99	8.20	0.95	0.62	*0.91*	-	*5.57*
6 Red crab	2.3	24.02	*0.06*	9.67	0.96	-	-	-	*7.68*
7 Abalone	2.2	*1.12*	0.62	2.00	0.95	0.04	*0.37*	-	*0.98*
8 Shrimp	2.4	*0.07*	4.03	10.20	0.95	0.10	*1.43*	-	*4.13*
9 Clam	2.1	*0.33*	1.32	5.00	0.95	0.23	*0.70*	-	*2.68*
10 Ariidae	3.2	*0.003*	0.67	3.46	0.95	-	-	-	*2.10*
11 Carangidae	3.1	*0.007*	0.80	3.65	0.95	-	-	-	*2.12*
12 Gerreidae	3.0	*0.06*	2.31	9.06	0.95	-	-	-	*4.94*
13 Haemulidae	3.1	*0.04*	2.85	14.40	0.95	-	-	-	*8.67*
14 Lenguados ('soles')	2.9	*0.36*	0.40	2.40	0.95	-	-	-	*1.52*
15 Sciaenidae	3.0	*0.0002*	2.95	12.00	0.95	-	-	-	*6.65*
16 Serranidae	3.4	*0.22*	0.79	3.60	0.95	-	-	-	*2.09*
17 Elasmobranches	3.5	*0.005*	0.52	5.71	0.75	-	-	-	*4.05*
18 Triglidae	3.1	*0.004*	0.43	2.40	0.95	-	-	-	*1.48*
19 Merluccidae	3.3	*0.23*	0.36	2.00	0.95	-	-	-	*1.24*
20 Sardine	2.2	55	*2.21*	15.00	0.95	9.17	*0.33*	-	*9.79*
21 Other fish	3.1	*0.05*	0.80	5.00	0.95	-	-	-	*3.20*
22 Birds	3.3	0.001	0.95	77.76	*0.08*	-	-	-	*61.26*
23 Dolphins	4.0	0.004	0.16	11.48	*0.00*	-	-	-	*9.02*
24 Whales	3.2	1.57	0.02	3.83	*0.00*	-	-	-	*3.05*
25 Sea lions	3.6	0.012	0.06	13.53	*0.03*	-	-	-	*10.76*
26 Detritus	1.0	100	-	-	*0.01*	-	-	-	-

TL: trophic level; B: biomass; P/B: production consumption ratio; Q/B: consumption biomass ratio; F: fishing mortality; EE: ecotrophic efficiency; EX: export; and R/B: respiration biomass ratio; Y: catch.

Table 4 summarizes the main ecosystem attributes of the GU. Total production is 128,628 $t{\cdot}km^{-2}{\cdot}year^{-1}$, of which 3% is consumed within the system, 50% is exported (including fisheries), 2% is used in respiration and the rest flows to detritus. Primary production-respiration (PP/R) and PP/B ratios indicate that the GU is an unusually highly productive system. The proportion of actual flows with respect to all potential flows, indicated by the connectance index, is 0.2; the percentage of the total production that is recycled within the system, the Finn's index, is 0.16%; and the average transfer efficiency between discrete trophic levels is 3.5%; the PPR to sustain regional fisheries from 1980 to 1990 is slightly less than 2%.

Table 4. Gulf of Ulloa main ecosystem properties, derived from Ecopath.

Attribute	Value	Units
Total system production (throughput)	128,628	$t{\cdot}km^{-2}{\cdot}year^{-1}$
Total primary production (PP)	65,089	$t{\cdot}km^{-2}{\cdot}year^{-1}$
Primary production/respiration	33	
Primary production / total biomass	46	
Mean trophic level	2.2	
Connectance index	0.2	
Omnivory index	0.15	
Finn's recycling index	0.16	% (of total flows)
Average transfer efficiency	3.5	%
Primary production required /PP	0.6	
Ascendancy	65 (129,235)	% (flowbits)
Overhead	35 (84,002)	% (flowbits)
Pedigree index	0.5	

The ascendancy (A=129,235 flowbits) represents 65% of the system total capacity (C) and the overhead (O=C-A, 49.8 flowbits) is 25.3%. The ascendancy is a measure of the ecosystem information content, derived from the information theory (Ulanowicz and Norden, 1990). Since 'A' has the same value whether it is calculated from the inputs or the outputs, it is considered symmetric. The upper limit of A corresponds to the system development capacity (196,783 flowbits) and O is the system potential to endure external perturbations (Ulanowicz, 1986).

Ecosim results

The Ecosim estimated time series of CPUE for blue abalone were relatively good. As for the Pacific sardine, estimated time series were especially sensitive to the interannual frequency of forcing factors, with exception of the 1994–1996 period, during which the index of abundance (landings) increased an order of magnitude. Figure 6 shows Ecosim simulations for abalone and sardine.

In the case of the blue abalone, the best biomass estimation resulted from the incorporation of the inverse value of the sea level height as forcing factor, a vulnerability field (equal vulnerability for all predator/prey relationships) of 1 and an individual vulnerability (for a single predator/prey relationship) of 1.2. These vulnerabilities define the flow control in the model: the smaller the value, the higher the control from prey to predators (bottom-up). The best fit for time series of abundance of sardine resulted from the combination of two forcing factors, the upwelling index and sea surface temperature, a vulnerability field of 1 and an individual vulnerability of 3.

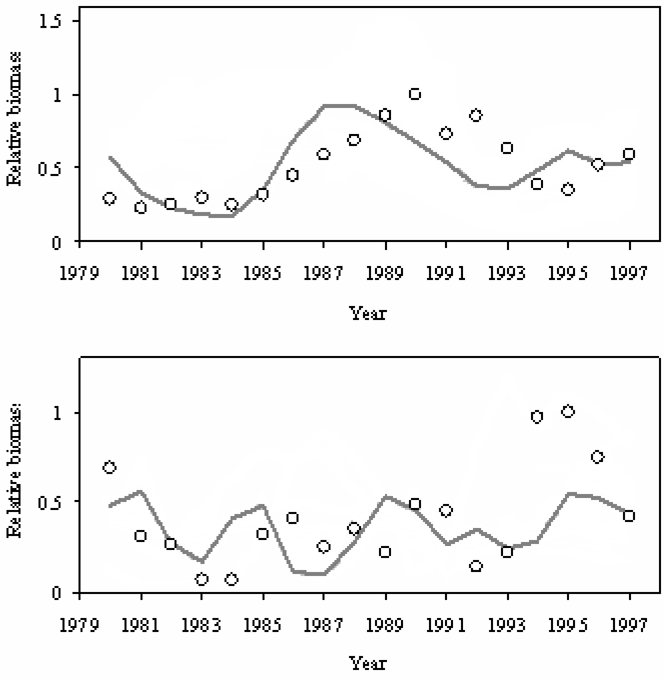


Figure 6. Ecosim model outputs. Observed (white dots) and estimated (lines) index of abundance of abalone (upper graph) and Pacific sardine (lower graph) in the Gulf of Ulloa

Ecospace results

The phytoplankton distribution pattern (Figure 7) estimated by Ecospace shows considerable improvement with respect to previous estimates (Figure 7, B) when compared with observed distribution patterns obtained from independent data (Figure 7, C). This is most probably due to the incorporation of an uneven distribution of primary producers P/B ratio. Figure 7 shows the phytoplankton distribution pattern only; the zooplankton pattern is not shown since it is indistinguishable from the former.

Each cell in Ecospace represents the average biomass that occurs in that particular space and time. Therefore we can calculate the mean longitudinal and latitudinal plankton abundance in the spatial grid by averaging all columns and rows, respectively. The resulting profiles, in which geographic positions (longitude or latitude) would be the X axis and the respective abundance the Y axis, can be extrapolated in order to estimate the amount of biomass that can be expected outside the ecosystem. We calculated these profiles for phytoplankton and zooplankton and fitted them by means of quadratic equations where the intercept with the Y axis, which geographically would be outside the GU, represents the exported biomass itself. By summing up both values, the estimated exportation is quite similar to that estimated from independent data. This figure calculated with Ecospace is 1,000 t·year^{-1} compared to 1,300 t·year^{-1} obtained from the SEAWIFS and Calcofi datasets (del Monte Luna, 2004).

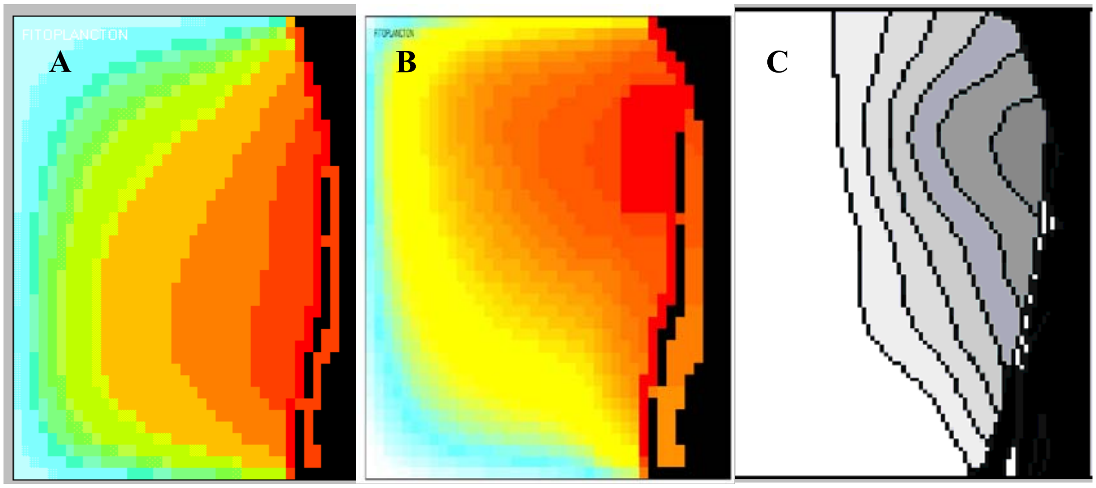


Figure 7. (A) Geographical distribution of phytoplankton biomass as calculated with Ecospace by del Monte-Luna (2004); (B) improved estimation of the same group in the present study; and (C) observed joint distribution of both phytoplankton and zooplankton average annual abundance (taken from Lluch-Belda (2000)).

Discussion

Ecopath

From all input data for the Ecopath model of the GU, the magnitude of phytoplankton biomass turns out to be particularly large. This was derived from the Vertically Generalized Production Model of Behrenfeld and Falkowski (1997). This quantity of 5,200 t·km^{-2} had to be reduced in a reciprocal balancing process, as a function of the P/B ratio, to avoid compromising the condition of EE<1. One of the problems of the balancing process according to the Ecopath master equation is that if the EE is fixed at, for instance, 0.95, a biomass as high as 5,200 tonnes cannot possibly be accompanied by an equally high P/B ratio; this assumption may be questionable when we are dealing with functional groups whose average biomass is enormous but that also have very high turnover rates, such as the phytoplankton of upwelling systems (Arreguín-Sánchez, 1999). Once the model was properly balanced, the resulting phytoplankton biomass was 4,000 tonnes with a P/B ratio of 17.5 year^{-1}.

The values estimated by Ecopath of fishing mortality for the shrimp (F=1.43), blue abalone (F=0.33) and sardine (0.37) fisheries were almost the same as those derived from single species methods: the surplus production model for the shrimp fishery (F=1.15; Sepúlveda-Medina, 1999), catch at age model for Pacific sardine (F=0.2; Morales-Bojórquez, 2004), and biomass dynamic model for abalone (F=0.3; Ponce-Díaz, 2004). Moreover, the mean trophic level of the catch is 2.2, a level consistent with what is found in other upwelling zones (Jarre-Teichman and Christensen, 1998; Duarte and García, 2004). This may be due to the effect of dominant, low trophic level species, such as small pelagics, as in other highly productive ecosystems.

Ecosystem characterization

In general, ecosystem statistics derived from the Ecopath model indicate that the GU is an immature, exceptionally productive system, even when compared to other upwelling areas; the system also presents short, inefficient trophic chains (mean transfer efficiency of 3.5%). These features are expected in ecosystems that are subject to external, periodic perturbations that lead to non-equilibrium conditions, as in the California Current System (Bernal, 1981).

Ecosim

In Ecosim, the best estimations resulted from those scenarios including environmental variables and bottom-up ecosystem properties, as very likely occur in the GU. The best fit was for the abalone CPUE time series provided the effect of the inverse value of sea level height; and for the sardine, the sea temperature and upwelling index. For both cases, the vulnerability field for all groups was of (1) and individual vulnerabilities (v_i) were 1.2 and 3.0 respectively.

Abalone

A time series of relative abundance of blue abalone shows an inverse relationship with sea level height (see Figure 4). Considering that this variable is strongly influenced by ENSO conditions in the GU, then the maximum CPUE values of abalone may be related to a cold episode that occurred at the end of 1990 (Lluch-Cota *et al.*, 2003). Such an effect is presumably via primary benthic producers, since these are the main item in the abalone diet (Serviere-Zaragoza *et al.*, 1998). Changes in intensity and position of sea level pressure fields over the North and Central Pacific during cold episodes may enhance the upwelling process, increasing available nutrients for benthic primary producers by sediment removal (Nidzgorski, 2000), as has been seen in other areas of California (Tegner *et al.*, 1996; Hernández-Guerrero, *et al.*, 1999). In turn, a high concentration of benthic algae, via the trophic web, may produce suitable conditions for the blue abalone (Tegner *et al.*, 1996; California Department of Fish and Game, 2004).

Sardine

The relationship between small pelagics and environmental variability has been broadly documented (Lluch-Belda *et al.*, 1989 and latter; Schwartzlose, *et al.*, 1999; Chávez *et al.*, 1993). In the Baja California Peninsula, sardine biomass fluctuations are associated with the migration of individuals between Ensenada, during summer and autumn, and the GU (Magdalena Bay) during winter and spring. It seems to be that this interchange, while seasonal in nature, depends to some extent on interannual variations of SST (Félix-Uraga *et al.*, 1996). After warm episodes (1982, 1993), there are important migrations from Ensenada to the GU, although there are no estimations of the magnitude of these movements. After the 1993 ENSO episode, sardine landings increased from 5,000 tonnes in 1992 to 34,000 tonnes in 1994. Such behavior was virtually impossible to replicate with Ecosim, even using a high-sensitive individual vulnerability of 9.

Ecospace

The present proposal concerning the existence of a 'theoretical belt' for the upwelling process as an empirical criterion for habitat definition is based upon the following premises: 1) in a given coastal zone, the prevailing wind system will exert a friction over the water surface such as to promote its displacement; 2) the water displaced offshore by the effect of the wind and the earth's rotation, leaves a 'vacuum' which is filled by subsurface waters; 3) both displaced and compensating water must come from a near coastal zone of certain depth so that the upwelling process can take place; and 4) according to some hydrodynamic models, the minimum depth for the wind stress to trigger the upwelling process is 50 m (Oke and Middleton, 2000). Most probably, the characteristics of the GU fulfill the first three premises. The fourth premise can also be satisfied since the extension of the 'theoretical belt' in the map of the GU corresponds to 3 km offshore, where the depth is between 100 m and 150 m.

As showed in graph C of Figure 7, there is considerable overlap of the concentration gradients of phytoplankton and zooplankton. This suggests a very rapid ecological response to the food abundance and an immediate trophic transfer. This coincidence of distribution patterns of primary producers and consumers has been reported by other authors (MacGowan *et al.*, 1996; Lluch-Belda, 1999).

The Ecopath, Ecosim and Ecospace model complex are useful tools for describing key aspects of the structure, functioning and organization of ecological systems in a comprehensible and uniform language from a limited amount of information, descriptions that otherwise would be difficult to derive from techniques focused on single species or groups of exploited species. Indeed, it would not be possible to classify the GU as a BAC on the basis of single-species models.

Adopting ecosystem models, however, does not imply that an Ecosystem-Based Fisheries Management is being done (the concept of BAC is also an ecosystem model). It does not imply either a replacement of typical quantitative techniques, but establishing a dialogue between methods that eventually will allow us to: 1) complement the results of evaluation models by measuring ecosystem level effects of traditional management strategies (catch quotas, proportion of exploitable biomass, etc.); and 2) improve the performance of holistic approaches by explicitly considering, for instance, non-linear relationships between environmental variables, i.e., forcing factors, and functional groups. By merging ecosystem approaches, we will have better descriptions of the relative effects of fishing pressure and environmental variability for key fish resources and the ecosystem-level effects of such variability.

ACKNOWLEDGEMENTS

Authors thank the Incofish project financed by the European Commission (contract EC-003739) for partial support, SEMARNAT-CONACyT (project 1231), SIP-IPN (20070767 and 20070254) as well as the National Polytechnic Institute through EDI and COFAA.

REFERENCES

Alvarez-Hernández, J.H. 2003. Trophic Model of a Fringing Coral Reef in the Southern Mexican Caribbean. Fisheries Centre Res Rep. 11: 227-235.

Arreguín-Sánchez, F. 1999. Modelos de flujos de biomasa en Centros de Actividad Biológica, p. 13-28. En: Lluch-Belda, D., J. Elorduy-Garay, S. E. Lluch-Cota y G. Ponce-Díaz (eds) BAC's: Centros de Actividad Biológica del Pacífico Mexicano. CIBNOR-CONACyT. 357 pp.

Arreguín-Sánchez, F., Arcos, E. and Chávez, E.A. 2002. Flows of biomass and structure in an exploited benthic ecosystem in the Gulf of California, Mexico. Ecological Modelling 156: 167-183.

Arreguín-Sánchez, F., Seijo, J.C. and Valero-Pacheco, E. 1993. An application of ECOPATH II to the North Continental Shelf Ecosystem of Yucatan, México p. 269-278. In: Christensen V and Pauly D (eds.) Trophic models of aquatic ecosystems. ICLARM Conf Proc 26, 390 pp.

Aurioles-Gamboa, D. and Balart, F.E. 1995. La langostilla: biología, ecología y aprovechamiento. CIBNOR 233 pp.

Aydin, K.Y., McFarlane, G.A., King, J.R. and Megrey, B.A. (comp y eds) 2003. PICES-GLOBEC International Program on Climate Change and Carrying Capacity The BASS/MODEL Report on Trophic Models of the Subarctic Pacific Basin Ecosystems. PICES Scientific Report No. 25. 97pp. URL: http://www.pices.int/publications/scientific_reports/Report25.

Bakun, A. 1973. Coastal upwelling índices, west coast of North America, 1946-71.NOAA Tech Rep NMFS, SSRF: 103 pp.

Bakun, A. 1996. Paterns in the ocean. Ocean processes and marine population dynamics. California Sea Grant/CIB. 323 pp.

Bakun, A. and Nelson, C.S. 1976. Climatology of upwelling related process off Baja California. CalCOFI Rep. 19: 107-127.

Barange, M. 2003. Ecosystem sciende and the sustainable management of marine resources: from Rio to Johannesburg.. Frontiers Ecol Environ, 1: 190-196.

Behrenfeld, M.J. and Falkowski, P.G. 1997. Photosynthetic Rates Derived from Satellite-based Chlorophyll Concentration. Limnol. Oceanogr., 42(1), 1-20.

Bernal, P. 1981. A review of the low frequency response of the pelagic ecosystem in The California Current. CalCOFI Rep, 22: 49-62.

Bundy, A., Lilly, G.R. and Shelton, A. 2000. A mass balance model of the Newfoundland-Labrador Shelf. Can Tech Rep Fish Aquat Sci, 2310:xiv + 157 p.

California Department of Fish and Game. 2004. Abalone Recovery and Management Plan. Draft. URL: http://www.dfg.ca.gov/mrd/armp. Fecha de acceso: septiembre 2004.

Chávez, E.A., Garduno, M. and Arreguín-Sánchez, F. 1993. Trophic dynamic structure of Celestun Lagoon, Southern Gulf of Mexico, p. 186-192. En: V. Christensen and D. Pauly, (Eds). 1993. Trophic models of aquatic ecosystems. ICLARM Conf. Proc. 26, 390 p.

Chávez-Rosales, S. 2006. El papel de los manglares en la producción de las comunidades acuáticas de Bahía Magdalena, BCS. PhD Thesis. CICIMAR-IPN. 127pp.

Christensen, V. and Pauly, D. 1992. Ecopath II - a software for balancing steady-state ecosystem models and calculating network characteristics. Ecological Mod, 61: 169-185.

Christensen, V. and Pauly, D. 1998. Changes in models of aquatic ecosystems approaching carrying capacity. Ecol App, 8 (supl): s104-s109.

Christensen, V., Walters, C.J. and Pauly, D. 2000. Ecopath with Ecosim: a User's Guide. Fisheries Centre, University of British Columbia, Vancouver, Canada and ICLARM, Penang, Malaysia. 130 p.

Christensen, V. and Walters, C.J. 2004. Ecopath with Ecosim: methods, capabilities and limitations. Ecological Modelling, 172: 109-139.

Cruz-Escalona, V. 1998. Análisis trófico de la ictiofauna de Laguna San Ignacio, Baja California Sur, México. CICIMAR-IPN. México. Tesis de Maestría. 128 pp.

Del Monte-Luna, P. 2004. Caracterización del Centro de Actividad Biológica del Golfo De Ulloa, BCS, México, bajo un enfoque de modelación ecológica. PhD Thesis. CICIMAR-IPN. México. 86pp.

Duarte, L.O., García, C.B. 2004. Trophic role of small pelagic fishes in a tropical upwelling ecosystem. Ecol Modelling, 172: 323-338.

FAO. 2004. Código de Conducta para la Pesca Responsable. URL: http://www.fao.org/fi/agreem/codecond/codecons.asp . Fecha de acceso: septiembre 2004.

Félix-Uraga, R., Alvarado-Castillo, R.M. and Carmona-Piña, R. 1996. The sardine fishery along the western coast of Baja California, 1981 to 1994. CalCOFI Rep, 37: 188-192.

Félix-Uraga, R. 2006. Dinámica poblacional de la sardine del Pacífico *Sardinops sagax* (Jenyns 1842) (Clupeiformes: Clupeidae) en la costa oeste de Baja California Sur y el sur de California. Tesis de Doctorado. CICIMAR-IPN. 85pp.

Froese, R. and Pauly, D. (Editors). 2001. FishBase. World Wide Web electronic publication.URL: www.fishbase.org, Access date: September 2001.

Funes-Rodríguez, R., Hernández-Rivas, M.E., Saldierna-Martínez, R.J., Hinojosa-Medina, A.T., Avendaño-Ibarra, R. and Jiménez-Rosenberg, S.P.A. 2000. Composición y abundancia del ictioplancton del Golfo de Ulloa, Baja California Sur, un Centro de Actividad Biológica. En: BAC: Centro de Actividad Biológica del Pacífico Mexicano. Lluch-Belda, D., Elorduy-Garay, J., Lluch-Cota, S.E., and Ponce-Díaz, G. p. 185-197. Centro de Investigaciones Biológicas del Noroeste. 367pp.

Guzmán del Proo, S. 1994. Biología, ecología y dinámica de la población del abulón (*Haliotis* spp.) de Baja California, México. ENCB-IPN, México. Tesis doctoral. 173 pp.

Hernández-Guerrero, C., Casas-Valdez, M. and Ortega-García, S. 1999. Cosecha comercial del alga roja *Gelidium robustum* en Baja California Sur, México. Rev Biol. Mar Oceanogr, 34: 91-97.

Jarre-Teichmann, A. and Christensen, V. 1998. Comparative modeling of trophic flows in four large upwelling ecosystems: global versus local effects. p. 423-443. En: Durand M, Cury P, Mendelssohn R, Roy C, Bakun A and Pauly D (eds.) Global versus local changes in upwelling systems, Orstom, Paris, 594 pp.

Jarre-Teichmann, A. and Pauly, D. 1993. Seasonal changes in the Peruvian Upwelling ecosystem, p. 307-314. En: V. Christensen and D. Pauly, (Eds). 1993. Trophic models of aquatic ecosystems. ICLARM Conf. Proc. 26, 390 p

Krebs, C.J., Danell, K., Angerbjorn, A., Agrell, J., Berteaux, D., Brathen, K.A., Danell, O., Erlinge, S., Fedorov, V., Fredga, K., Hjalten, J., Hogstedt, G., Jonsdottir, I.S., Kenney, A.J., Kjellen, N., Nordin, T., Roininen, H., Svensson, M., Tannerfeldt, M. and Wiklund, C. 2003. Terrestrial trophic dynamics in the Canadian Arctic. Can J Zool, 81: 827–843.

Latour, R.J., Brush, M.J. and Bonzek, C.F. 2003. Toward ecosystem-based fisheries management: strategies for multispecies modeling and associated data requirements. Fisheries 28:10-22.

Le Boeuf, B.J., Aurioles, D.A., Condit, R., Fox, C., Gisiner, R., Romero, R. and Sinsel, F. 1983. Size and distribution of the California sea lion population in Mexico. Proc Calif Acad Sci, 43: 77-85.

León-Carballo, G. and Muciño-Díaz, M. 1996. Pesquería de abulón, p. 15-41. En: Casas-Valdez, M y. Ponce-Diaz G (eds.) Estudio del potencial pesquero y acuícola de Baja California Sur. CIBNOR, México. 350 pp.

Lluch-Belda, D. 1998. A proposal for IAI phase II research: Biological Actions Centers. Informe técnico. CIBNOR/CICIMAR/IAI. 35 pp.

Lluch-Belda, D. 1999. Centros de Actividad Biológica en la costa de Baja California. p. 49-64. En: Lluch-Belda, D., J. Elorduy-Garay, S. E. Lluch-Cota y G. Ponce-Díaz (eds) BAC's: Centros de Actividad Biológica del Pacífico Mexicano. CIBNOR-CONACyT.

Lluch-Belda, D., Crawford, R.J., Kawasaki, T., MacCall, A.D., Parrish, R.H., Schwartzlose, R.A. and Smith, P.E. 1989. World-wide fluctuations of sardine and anchovy stocks: The regime problem. South Afr J Mar Sci, 8:195-205.

Lluch-Belda, D., Hernández-Rivas, M., Saldierna-Martínez, R. and Guerrero-Caballero, R. 2000. Variabilidad de la temperatura superficial del mar en Bahía Magdalena, BCS. Oceánides, 15: 1-23.

Lluch-Belda, D. 2000. Centros de Actividad Biológica en la costa occidental de Baja California. En: BAC: Centro de Actividad Biológica del Pacífico Mexicano. Lluch-Belda, D., Elorduy-Garay, J., Lluch-Cota, S.E., and Ponce-Díaz, G. p. 49-64. Centro de Investigaciones Biológicas del Noroeste. 367pp.

Lluch-Belda, D., Lluch-Cota, D.B. and Lluch-Cota, S.E. 2003. Scales of Interannual Variability in the California Current System: associated physical mechanisms and ecological impacts. CalCOFI Rep, 44: 76-85.

Lluch-Cota, D.B., Wooster, W.S., Hare, S.R., Lluch-Belda, D. and Pares-Sierra, A. 2003. Principal modes and related Frequency of Sea Surface Temperature Variability in the Pacific Coast of North America. J Oceanogr, 59: 477-488.

Machena, C., Kolding, J. and Sanyanga, R.A. 1993. A preliminary assessment of the tropic structure of Lake Kariba, Africa, p. 130-137. En: Christensen V and Pauly D (eds). Trophic models of aquatic ecosystems. ICLARM Conf. Proc. 26, 390 p.

Maeda-Martínez, A., Reynoso-Granados, T., Solís-Marín, F., Leija-Tristán, A., Aurioles-Gamboa, D., Salinas-Zavala, C.A., Lluch-Cota, D.B. and Castro-Ormart, P. 1993. A modelo to explain the formation of catarina scallop, Argopecten circularis (Sowerby, 1835) beds, in Magdalena Bay, México. Aquaculture and Fisheries Management, 24: 323-339.

Mangels, K.F. and Gerrodette, T. 1994. Report on cetacean sightings during a marine mammals survey in the Eastern Pacific Ocean and the Gulf of California aboard the NOAA ships MacArthur and David Starr Jordan, July 28 – November 2, 1992. Technical memorandum NOAA-TM-SWFC-200. NOAA, 52 pp.

Mantua, N.J. 2000. Pacific Decadal Oscillation Index. URL: http://jisao.washington.edu/pdo/. Access date: April 2004.

Martell, S.J., Essington, T.E., Lessard, B., Kitchell, J.F., Walters, C.J. and Boggs, C.H. 2005. Interactions of productivity, predation risk, and fishing effort in the efficacy of marine protected areas for the central Pacific. Canadian Journal of Fisheries and Aquatic Sciences 62: 1320-1336.

Massó-Rojas, J.A. 1996. Pesquería de almeja catarina, p 71-85. En: Casas-Valdez M y Ponce-Diaz G (eds). Estudio del potencial pesquero y acuícola de Baja California Sur. CIBNOR, México. 350 pp.

McGowan, J.A., Chelton, D.B. and Conversi, A. 1996. Plankton patterns, climate and change in the California Current. CalCOFI Rep, 37: 45-68.

Medley, P.K. 2002. Climate change and long-term fluctuations of commercial catches: the possibility of forecasting. FAO Fish. Tech Pap, No 410.

MFAC. 2003. Technical Guidance for Implementing an Ecosystem-based Approach to Fisheries management. Final Draft. NOAA. URL: www.nmfs.noaa.gov/mafac/Documents/mafac_rev_5th_7Final%20wref.pdf.

Morales Bojórquez, E. 2004. Estimación del rendimiento de la pesquería de sardina Monterrey (*Sardinops caeruleus*) de Bahía Magdalena, Baja California Sur, México: un análisis de riesgo e incertidumbre basado en el teorema de Bayes. Tesis de Doctorado. CICIMAR-IPN. México. 412pp.

Morales-Zárate, M.V., Arreguín-Sánchez, F., López-Martínez. J, and Lluch-Cota, S.E. 2004. Ecosystem trophic structure and energy flux in the Northern Gulf of California, México. Ecol Mod, 174: 331-345.

Nidzgorski, D.A. 2000. Carbon export from surface waters of Monterey Bay. PhD Thesis. Stanford University, MABARI. URL: www.mbari.org/education/internship/ 00interns/00internpapers/dan.pdf. Access date: August 2004.

Oke, P.R. and Middleton, J.H. 2000. Topographically induced upwelling off eastern Australia. Journal of Physical Oceanography 30: 512-531.

Odum, E.P. 1969. The Strategy of Ecosystem Development. Science, 164: 262-270.

Olivieri, R.A., Cohen, A. and Chavez, F.P. 1993. An ecosystem model of Monterey Bay, California, p. 315-322. En: Christensen, V. and Pauly, D. (eds) Trophic models of aquatic ecosystems. ICLARM Conf. Proc. 26, 390 p.

Pauly, D. 1980. On the interrelationships between natural mortality, growth parameters, and mean environmental temperature in 175 fish stocks. J Cons Int Explor Mer, 39: 175-192.

Pauly, D. and Christensen, V. 1995. Primary production required to sustain global fisheries. Nature, 374: 255-257.

Pauly, D., Trites, A.W., Capuli, E. and Christensen, V. 1998. Diet composition and trophic levels of marine mammals. ICES J Mar Sci, 55:467-481

Platt, T. and Sathyendranath, S. 1988. Oceanic primary production: estimation by remote sensing at local and regional scales. Science, 241:1613-1620.

Polovina, J.J. 1984. Model of a coral reef ecosystems I. The ECOPATH model and its application to French Frigate Shoals. Coral Reefs, 3: 1-11.

Ponce-Díaz, G. 2004. Efecto de la mortalidad por pesca y la variabilidad ambiental en la pesquería de abulón. PhD Thesis. CICIMAR-IPN. México. 130pp.

Schwartzlose, R., Alheit, J., Bakun, A., Baumgartner, T.R., Cloete, R., Crawford, R.J.M., Fletcher, J., Green-Ruiz, Y., Hagen, E., Kawasaki, T., Lluch-Belda, D., Lluch-Cota, S.E., MacCall, A.D., Matsuura, Y., Nevarez-Martínez, M.O., Parrish, R.H., Roy, C., Sierra, R., Shust, K.V., Ward, M.N. and Zuzunaga, Z. 1999. Worldwide large-scale fluctuations of sardine and anchovy populations. S. Afr. J. mar. Sci. 21: 289-347.

Sepúlveda-Medina, A. 1999. Dinámica poblacional de los peneidos comerciales en el alto, centro Golfo de California, Topolobampo y costa occidental de la Baja California en el litoral del Pacífico mexicano. ICML-UNAM, México. Tesis doctoral. 147 p.

Serviere-Zaragoza, E., Gomez-Lopez, D. and Ponce-Diaz, G. 1998. The natural diet of the green abalone (*Haliotis fulgens* Philippi) in the southern part of its range, Baja California Sur, Mexico, assessed by an analysis of gut contents. J. Shellfish Res, 17: 777-782.

Shannon, J.L., Field, J.G. and Moloney, C.L. 2004. Simulating anchovy-sardine regime shifts in the southern Benguela ecosystem. Ecological Mod, 172: 269-281.

Shannon, L.J., Moloney, C.L., Jarre-Teichmann, A. and Field, J.G. 2003. Trophic flows in the southern Benguela during the 1980s and 1990s J Mar Syst, 39: 83-116.

Steven, J., Martell, D., Beattie, A.I., Walters, C.J., Nayar, T. and Briese, R. 2002. Simulating Fisheries Management Strategies in the Strait of Georgia Ecosystem using Ecopath and Ecosim. Fisheries Centre Research Reports. 10, 2: 155pp.

Tegner, M.J., Dayton, P.K., Edwards, P.B. and Riser, K.L. 1996. Is there evidence for long-term climatic change in southern California kelp forests? CalCOFI Rep, 37: 111-126.

Trites, A.W., Livingston, P.A., Mackinson, S., Vasconcellos, M.C., Springer, A.M. and Pauly, D. 1999. Ecosystem Change and the Decline of Marine Mammals in the Eastern Bering Sea: Testing the Ecosystem Shift and Commercial Whaling Hypotheses. The Fisheries Centre Research Reports, 7, 1: 106pp.

UHSLC. 2004. University of Hawaii Sea Level Center. URL: http://uhslc.soest.hawaii.edu/. Access date: May 2004.

Ulanowicz, R.E. 1986. Growth and Development: Ecosystem Phenomenology. Springer Verlag (reprinted by iUniverse, 2000), New York. 203 pp.

Ulanowicz, R.E. and Norden, J.S. 1990. Symmetrical overhead in flow and networks. Int J Systems Sci, 21: 429-437.

Vega-Velázquez, A., Espinoza-Castro, G. and Gómez Rojo, C. 1996. Pesquería de langosta Panulirus spp. p 227-262. En: Casas-Valdez M y Ponce-Diaz G (eds). Estudio del potencial pesquero y acuícola de Baja California Sur. CIBNOR, México. 350 pp.

Walters, C., Christensen, V. and Pauly, D. 1997. Structuring dynamic models of exploited ecosystems from trophic mass-balance assessments. Reviews in Fish Biology and Fisheries, 7: 139-172.

Walters, C., Pauly, D. and Christensen, V. 1999. Ecospace: Prediction of mesoscale spatial patterns in trophic relationships of exploited ecosystems, with emphasis on the impacts of marine protected areas. Ecosystems, 2:539-554.

Walters, C.J., Kitchell, J.F., Christensen, V. and Pauly, D. 2000. Representing density dependent consequences of life history strategies in aquatic ecosystems: EcoSim II. Ecosystems, 3: 70-83.

Zetina-Rejón, M.J., Arreguín-Sánchez, F. and Chávez, E. 2004. Exploration of harvesting strategies for the management of a Mexican coastal lagoon fishery. Ecological Mod 172: 361-372.

Appendix A. Ecopath predator-prey (diet) matrix for the Gulf of Ulloa (unbalanced model).

	Prey/predator	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
1	Phytoplankton	0.88	0.25				0.09	0.09											0.96					
2	Phytobenthos	0.04	0.28	0.00				0.08			0.01							0.00		0.00				
3	Zooplankton	0.00	0.00		0.03					0.10	0.01		0.10	0.07				0.01	0.04	0.00	0.02			
4	Zoobenthos		0.15	0.70	0.21	1.00	0.62	0.10	0.83	0.82	0.98	1.00	0.70	0.64	0.68	0.41	1.00			1.00			0.76	
5	Lobster														0.01	0.00								0.00
6	Red crab			0.07									0.04			0.00		0.56	0.00				0.24	0.12
7	Abalone			0.02												0.07								0.08
8	Shrimp								0.10	0.05			0.06	0.10	0.06	0.09								0.08
9	Clam			0.08												0.25		0.18						0.43
10	Ariidae														0.01	0.01						0.02		
11	Carangidae															0.00					0.00	0.00		0.00
12	Gerreidae								0.04						0.07							0.00		
13	Haemulidae														0.03	0.07						0.02		
14	Lenguados (‘soles’)			0.03											0.10			0.25				0.12		
15	Sciaenidae															0.06						0.00		
16	Serranidae			0.00					0.04													0.06		0.00
17	Elasmobranches																							0.01
18	Triglidae									0.03					0.01	0.01						0.00		
19	Merluccidae			0.02											0.01							0.10		0.10
20	Sardine	0.00							0.00	0.00				0.09	0.00	0.00		0.00	0.00	0.00	0.12	0.02		0.05
21	Other fish														0.01	0.02					0.86	0.66		0.10
22	Birds															0.00								0.04
23	Dolphins															0.00								
24	Whales															0.00								
25	Sea lion															0.01								
26	Detritus	0.08	0.32	0.09	0.76		0.30	0.73					0.10	0.10										

Trophic Model for the Ecosystem of La Paz Bay, Southern Baja California Peninsula, Mexico[1]

Francisco Arreguín-Sánchez, Pablo del Monte-Luna, Juan G. Díaz-Uribe[2], Marisela Gorostieta, Ernesto A. Chávez and Rocío Ronzón-Rodríguez
Centro Interdisciplinario de Ciencias Marinas del IPN Apartado Postal 592, La Paz,
Baja California Sur, México

Abstract

A trophic ecosystem model of La Paz Bay, on the southern Baja California Peninsula, was improved from one previously constructed by adding 13 functional groups. In the bay, small-scale fisheries take place, which are aimed at finfish, shark and clams. Also there is a pilot shrimp trawl fishery. At the mouth of the bay, communicating with the Gulf of California, there is the insular complex of Espíritu Santo, which was declared as a protected area by the federal government. The aim for the construction of a model of La Paz Bay is to help run scenarios of the fleets and MPA operating together to support fisheries management within an ecosystem context. We present a full description of the ecosystem structure and basic functions based on Ecopath software. The Ecosim model is used to calibrate time series of relative abundance of several groups, which served as the basis for spatial modeling. Preliminary simulations suggest a limited effect of the MPA around Espiritu Santo Island on marine birds, sharks and red snapper.

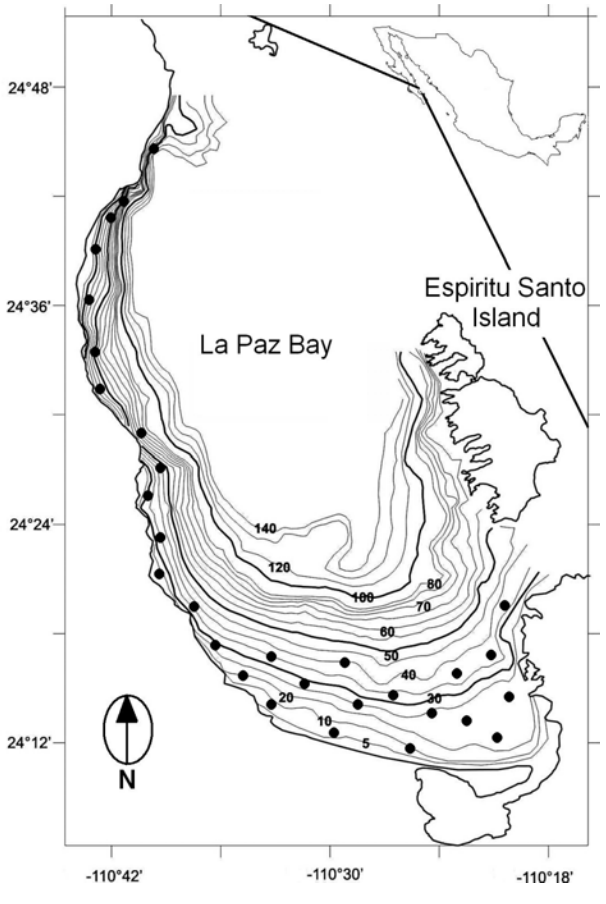


Figure 1. La Paz Bay. Lines refer to depth in meters and dots indicate data collection points for the experimental small-scale shrimp trawl fishing.

Introduction

La Paz Bay (Figure 1) is located on the south of the Peninsula of Baja California (24°06'–24°47' North and 110°16'–110°45' West), with an area of 1934 km^2. The Espiritu Santo Island partially closes the mouth of the bay, leaving a small opening to the south (about 6 km wide and 19 m deep) and a larger one to the north (27 km wide and 300 deep).

Ramírez-Rodríguez (1997) reported around 400 fishers using 7 m vessels with engines of 40–60 hp; hand-held hooks, hook-and-lines and gillnets are the most important fishing gears. Diving and fixed nets are also common fishing methods. The species caught can be grouped by their economic importance (Ramírez-Rodríguez and Rodríguez,

---

[1] Cite as: Arreguín-Sánchez, F., del Monte-Luna, P., Díaz-Uribe, J.G., Gorostieta, M., Chávez, E.A. and Ronzón-Rodríguez, R. 2007. Trophic model for the ecosystem of La Paz Bay, Southern Baja California Peninsula, Mexico, p. 134–160. *In*: Le Quesne, W.J.F., Arreguín-Sánchez, F. and Heymans, S.J.J. (eds.) INCOFISH ecosystem models: transiting from Ecopath to Ecospace. Fisheries Centre Research Reports 15(6). Fisheries Centre, University of British Columbia [ISSN 1198-6727].

[2] Centro Regional de Investigación Pesquera del Instituto Nacional de la Pesca, Km 1 carretera a Pichilingue, La Paz, Baja California sur, México

1990; Abitia-Cárdenas *et al.*, 1994; Ramírez-Urbán and Ramírez-Rodríguez, 1997); these are the target finfish species snappers (Lutjanidae) and groupers (Serranidae), and mollusks, including the clam, squalid callista (*Megapitaria squalida*) and recently the giant squid (*Dosidiscus gigas*).

Catches of target species fluctuate during the year, and fishers do not follow rigid fishing patterns. In practice, most fishers targeting finfish operate under an open access scheme. Controls to fishing are implemented through minimum legal sizes, based on local information and experience with similar stocks in adjacent regions. Arreguín-Sánchez *et al.* (2004) mentioned several problems associated to artisanal fisheries in La Paz Bay:

- annual catches tend to decrease and the number of fishers to increase;
- there is not a strong control in the number of boats that compose fleets;
- gillnets are claimed to be inefficient and to cause mortality of non-target species;
- habitats are being altered as a result of operation of some fishing gear;
- there are conflicts with other users of the coastal zone;
- illegal fishing occurs;
- there is a growing interest in conservation, particularly around islands, which are the preferred fishing grounds and were declared a natural reserve
- the market is unpredictable and fluctuates with no apparent pattern.

Fishing activities by the artisanal fishery occur along the bay with many landing places along the coast. Some well-known locations where concentration of landings is high are shown in Figure 2.

Recently, fishers organized in cooperatives claimed access to shrimp stock within the bay and asked the federal and state governments to evaluate the possibility of initiating a small-scale shrimp trawl fishery. Initial scientific information was required to evaluate the available shrimp biomass and potential allowable fishing rates. However, given the experience gained within the Incofish project (www.incofish.org) on the impact of bycatch mortality associated with shrimp trawling, we suggested the need to evaluate the potential impact of trawling. Even when Mexican laws prohibit trawling within bays and coastal waters, such a claim was based on the use of a low-impact net developed by the National Institute of Fishing known locally as 'Magdalena 1', which operates in Magdalena Bay on the Pacific coast of the southern Baja California Peninsula.

The aim of this contribution is the construction and description of a trophic model for the ecosystem of La Paz Bay, providing information on its structure, function and organization, as well as the basis for dynamic and spatial simulations.

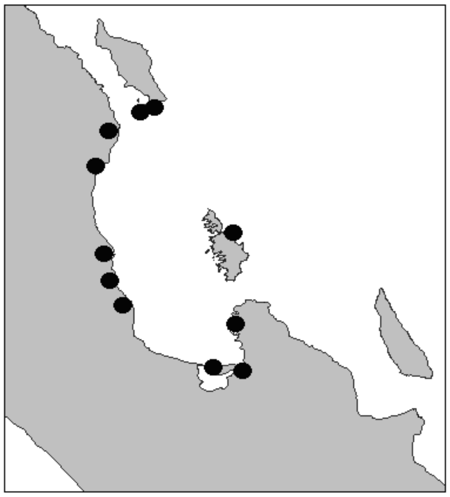


Figure 2. Location for the main fishing landing places in La Paz Bay associated to fishing grounds (adapted from Arreguín-Sánchez *et al.*, 2004)

MATERIALS AND METHODS

Based on two previous models by Arreguín-Sánchez *et al.* (2004) and Díaz-Uribe *et al.* (2007), an improved trophic model for the ecosystem of La Paz Bay (Figure 1) was constructed by adding 13 functional groups to the former contribution. New information consists of species of demersal communities that were captured through a shrimp trawl net operated by small boats with out-board engines. Presently, the model consists of a total of 48 groups: 29 fish, 3 marine mammals, 2 sharks, 1 marine bird, 5 macroinvertebrates including clams, shrimp and cephalopods, 2 epifauna, 2 zooplankton, 3 primary producers and 1 detritus (see Appendix A for species added to previous models that represent the new functional groups). The improved model also includes 20 commercial stocks captured by 5 gears: gillnet, hook, diving, shark-targeting and small-scale potential shrimp trawling (Table 1). Present models corresponded to the ecosystem during the period of 2005 and 2006.

Ecosystem models

To construct the trophic ecosystem model we used the suite of programs 'Ecopath with Ecosim' or EwE (Pauly *et al.*, 2000; Christensen and Walters, 2004); Ecopath describes and quantifies the trophic interactions and flows of biomass in an ecosystem (Christensen and Pauly, 1992). In order to evaluate the dynamics of fishing, we used the Ecosim model (Walters *et al.*, 1997), within which we can consider the effect of environmental forcing as well as changes in vulnerability to predation. For spatial representation we used the Ecospace model (Walters *et al.*, 2000) which describes distribution of biomasses of functional groups. Ecospace dynamically allocates biomass across a grid map and represents movements of organisms from a bad habitat to a better habitat. The quality of the habitat is given by the risk of predation and the amount of food available. The model considers relative dispersal rates, vulnerabilities to predation and relative feeding rate. For simulations, identification of habitats is required and habitats are represented by cells on the base map for biomass distribution. Functional groups are allocated to habitats and distribution of biomasses can be obtained as well as distribution of fleets. The design of the maps allows the representation of marine protected areas (MPAs) to simulate their impact on both individual and ecosystem levels.

Table 1. Commercial catch composition per fleet/gear in La Paz Bay ($g \cdot m^{-2}$)

Functional group / Species	Gill-net	Hook	Diving	Shark – targeting	Shrimp trawl	Shrimp trawl bycatch
Red grouper Adult		0.040				
Red grouper Juv.		0.007				0.0029
Sharks				0.019		0.0001
Groupers	0.003	0.001				0.0366
Jacks	0.003	0.005		0.001		0.0002
Whitefish		0.006				0.0002
Small sharks	0.001			0.005		
Snappers	0.002	0.004				0.0018
Triggerfish	0.002	0.002				0.0092
Parrotfish	0.003					
Sardines						0.0040
Large pelagics	0.001					
Haemulidae	0.020	0.001				0.0336
Taetrodontidae						0.0038
Labridae						0.0001
Priacanthidae	0.001					0.0001
Gerreidae (mojarras)	0.002					0.0165
Diodontidae						0.0331
Rhinobatidae						0.0078
Triglidae						0.0078
Batrachoididae						0.0052
Sparidae						0.0051
Ophidiidae						0.0014
Synodontidae						0.0185
Sciaenidae						0.0049
Ariidae						0.0044
Flatfishes	0.002					0.0131
Urolophidae						0.0038
Giant squid		0.402				
Squalid callista			0.028			
Brown shrimp					0.042	
Clams			0.002			
Crabs/octopus			0.001			0.0007

Groups definition and parameterization

Previous models were constructed emphasizing artisanal finfish fisheries, but in this contribution the addition of a potential artisanal shrimp trawling fleet involves the consideration of mortality from bycatch. In this sense 25 of the 48 functional groups appear as bycatch, and of those, about 14 species also appear as commercial catch in other fisheries. A report by Díaz-Uribe *et al.* (2007) considered shrimp bycatch from the industrial fleet whose operation stopped in the early 2000s. For this reason, the functional groups in the model presented here were defined by considering bycatch captured by the artisanal shrimp boats, the target species by commercial fleets as well as some charismatic species such as marine mammals and aquatic birds.

The main criterion for the balancing process, given biomass, catch, diets, production/biomass (P/B) and consumption/biomass (Q/B) ratios, was a value for ecotrophic efficiency, or EE<1. In some cases, when biomass was not an input, an EE value was assumed, the value taken from the same group in another model of a similar ecosystem. Once data were introduced the first time, the model was not balanced. In our case, some EE values were very high, and since diets are the most uncertain input data, we modified slightly the proportion of prey in diets. Once most EE were close but higher than unity, we used the automatic balance routine provided with EwE given variation to input data (40% in diets and biomasses, and 10% in P/B and Q/B ratios).

Table 2. Input data for Ecopath model of La Paz Bay. Bold italic numbers were estimated by the model (see Appendix A for species). P = production, B = biomass, Q = Consumption, EE = ecotrophic efficiency

Group name	Trophic level	Biomass ($t{\cdot}km^{-2}$)	P / B ($year^{-1}$)	Q / B ($year^{-1}$)	EE	P / Q
marine birds	***3.71***	0.0010	0.934	10.380	***0.256***	***0.090***
sea lion	***3.88***	0.0075	1.576	19.700	***0.110***	***0.080***
fin whale	***3.12***	0.2350	3.197	26.639	***0.001***	***0.120***
dolphin	***4.31***	0.0073	1.278	18.250	***0.119***	***0.070***
red snapper adults	***3.21***	0.1100	0.426	8.276	***0.957***	***0.051***
red snapper juv.	***3.74***	0.2110	0.331	3.000	***0.950***	***0.110***
deep grouper	***3.66***	0.0681	0.210	2.900	***0.730***	***0.072***
sharks	***4.21***	0.0271	1.050	9.700	***0.950***	***0.108***
groupers	***3.59***	0.1100	0.417	3.900	***0.978***	***0.107***
jacks	***3.81***	0.0511	1.360	9.000	***0.945***	***0.151***
whitefishes	***3.24***	0.1280	0.310	4.100	***0.873***	***0.076***
small shark	***4.04***	0.0293	0.440	5.300	***0.950***	***0.083***
snappers	***3.60***	0.0718	0.480	5.400	***0.927***	***0.089***
triggerfishes	***3.26***	0.1060	0.750	5.100	***0.945***	***0.147***
parrot fish	***2.12***	0.1170	0.890	12.000	***0.520***	***0.074***
sardines	***2.46***	5.4590	2.440	14.900	***0.911***	***0.164***
dolphinfish	***3.70***	0.1580	2.080	11.640	***0.950***	***0.179***
large pelagics	***4.27***	0.0287	0.320	6.800	***0.792***	***0.047***
grunts	***2.92***	1.5730	0.600	5.500	***0.950***	***0.109***
puffers	***2.77***	1.4740	0.510	8.000	***0.751***	***0.064***
deep demersals	***2.70***	5.8490	1.320	12.000	***0.950***	***0.110***
wrasses	***3.17***	***0.0371***	1.430	13.500	0.911	***0.106***
bigeyes	***2.45***	***0.0184***	0.630	9.300	0.672	***0.068***
mojarras	***3.03***	***0.2300***	0.900	7.300	0.660	***0.123***
porcupinefishes	***3.11***	***0.0823***	0.500	4.900	0.815	***0.102***
guitarfishes	***3.34***	***0.0418***	0.510	4.100	0.591	***0.124***
searobins	***3.17***	***0.5440***	0.400	6.100	0.712	***0.066***
toadfishes	***3.85***	***0.0775***	0.570	7.500	0.950	***0.076***
porgies	***3.22***	***0.3430***	0.410	5.100	0.950	***0.080***
cusk-eels	***2.48***	***0.1630***	0.700	23.200	0.714	***0.030***
lizardfishes	***4.03***	***0.0829***	0.880	8.100	0.943	***0.109***
croakers	***2.59***	***0.0474***	0.550	6.500	0.599	***0.085***
catfishes	***2.94***	***0.0267***	1.600	7.700	0.534	***0.208***
flatfishes	***3.07***	***0.2520***	1.300	11.700	0.561	***0.111***
round rays	***3.06***	***0.0530***	0.310	6.000	0.950	***0.052***
giant squid	***3.46***	0.4180	5.419	47.820	0.866	***0.113***
squalid callista	***2.43***	0.1150	2.121	10.604	0.855	***0.200***
brown shrimp	***2.24***	0.4140	4.068	25.733	0.900	***0.158***
clams	***2.36***	3.9400	2.350	10.604	0.695	***0.222***
crabs/octopus	***2.34***	4.3450	2.120	8.500	0.950	***0.249***
infauna	***2.00***	***1.6870***	8.120	27.000	0.853	***0.301***
polychaeta	***2.02***	***2.1390***	4.200	11.600	0.879	***0.362***
zooplankton	***2.16***	7.2510	21.550	119.700	0.950	***0.180***
jelly-zooplankton	***2.00***	3.1010	30.700	118.445	0.872	***0.259***
phytoplankton	***1.00***	8.5770	361.561		0.219	
macro algae	***1.00***	1.1330	20.142		0.657	
reef corals	***1.00***	2.7510	6.168		0.895	
detritus	28.00				0.222	

RESULTS

Ecopath model

After consideration of the functional groups in previous models, we disaggregated fish groups to consider more specifically the structure of shrimp trawl bycatch. With the inclusion of the new functional groups, input data are as shown in Table 2 for biomass, production/biomass and consumption/ biomass ratios and ecotrophic efficiency. The diet matrix is given in Appendix B. The previous model used as a base was that reported by Arreguín-Sánchez *et al.* (2004). Díaz-Uribe *et al.* (2007) reported some information on shrimp bycatch from about one decade ago, which was taken by industrial shrimp trawlers before prohibition of their operation. For the present model, we used part of the information in those models but we add explicitly some groups which appear in the small-scale trawl shrimp fishery, as represented in Table 3.

After the balancing process, several ecosystem parameters were estimated. The global ecosystem statistics are shown in Table 4, while key indices for the ecosystem are given in Appendix C.

The biological consistency of the trophic model was tested by examining key indexes (Christensen *et al.*, 2002); for example, the respiration/ assimilation (R/A) ratio cannot exceed 1, as respiration cannot exceed assimilation, and as expected this ratio is close to 1 for top predators and lower for low trophic levels. In this case, this ratio increased 9% with trophic level. On the other hand, the production/ respiration (P/R) ratio, which expresses the fate of the assimilated food, must take values much lower than 1 because of thermodynamic constraints.

Table 3. Sources of information for those functional groups not included in previous trophic models of La Paz Bay.

Group	Biomass (g·m^{-2})	Production / Biomass ratio (g·m^{-2}·y^{-1})	Consumption / Biomass ratio (g·m^{-2}·y^{-1})	Diet
Croaker	-	1	2	3
Guitarfish	-	3; 4	3; 4	3; 4
Cusk-eels	-	5	5	6
Flatfishes	-	5	7	8
Porgies	-	9	9	9
Dolphinfish	f.d.	1; 10	2; 10	11
Lizardfishes	-	1; 12	2; 12	13
Puffers	f.d.	5	5	14
Porcupinefish	-	1; 15	2; 15	15
Bigeyes	-	1; 15	2; 15	15
Wrasses	-	1; 15	2; 15	15
Toadfishes	-	1; 15	2; 15	15
Round rays	-	1; 15	2; 15	15

f.d. = field data; 1) Pauly (1980), using data reported by Allen and Robertson (1994); 2) Palomares and Pauly (1989), using data reported by Allen and Robertson (1994); 3) Arreguín-Sánchez *et al.* (2002); 4) Lercari (2006); 5) Galván-Piña and Arreguín-Sánchez (2007); 6) Godínez-Domínguez (1999) and Arreguín-Sánchez *et al.* (2002); 7) (P/B)/GE, assuming GE = 0.2; 8) Maeda-Martínez (1981) and Arreguín-Sánchez *et al.* (2002); 9) Arreguín-Sánchez *et al.* (1993) and Arreguín-Sánchez *et al.* (2004); 10) Alfaro (1996); 11) Aguilar- Palomino (1993); 12) Ruiz-Ramírez *et al.* (1997); 13) Hiatt and Strasburg (1960); 14) Raymundo-Huizar and Chiapa-Carrara (2000); 15) basic data taken from FishBase (Froese and Pauly, 2004)

Trophic level decomposition represented by trophic pyramids is shown in Figure 3, where system throughput, biomass and catch are compared. Essentially, the form of the pyramids indicates different structures according to how each attribute is distributed over the trophic levels, with the difference of the order of magnitude of the scale between attributes and the size of the pyramids' base being of relevance.

Table 4. Global statistics for the ecosystem of La Paz Bay, Mexico.

Parameter	Value	Units
Sum of all consumption	1619.344	t·km^{-2}·year^{-1}
Sum of all exports	2167.414	t·km^{-2}·year^{-1}
Sum of all respiratory flows	973.827	t·km^{-2}·year^{-1}
Sum of all flows into detritus	2784.688	t·km^{-2}·year^{-1}
Total system throughput	7545	t·km^{-2}·year^{-1}
Sum of all production	3461	t·km^{-2}·year^{-1}
Mean trophic level of the catch	3.32	t·km^{-2}·year^{-1}
Gross efficiency (catch/net p.p.)	0.000318	-
Calculated total net primary production	3140.849	-
Total primary production/total respiration	3.225	t·km^{-2}·year^{-1}
Net system production	2167.021	t·km^{-2}·year^{-1}
Total primary production/total biomass	58.501	t·km^{-2}·year^{-1}
Total biomass/total throughput	0.007	-
Total biomass (excluding detritus)	53.689	t·km^{-2}
Total catches	0.999	t·km^{-2}
Connectance Index	0.179	t·km^{-2}·year^{-1}
System Omnivory Index	0.178	-
Total market value	0.61	MXN
Total value	0.61	MXN
Total fixed cost	0.1	MXN
Total variable cost	0.14	MXN
Total cost	0.24	MXN
Profit	0.36	MXN

There are several ecosystem structure characteristics of interest; for example, the net efficiency, NE, decreases with trophic level, TL, which means that high TLs are less efficient than lower TLs, changing at a rate of 15% (Figure 4).

Figure 5 shows decreasing changes in production and respiration, with TL being the rate of change higher for respiration than production. Production decreases at a rate of 3% (expressed as log P), while respiration (log R) decreases at a rate of 22% per TL. A higher respiration rate with TL with respect to the production rate means that the loss of energy (respiration) through the TLs is higher than the loss of production. When both processes are associated as the log (P/R), the decreasing rate is about 20% per TL (Figure 6). The turnover rate, expressed as log (B/P) increases with TL at a rate of 50%, reflecting the biomass accumulation process increasing to higher TLs (Figure 7).

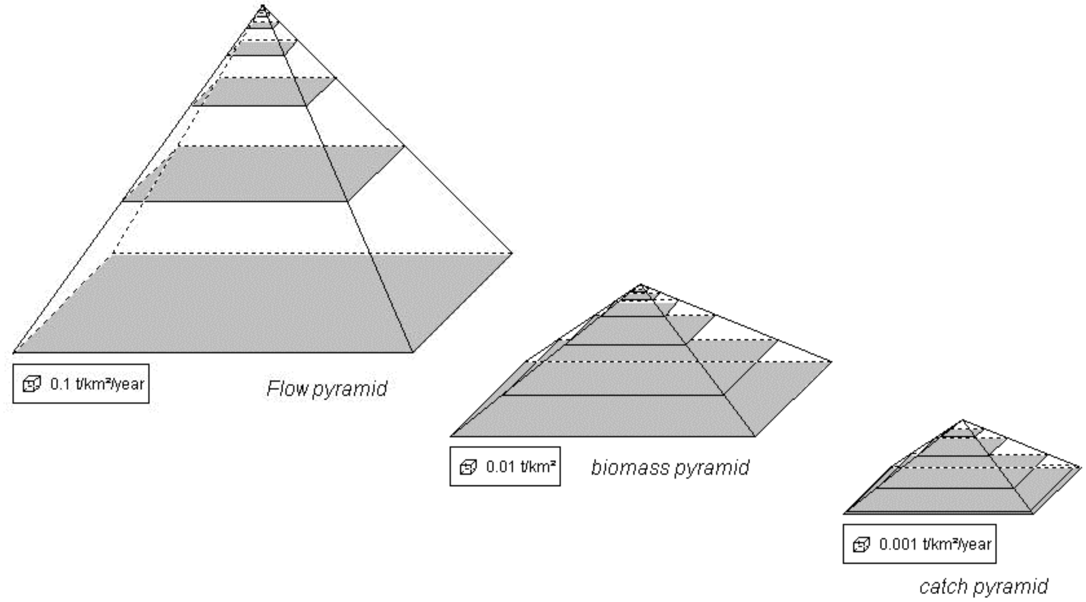
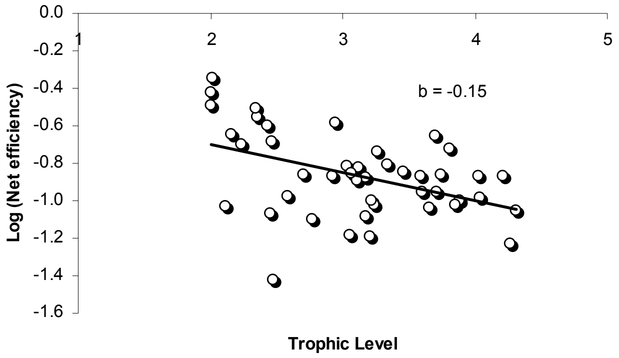


Figure 3. Trophic pyramids of flow, biomass and catch, for the La Paz Bay ecosystem. Note the difference of one order of magnitude in the scale for each pyramid.



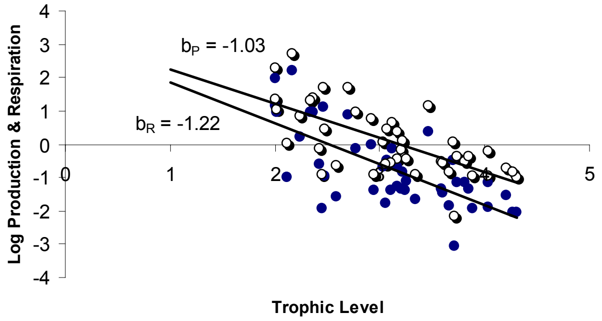


Figure 4. Changes in the net efficiency with trophic level. Net efficiency decreases at a rate of 15% per trophic level.

Figure 5. Rate of change of production and respiration with trophic level for the ecosystem of La Paz Bay, Mexico.

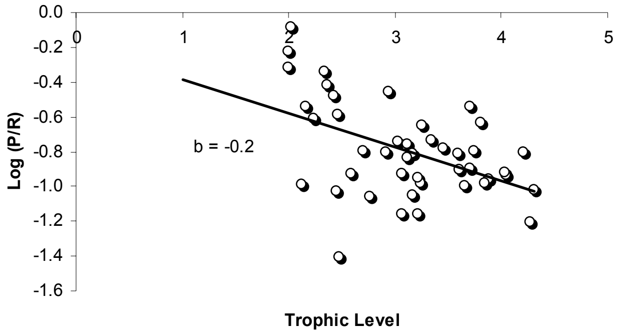


Figure 6. Decreasing of production/respiration ratio with trophic level.

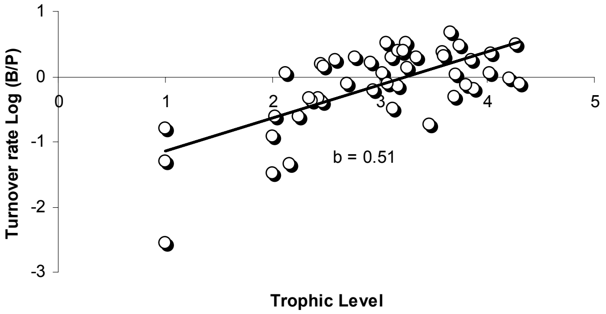


Figure 7. Trend of the turnover rate over the trophic levels. Slope indicates biomass accumulation and less production at a rate of 50% towards higher trophic levels.

Mixed trophic impact shows the positive or negative effects between groups through direct or non-direct prey-predator type relationships. Mixed impacts for selected commercial target species and marine mammals are shown in Figure 8; observe, for example, the positive impact of sardine as prey for several predators, the negative impact of the giant squid including the well-known cannibalism process, and the positive effect of shark exploitation on marine mammals.

Regarding shrimp trawling gear, Figure 9 shows how shrimp stock, as a target species, is related to others through a connectance diagram, where predation strength is represented by line thickness. Flounders, porgies, mojarras, grunts and croakers are the fish species that strongly predate on shrimp.

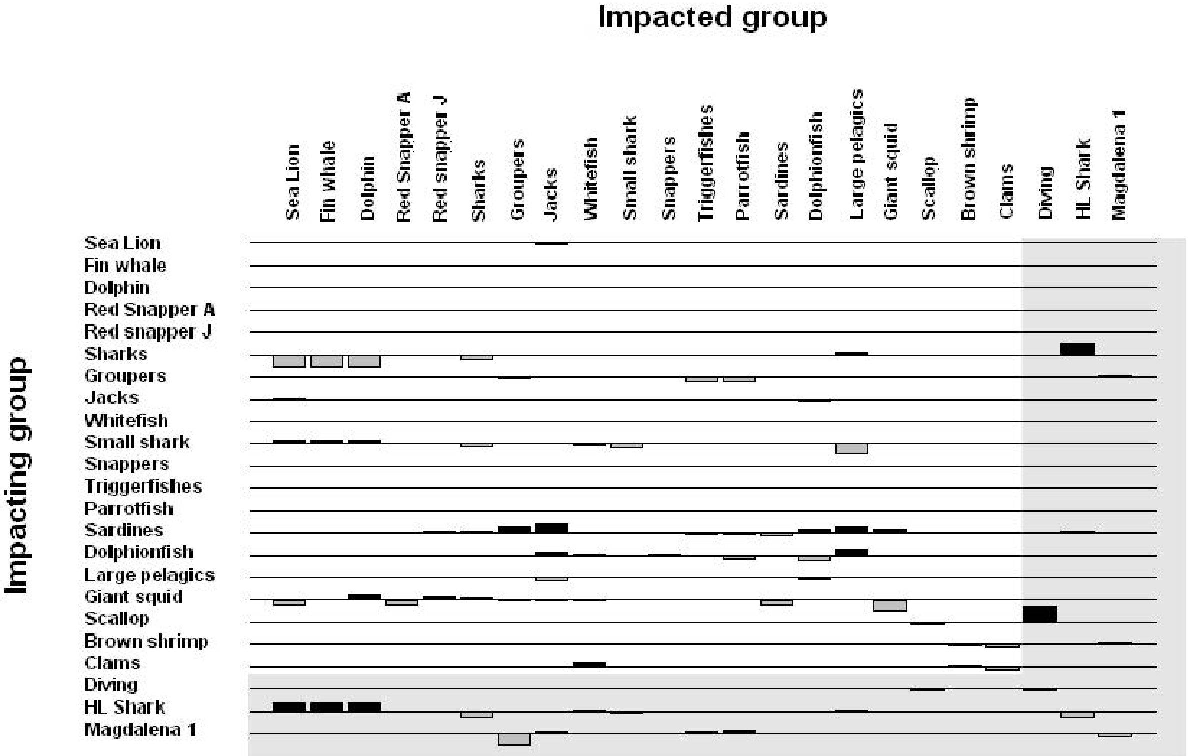


Figure 8. Mixed trophic impacts for selected commercial species and marine mammals in La Paz Bay, Mexico. Shadowed areas show the effects of fishing fleets.

The primary production required (PPR) to sustain the system is a measure of the minimum amount of production required for ecosystem functioning at the present state. The PPR per unit of biomass increases with TL, notably around TL≅4 (Figure 10).

The PPR to sustain consumption increases at a rate of 20% with TL, while the PPR to sustain harvest increases at a rate of 27%. In general terms, this suggests that ecosystems require more energy to sustain a fishery than consumption (Figure 11).

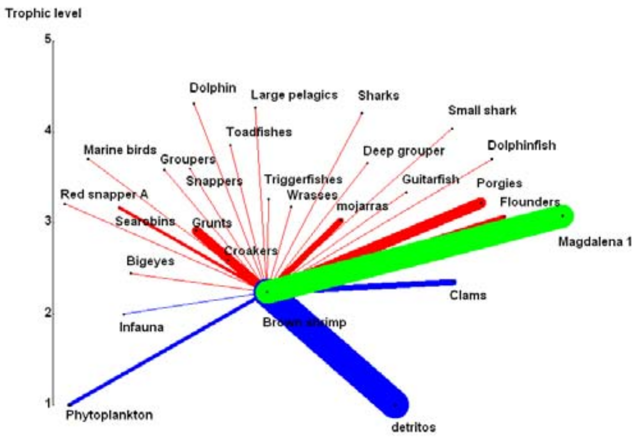


Figure 9. Connectance diagram emphasizing the relationships of the brown shrimp as potential target stock of a small-scale shrimp trawl fishery, with other functional groups in the ecosystem of La Paz Bay, Mexico. The thickness of line indicates the scale after predation strength, including the fishery.

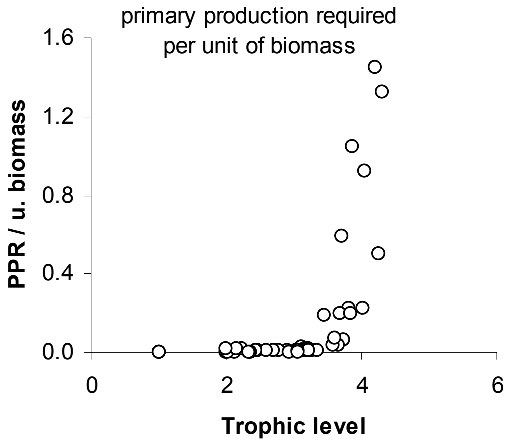


Figure 10. Primary production required per unit of biomass through trophic levels for La Paz Bay ecosystem, Mexico.

Figure 12 shows how fast the number of paths increases with TL. This is probably an intrinsic characteristic of the ecosystem since number of paths is associated to structure and complexity.

The ascendancy is a measure of ecosystem information weighted by the ecosystem size (given by the total system throughput). It decreases with TL as well as the overhead and capacity. Following Figure 13, ascendancy decreases at a rate of 30% higher than overhead over trophic levels which probably reflects differences in resilience by TL. Capacity, however, slightly increases with TL suggesting potential information that can be accumulated towards higher TL.

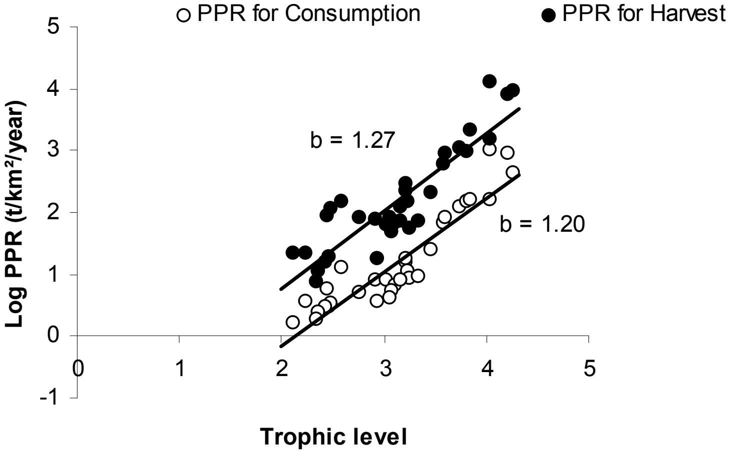


Figure 11. Primary production required to sustain consumption and harvest. Slopes indicates a rate of increase of primary production required by trophic level of 20% and 27%, respectively.

Ecosim model

There are no industrial fisheries operating in La Paz Bay. All fisheries are based on small boats, usually operating on a daily basis, even when the trips frequently involve overnight camping. Four fleets were identified with more than 20 stocks captured; however, statistical records go back no more than a decade and only for the most important species.

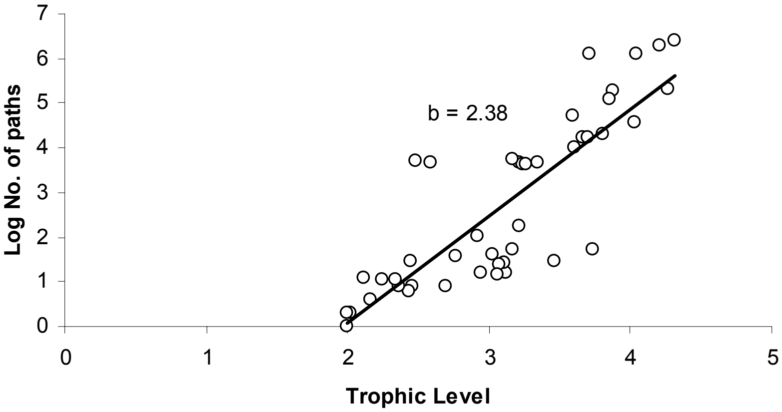


Figure 12. Change of the number of paths with trophic level indicating a strong increase of complexity of top predators.

We are including as a fifth gear the shrimp trawling net, which was operated as a pilot experiment to evaluate the possibility of development of a commercial activity. In this case, there are no records of yields with exception of those given in Appendix A corresponding to the 2005–2006 fishing season.

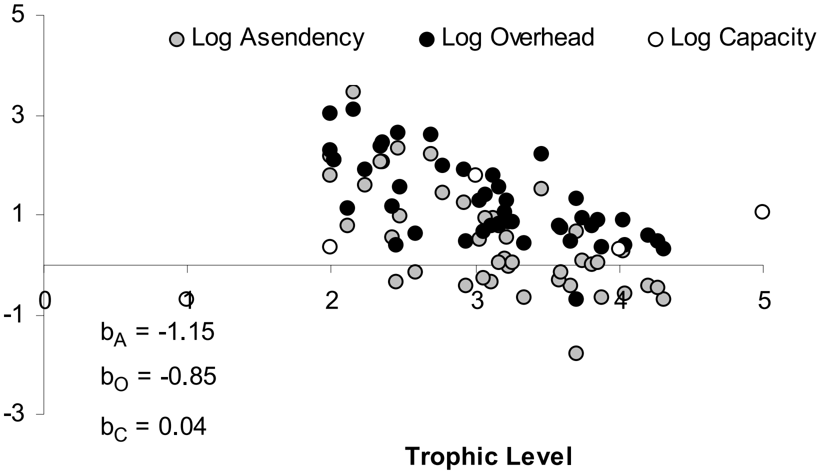


Figure 13. Changes in ascendancy, overhead and capacity with trophic level.

We used available records of catch per unit of effort of the main species as an index of relative abundance. Figure 14 shows the relative abundance for squalid callista, red snapper, grouper and shark, as well as changes in fishing effort measured as the number of fishing days. Fishing effort is given by arrival records, and since there is no specific information, we assume the fishing day as a measure of fishing effort. Figure 15 shows other target species for La Paz Bay. Relative cost of fleet/gear operation and corresponding profits were taken from Arreguín-Sánchez *et al.* (2004) and re-estimated when necessary considering the typical operation of boats and catch value (Table 5).

Effort and catch per unit of effort as a measure of relative abundance were used to fit simulated biomasses, using mean annual temperature as a forcing factor acting on primary producers. This forcing was introduced under the assumption that the production rate of primary producers is affected by the environment (Lluch-Cota *et al.*, 2007). Initial fitting results are shown in Figure 16. Fitting must be taken as a preliminary approach, since there are some aspects that must be considered for interpretation, especially prior to a management analysis. Time series were complete for 1992 to 2004 in only 4 stocks, while in another 5 species only the first 7 years of that period were available. For incomplete series, fitting could produce a bias on the simulated biomasses for recent years, as appears to occur with parrotfish.

Table 5. Distribution of costs (%) for operation of the small scale fleets in La Paz Bay, Mexico

Name of fleet	Fixed cost (%)	Effort related cost (%)	Sailing related cost (%)	Profit (%)
Gill net	19.5	0.2	19.4	60.9
Hook & line	19	20	0.3	60.7
Diving	4	15	15	66
Shark-targeting	4	15	25	56
Magdalena 1	5	35	15	45

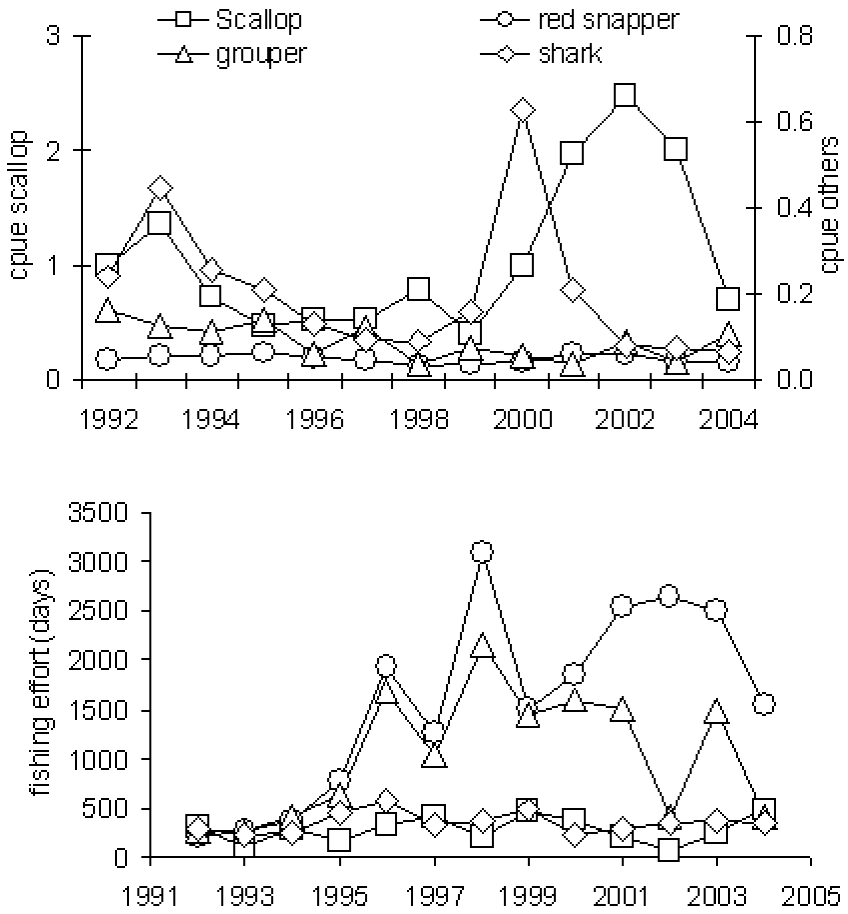


Figure 14. Relative abundance for squalid callista, red snapper, grouper and sharks expressed by the catch per unit of effort in La Paz Bay (top panel) and fishing effort expressed as fishing days (bottom panel).

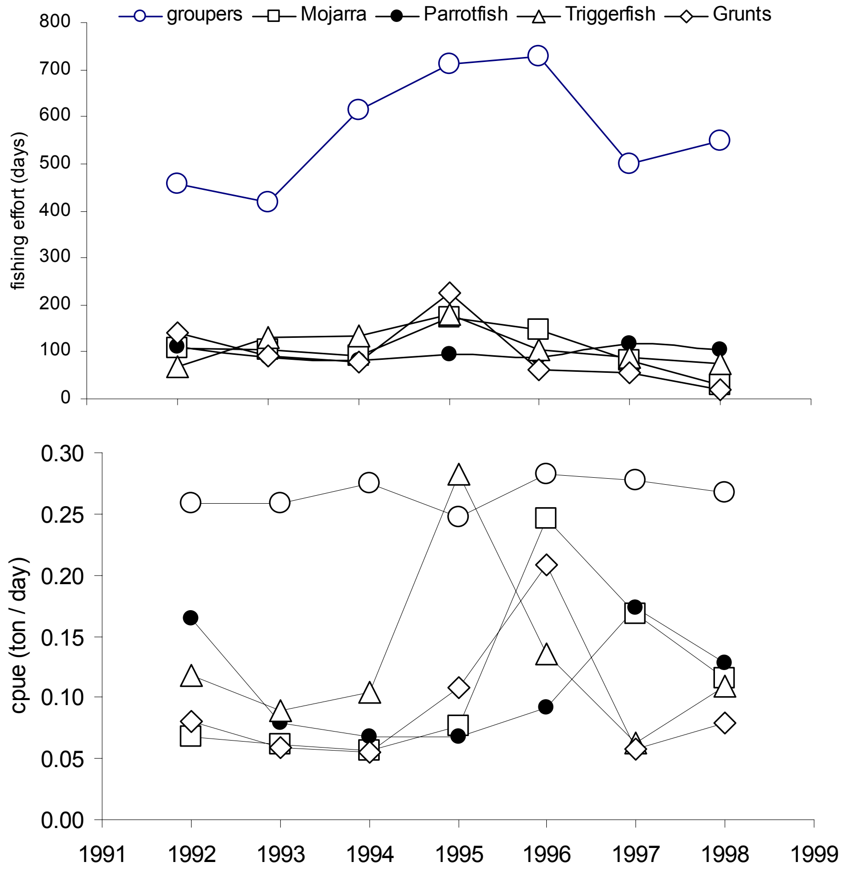


Figure 15. Effort (top) and catch per unit of effort (bottom) for some commercially important species of fish captured in La Paz Bay.

Ecospace model

La Paz Bay covers an area of approximately 1,970 km^2 including the marine areas around the Espiritu Santo Island. For the construction of the basemap in Ecospace, we selected a matrix of 70 x 52 squared cells with a length of 1.08 km on each side.

As part of the model construction, we identified 9 habitats to which species were allocated. For species allocation, we used information about their biology and behavior. Habitats were defined by considering the type of substrate or community as well as depth ranges.

Nine habitats were identified, as indicated in Table 6, which also shows how functional groups were allocated. Considering information reported by Cruz-Orozco *et al.* (1996), Alvarez *et al.* (1997) and Castro-Aguirre and Balart (1997), we drew habitats (sandy, muddy, rocky, mangrove and depth ranges) and 4 regions considering distribution sediments (Figure 17).

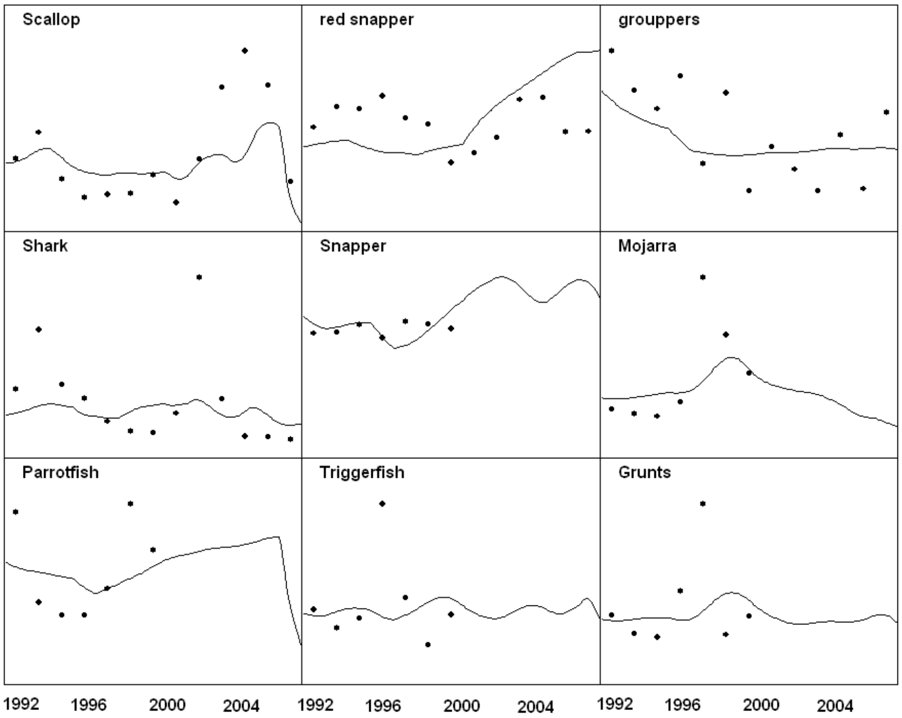


Figure 16. Fitting output of Ecosim for some commercial species of La Paz Bay, Mexico.

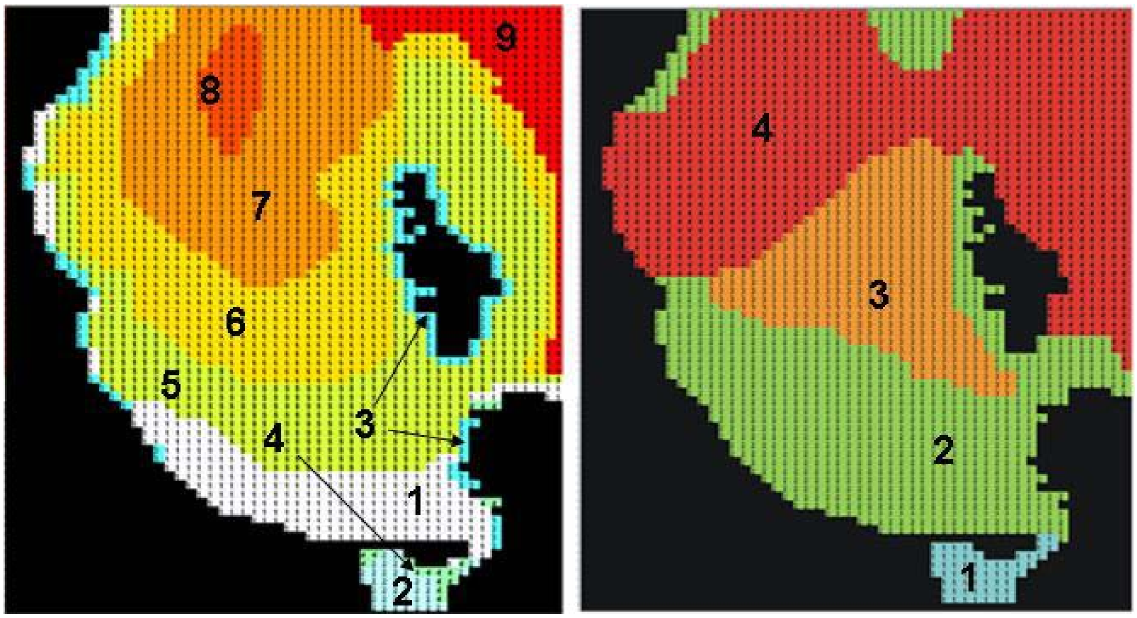


Figure 17. Left panel: representation of habitat distribution in La Paz Bay: 1) Sandy (0–30 m); 2) Mud (0–30 m); 3) Rocky (0–30 m); 4) Mangrove (0–30 m); 5) Depth I (30–70 m); 6) Depth II (70–200 m); 7) Depth III (200–400 m); 8) Depth IV (>400 m) and 9) Gulf (oceanic). Right panel: distribution of habitats defined by the type of bottom: 1) Fine sand, 2) Gross sand, 3) Lime and 4) Not defined (deeper areas with influence of the Gulf of California waters).

Table 6. Habitat allocation for the functional groups in La Paz Bay.

Group / Habitat #	All habitats	Sandy (0-30m)	Muddy (30m)	Rocky (0-30m)	Man-grove	Depth I 30-70m	Depth II 70-200m	Depth III 200-400m	Depth IV >400m	Gulf
sea birds		+	+	+	+	+				
sea lion		+		+	+	+	+	+	+	+
toothed whale						+	+	+	+	+
dolphin		+	+	+		+	+	+	+	+
red snapper adult						+	+			
red snapper juvenile		+								
deep groupers						+	+			
shark		+		+		+	+	+	+	+
groupers		+		+						
jacks		+		+		+	+	+	+	+
pierna						+	+			
joung sharks		+		+		+	+	+	+	+
snapper		+		+	+					
trigger fish				+	+					
parrot fish				+						
sardine	+									
dolphin fish		+		+		+	+	+	+	+
large pelagics		+		+		+	+	+	+	+
Haemulidae		+	+	+	+					
Tetrodontidae				+	+					
demersal fish						+	+	+	+	+
Labridae		+		+						
Priacanthidae				+						
Gerreidae		+			+					
Diodontidae		+		+						
Rhinobatidae		+	+		+	+				
Triglidae		+				+	+			
Batrachoididae						+	+	+	+	
Sparidae		+		+						
Ophidiidae		+								
Synodontidae		+				+				
Sciaenidae		+				+				
Ariidae		+			+					
flatfishes		+	+		+					
Urolophidae		+			+	+				
giant squid						+	+	+		
squalid callista		+	+		+					
brown shrimp		+				+				
clams		+	+		+					
crabs & octopus		+	+	+	+	+				
infauna		+	+	+	+	+				
polychaetes		+	+	+	+					
zooplankton	+									
jelly zooplankton	+									
phytoplankton	+									
benthic primary producers		+								
benthic producers in reef corals				+						
detritus	+									

Dispersal rates express the mobility of individuals but do not account for migrations, which can be accounted for independently. This parameter is of relevance because distribution of biomass depends to a great extent on dispersal rates. Information associated with dispersal rates is scarce in literature, and we initially adapted dispersal rates reported by Pitcher and Buchary (2002) considering the biology and taxonomic closeness among the species used. Specific values are given in Table 7.

Table 7. Dispersal rate values for functional groups of La Paz Bay, following Pitcher and Buchary (2002)

Functional group	Dispersal rate (km·year^{-1})	Functional group	Dispersal rate (km·year^{-1})
marine birds	-	porcupinefishes	60
sea lion	300	guitarfishes	70
fin whale	300	searobins	70
dolphin	300	toadfishes	70
red snapper adults	83	porgies	70
red snapper juveniles	83	cusk-eels	70
deep grouper	80	lizardfishes	70
sharks	300	croakers	70
groupers	78	catfishes	60
jacks	81	flounders	80
whitefishes	76	round rays	65
small shark	300	giant squid	93
snappers	76	squalid callista	0.6
triggerfishes	70	brown shrimp	53
parrot fish	73	clams	0.6
sardines	63	crabs and octopus	60
dolphinfish	93	infauna	0.5
large pelagics	93	polychaeta	0.5
grunts	73	zooplankton	1
puffers	-	jelly zooplankton	2
deep demersals	80	phytoplankton	1
wrasses	70	benthic primary producers (macroalgae & reefs)	0.1
bigeyes	75		
mojarras	60	detritus	1

Marine protected area in La Paz Bay

In November 2006, an area for protection of biodiversity was established around the Espiritu Santo Island (Figure 18) as Espiritu Santo National Park (marine region); however, there are no criteria to assess how such an objective can be reached.

Simulated biomass distribution for functional groups is shown in Figure 19 with and without the presence of the MPA around Espiritu Santo Island. Initially there were no apparent differences. On the other hand, Figure 20 shows the simulated distribution of fleets/gears in accordance with their habitat allocation and biomass distribution of target species.

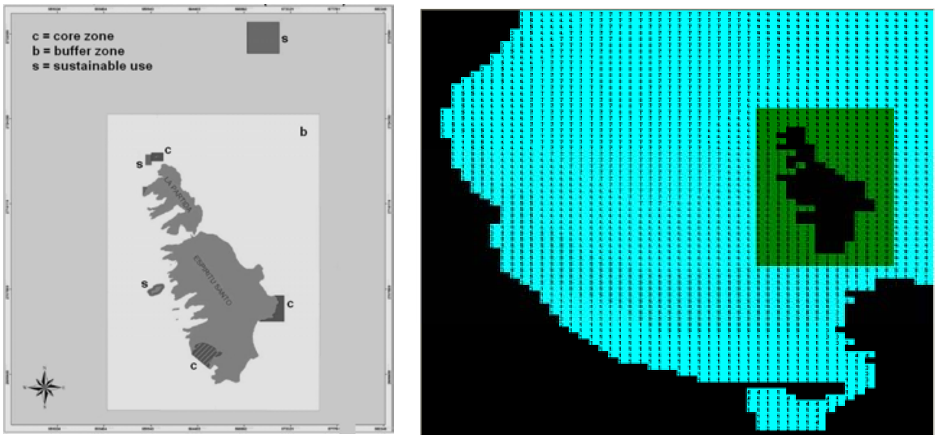


Figure 18. Area defined as Espiritu Santo National Park (taken from CONANP, 2000) on the left, and drawn in Ecospace map on the right.

Simulations were conducted over a period of 20 years to evaluate the possible effects of the MPA. Figure 21 shows the tendencies in biomass in both scenarios, with those species of interest for conservation showing no significant difference. Figure 22 illustrates the resulting scenarios on species of commercial interest. It is interesting that red snapper is the unique species among the primary targets that benefited from the MPA in terms of abundance, while sharks benefited in terms of decreased catch.

DISCUSSION

The Ecopath model description gives a quantitative picture of the state of the ecosystem structure at the present time. In general terms, ecosystem indicators given by changes in P, R, P/R, net efficiency and the turnover rate suggest a reasonably good ecosystem health where production dominates along the ecosystem structure over energy dissipation given by respiration rate.

Figure 19. Maps showing biomass distribution of the functional groups in the La Paz Bay ecosystem. Top panel without MPA (as defined in Figure 18); bottom panel with MPA.

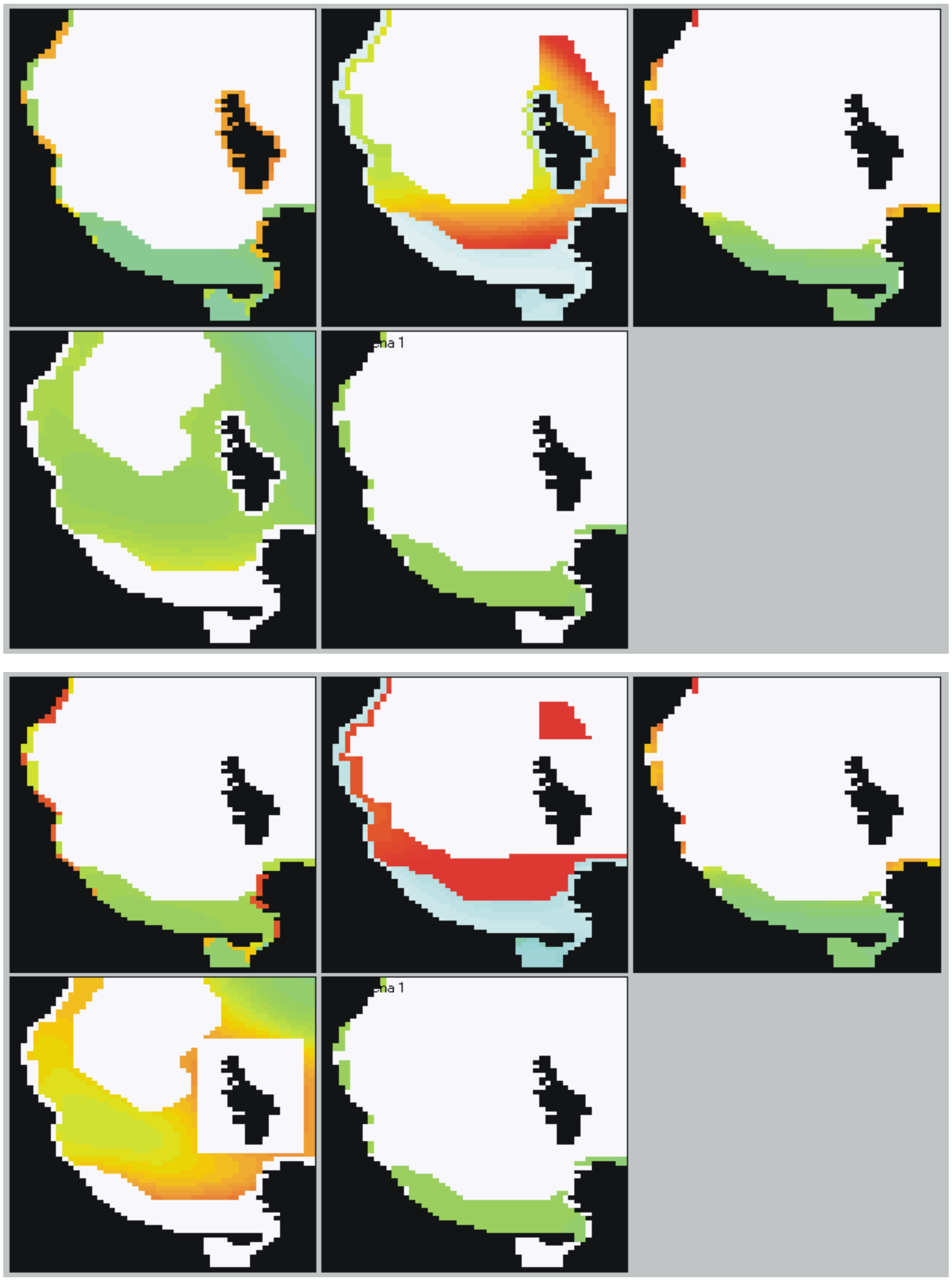


Figure 20. Distribution of effort by fishing gear: without MPA (top) and with MPA (bottom). From left to right starting on the top: 1) gillnet, 2) hook-and-line, 3) diving, 4) drifting nets and longlines targeting sharks and 5) small-scale shrimp trawling.

Apparently, fishing has little significant negative impact on the processes of the ecosystem. Mixed trophic impacts represent cascade effects with a logical biological response to positive or negative effects among groups. However, fishing appears to have the strongest effects, which could serve to prevent negative effects. The authorization for a potential commercial shrimp trawling fishery should be taken with care in the context of biodiversity. Shrimp as prey is trophically associated to a number of predators, but probably most relevant could be the potential effect on biodiversity, given the number of species appearing as bycatch.

It is interesting that the primary production required to sustain the fisheries is energetically costlier that that required for sustaining consumption by predators. This concept is of interest in terms of optimum fishing schemes, which traditionally assume that the fishery plays a role as a predator and implicitly assumes the same energetic cost.

Organization indicators also suggest an ecosystem balanced in terms of how information is spread throughout TLs. Low TLs represent a higher amount of information in terms of ascendancy and overhead, since most flows come from them and differences between their slopes with respect to TLs (Figure 13) indicates that groups with higher TLs are closer to their capacity than groups with low TLs. This means that high TLs are less resilient than low TLs.

Dynamic simulation through Ecosim was used to calibrate estimated biomasses with respect to observed data as a previous step for spatial simulation. In general terms, primary target species (squalid callista, red snapper, groupers and sharks) fit reasonably well. However, for other species, particularly mojarras and parrotfishes, fitting is not satisfactory since the absence of data for the second half of the simulated period could incorporate a bias, which we are not able to evaluate with the information available. In this sense, the model could be improved in the future. A second consideration here is that we need to explore properly the potential influence of other forcing functions, such as changes in primary production on short and long term effects.

For Ecospace, the map of habitats and regions representing the state of our knowledge and species distribution looks reasonable. The model could be improved by considering spatial patterns of primary production as well as advection fields. However, representation of the role of an MPA around the Espiritu Santo Island should be taken as preliminary. Simulated trajectories over time suggest some benefits to marine birds at the end of the period (20 years). Red grouper abundance also benefited from catch reduction. The sharks appear to benefit from reduced fishing pressures but do not show great change in abundance. It is highly recommended to interpret these outputs with care until model validation.

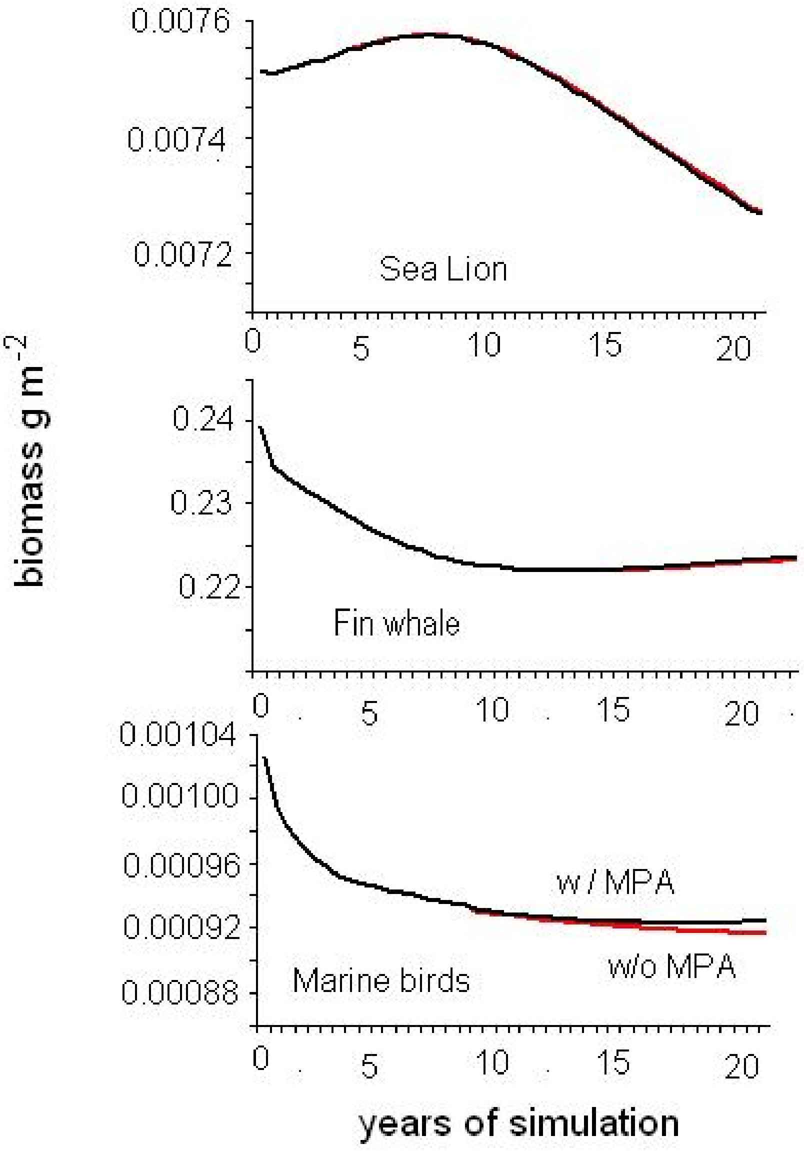


Figure 21. Changes of biomass with (black) and without (red) MPA for three species of interest for conservation in La Paz Bay.

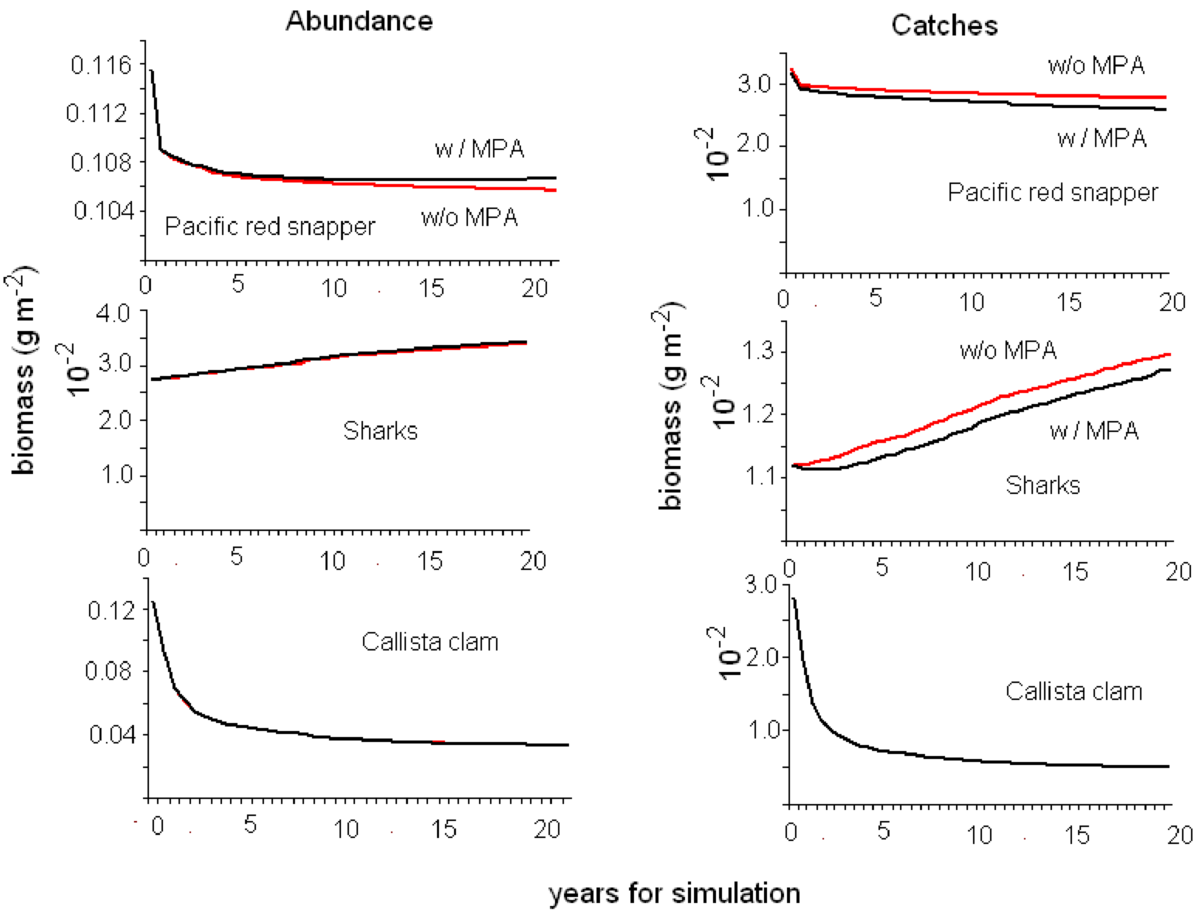


Figure 22. Changes of biomass with (black line) and without (red line) MPA for three commercially important species in La Paz Bay.

Globally, the EwE suite of programs is useful to represent different aspects of ecosystem structure, function, organization as well as time and space dynamics. However, the current model of La Paz Bay should be taken as a first approach to ecosystem representation, since there are different aspects that should be improved prior to its use for management purposes.

ACKNOWLEDGEMENTS

The authors thank the INCOFISH project for support, financed by the European Commission (contract EC-003739), SEMARNAT-CONACyT (project 1231), SAGARPA-CONACyT (project 12004), DPI-IPN (20070767), as well as the National Polytechnic Institute through EDI and COFAA. Thanks also to CONAPESCA, to the State Government of Baja California Sur and the Federación de Cooperativas de la Capital del Estado de B.C.S. for their support during fieldwork.

REFERENCES

Abitia-Cárdenas, L.A., Rodríguez-Romero, J., Galván-Magaña, F., De La Cruz-Agüero, J. and Chávez Ramos, H. 1994. Lista sistemática de la ictiofauna de Bahía de La Paz, Baja California Sur, México. Ciencias Marinas 20(2):159-181.

Aguilar-Palomino, B. 1993. Espectro trófico del dorado *Coryphaena hippurus* Linnaeus 1758 (Osteichthyes: Coryphaenidae), capturado en la Bahía de La Paz y Cabo San Lucas, Baja California Sur, México, durante 1990 y 1991. Tesis de Maestría CICIMAR La Paz. 101 pp.

Alfaro, G.M.T. 1996. Edad y crecimiento de *Coryphaena hippurus* (Linnaeus 1758) (Ostichthyes: Coryphaenidae), en el sur de la península de Baja California, México. . Master´s thesis, Instituto Politécnico Nacional, CICIMAR, México.

Allen, G.R. and Robertson, D.R. 1994. Fishes of the tropical eastern Pacific. University of Hawaii Press, Honolulu.

Álvarez, A. D., Rojas, H. and Prieto, J.J. 1997. Geología de la Bahía de La Paz y áreas adyacentes. En: La Bahía de La Paz, investigación y conservación. Eds. Urbán R., J. and M. Ramírez R. UABCS, CICIMAR, SCRIPPS. pp 13-29.

Arreguín-Sánchez, F., Arcos, E. and Chávez, E.A. 2002. Flows of biomass and structure in an exploited benthic ecosystem in the gulf of California, Mexico. Ecol. Model. 156: 167–183.

Arreguín-Sánchez, F., Hernández-Herrera, A., Ramírez-Rodríguez, M. and Pérez- España, H. 2004. Optimal management scenarios for the artisanal fisheries in the ecosystem of La Paz Bay, Baja California Sur, México. Ecological Modelling 172:373- 382.

Arreguín-Sánchez, F., Hernández-Herrera, A., Ramírez-Rodríguez, M. and Pérez-España, H. 2004. Optimal management scenarios for the artisanal fisheries in the ecosystem of La Paz, Baja California Sur, Mexico. Ecol. Modelling, 172:373-382.

Arreguín-Sánchez, F., Seijo, J.C. and Valero-Pacheco, E. 1993. An Application of ECOPATH II to the North Continental Shelf Ecosystem of Yucatan, Mexico , p. 269-278. En V. Christensen and D. Pauly (eds) Trophic models of aquatic ecosystem. ICLARM Conf. Proc. 26, 390 p.

Castro-Aguirre, J.L. and Balart, E.F. 1997. Contribución al conocimiento de la ictiofauna de fondos blandos y someros de la Ensenada de La Paz y Bahía de La Paz, B. C. S., En: J. Urbán y M. Ramírez (eds), La Bahía de La Paz: Investigación y Conservación, UABCS-CICIMAR-SCRIPPS: 139-150.

Christensen, V. and Pauly, D. 1992. ECOPATH II -a software for balancing steady state ecosystem models and calculating medeval characteristics. Ecol. Modelling, 1:169-185.

Christensen, V., Walters, C.J. and Pauly, D. 2000. Ecopath with Ecosim Version 4, Help system [Built in EwE].

Christensen, V. and Walters, C.J. 2004. Ecopath with Ecosim: methods, capabilities and limitations. Ecological Modelling, 172(2-4):109-139.

CONANP. 2000. Programa de Manejo Complejo Insular del Espiritu Santo. Copmisión Nacional de Áreas Naturales Protegidas, SEMARNAT, México. 194 p.

Cruz-Orozco, R., Martínez-Noriega, C. and Mendoza-Maravillas, A. 1996. Batimetría y sedimentos de la Bahía de La Paz, B. C Sur, México. Oceánides, 11(1):21-27.

Díaz-Uribe, J.G., Arreguín-Sánchez, F. and Cisneros-Mata, M.A. 2007. Multispecies perspective for small-scale fisheries management: a trophic analysis of La Paz Bay in the Gulf of California, Mexico. Ecological Modelling, 201: 225-222.

Froese, R. and Pauly, D. (Eds.). 2004. FishBase, concepts, design and data sources. ICLARM, Los Baños, Philippines (www.fishbase.org).

Galván-Piña, V.H. and Arreguín-Sánchez, F. 2007. Interacting industrial and artisanal fisheries and their impact on the ecosystem of the continental shelf on the central Pacific coasts of Mexico. Proc IV World Fish. Congr. AFS (in press)

Godínez-Domínguez, E., Raymundo, A.R., Rodríguez, L.E., Saucedo-Lozano, M. and González-Sansón, G. 1999. Un modelo preliminar de flujos tróficos para las comunidades de fondos blandos del Pacífico Central de México. Universidad def Guadalajara, México (mimeo).

Hiatt, R W. and Strasburg, D.W. 1960. Ecological relationships of the fish fauna on coral reefs of the Marshall Islands. Ecol. Monogr. 30 (1): 65-126.

Lecari, D. 2006. Manejo de los recursos del ecosistema del norte del Golfo de California: integrando explotación y conservación. Disertación Tesis Doctor en Ciencias. Centro Interdisciplinario de Ciencias Marinas del IPN. México.

Lluch-Cota, S.E., Aragón-Noriega, E.A., Arreguín-Sánchez, F., Aurioles-Gamboa, D., Bautista-Romero, J.J., Brusca, R.C., Cervantes-Duarte, R., Cortés-Altamirano, R., Del-Monte-Luna, P., Esquivel-Herrera, A., Fernández, G., Hendrickx, M.E., Hernández-Vázquez, S., Herrera-Cervantes, H., Kahru, M., Lavín, M., Lluch-Belda, D., Lluch-Cota, D.B., López-Martínez, J., Marinone, S.G., Nevárez-Martínez, M.O., Ortega-García, S., Palacios-Castro, E., Parés-Sierra, A., Ponce-Díaz, G., Ramírez-Rodríguez, M., Salinas-Zavala, C.A., Schwartzlose, R.A. and Sierra-Beltrán, A.P. 2007. The Gulf of California: Review of ecosystem status and sustainability challenges. Progress in Oceanography. 73: 1–26.

Maeda-Martínez, A. 1981. Composición abundancia y alimentación de la ictiofauna en tres lagunas costeras del Golfo de California. UANL. 140 p.

Palomares, M.L. and Pauly, D. 1989. A multiple regression model for predicting the food consumption of marine fish populations. Aust. J. Mar. Freswat. Res. 40: 259-273.

Pauly, D., Christensen, V. and Walters, C.J. 2000. Ecopath, Ecosim, and Ecospace as tools for evaluating ecosystem impact of fisheries. ICES Journal of Marine Science, 57(3):697-706.

Pauly, D. 1980. On the interrelationships between natural mortality, growth parameters, and mean environmental temperature in fish stocks. Jour. Cons. Int. Explor. Mer. 39(2):175-192.

Pitcher, T.J. and Buchary, E.A. 2002. Spatial Simulations of Hong Kong's Marine Ecosystem: Ecological and Economic Forecasting of Marine Protected Areas with Human-Made Reefs. Fisheries Centre Research Reports Volume 10 Number 3. 75pp.

Ramírez-Rodríguez, E.M. 1997. Producción pesquera en la Bahía de La Paz. En: J. Urbán y M. Ramírez (eds), La Bahía de La Paz: Investigación y Conservación, UABCS-CICIMAR-SCRIPPS:

Ramírez-Rodríguez, E.M and Rodríguez, M.C. 1990. Composición específica de la captura artesanal de peces en la Isla Cerralvo, BCS., México. Inv. Mar. CICIMAR 5(2): 137-141 pp.

Ramírez-Urban, J. and Ramírez-Rodríguez, M. 1997. La Bahía de La Paz. Investigación y conservación. UABCS, CICIMAR, SCRIPPS I.O. 345p.

Raymundo-Huizar, A.R. and Chiapa Carrara, X. 2000. Hábitos alimentarios de *Diodon histrix* y *Diodon holocanthus* (Pisces: Diodontidae), en las costas de Jalisco y Colima, México. Bol. Centro Invest. Biol.34 (2): 181-210.

Ruíz-Ramírez, S., Lucano-Ramírez, G. and Mariscal-Romero, J. 1997. Length-weight relationships of soft-bottom demersal fishes from Jalisco and Colima States, México. Naga. ICLARM Q. 20 (3/4): 62-63

Walters, C. J., Christensen, V. and Pauly, D. 1997. Structuring dynamic models of exploited ecosystems from trophic mass balanced assessments. Reviews in Fish Biology and Fisheries, 7: 139–172.

Walters, C. J., Christensen, V., Pauly, D. and Kitchell, J.F. 2000. Representing density dependent consequences of life history strategies in aquatic ecosystems: Ecosim II. Ecosystems, 3: 70–83.

Appendix A. Functional groups of fish species included in the present version of the trophic model for La Paz Bay, Mexico.

Functional group	Family	Species	Density (g·m^{-2})
bigeyes	Priacanthidae	*Pristigenys serrula*	0.0001
catfish	Ariidae	Ariidae	0.0006
		Arius platystomus	0.0036
		Bagre panamensis	0.0002
croakers	Sciaenidae	*Bairdiella incistia*	0.0003
		Menticirrhus spp	+
		Larimus pacificus	0.0001
		Micropogonias ectenes	0.0035
		Umbrina maculatus	0.0002
		Umbrina xanti	0.0008
cusk-eels	Ophidiidae	*Lepophidium prorratees*	0.0009
		Lepophidium stigmatistium	0.0004
		Ophidion iris	0.0001
		Ophidium iris	+
flounders	Achiridae	*Achirus mazatlanus*	0.0061
	Bothidae	*Bothus constellatus*	+
		Bothus leopardinus	0.0001
		Bothus sp	+
	Paralichthyidae	*Citarishthys* sp	0.0011
		Citharichthys xanthostigma	+
		Cyclopsetta panamensis	0.0017
		Cyclopsetta querna	0.0002
		Etropus crossotus	0.0052
		Hippoglossima tetrophthalma	0.0028
		Paralichthys aestuarius	0.0001
		Paralichthys californias	0.0003
		Syacium latifrons	0.0006
		Syacium ovale	0.0006
	Pleuronectidae	*Glyptocephalus zachirus*	0.0001
		Pleuronichthys guttulatu	+
		Pleuronichthys ocellatus	0.0001
groupers	Serranidae	*Dermatolepsis dermatolepsis*	+
		Diplectrum pacificum	0.0197
		Diplectrum sp	0.0024
		Hemanthias peruanus	0.0001
		Paralabrax maculatofasciatus	0.0143
depth groupers		*Epinephelus niphobles*	0.0001
grunts	Haemulidae	*Conodon serrifer*	+
		Haemulidae	0.0049
		Haemulon elongatus	0.001
		Haemulon maculacaudi	0.0017
		Haemulon steindachneri	0.0129
		Haemulopsis elongatus	0.0036
		Haemulopsis elongatus	0.0001
		Haemulopsis leuciscus	0.0002
		Orthopristis chalceus	0.0001
		Orthopristis reddingi	0.008
		Orthropristis reddingi	0.0001
		Pomadasys macracanthus	0.0003
		Pomadasys panamensis	0.0007
		Xenichthys xanti	0.0001
		Xenistius californienses	0.0001
guitarfishes	Rhinobatidae	*Platyrhinoidis triseriata*	0.0002
		Rhinobatos glaucostigma	0.007
		Rhinobatos productus	0.0006

Appendix A. Continued.

Functional group	Family	Species	Density (g·m^{-2})
jacks	Carangidae	*Alectis ciliaris*	+
		Carangidae juvenil	+
		Caranx vinctus	+
		Decapterus macrosoma	0.0001
		Selene oerstedii	0.0001
lizardfishes	Synodontidae	*Synodus evermani*	0.0003
		Synodus evermanni	0.0006
		Synodus scituliceps	0.0176
mojarras	Gerreidae	*Diapterus peruvianus*	0.0013
		Eucinostomus currani	0.0001
		Eucinostomus dowii	0.0143
		Eucinostomus entemola	0.0001
		Eucinostomus entomelas	0.0001
		Eucinostomus gracilis	0.0007
porcupinefishes	Diodontidae	*Chilomycterus* sp	0.0005
		Diodon holocanthus	0.0321
		Diodon hystrix	0.0005
porgies	Sparidae	*Calamus brachysomus*	0.0051
puffers	Tetraodontidae	*Sphoeroides annulatus*	0.0007
		Sphoeroides lispus	0.0002
		Sphoeroides lobatus	0.0017
		Sphoeroides sp	0.0012
red snapper		*Lutjanus peru*	0.0029
roundrays	Urolophidae	*Urobatis concentricus*	+
		Urobatis halleri	0.0027
		Urobatis maculatus	0.0009
		Urotrygon rogersi	0.0002
searobins	Triglidae	*Bellator xenisma*	0.0005
		Prionotus albirostris	0.0001
		Prionotus birostratus	0.0009
		Prionotus ruscarius	0.0014
		Prionotus sp	0.0003
		Prionotus stephanophrys	0.0043
		Triglidae	0.0003
small pelagics	Clupeidae	*Opisthonema libertate*	0.0004
snappers	Lutjanidae	*Alphestes immaculatus*	+
		Lutjanus guttatus	0.0018
		Lutjanus sutteatus	+
tilefishes	Malacanthidae	*Caulolatilus affinis*	0.0002
toadfishes	Batrachoididae	*Porichthys analis*	0.0049
		Porichthys sp	0.0003
triggerfish	Balistidae	*Balistes polylepsis*	0.0092
wrases	Labridae	*Halichoeres chierchiae*	0.0001

+ species with a relative abundance less than 0.0001 g·m^{-2}.

Appendix B. Prey-predator matrix for La Paz Bay ecosystem, Mexico.

Prey \ Predator	1	2	3	4	5	6	7	8	9	10	11	12
marine birds								0.0009				
sea lion								0.0050				
fin whale								0.0030				
dolphin								0.0040				
red snapper adults				0.0020				0.0050				0.0100
red snapper juveniles				0.0070				0.0140				0.0420
deep grouper				0.0070				0.0140				0.0380
sharks				0.0070								0.0450
groupers	0.0100			0.0010				0.0010				0.0050
jacks	0.0010	0.0650		0.0080				0.0170	0.0080			0.0440
whitefishes				0.0070				0.0110				0.0390
small shark	0.0200			0.0060				0.0020				0.0310
snappers	0.0100			0.0030				0.0040				0.0160
triggerfishes				0.0080				0.0120	0.0590			0.0340
parrot fish				0.0070				0.0090	0.0420			0.0290
sardines	0.5160	0.1810	0.1000	0.0080	0.1980	0.0570	0.5220	0.0940	0.3760	0.5890	0.0560	0.0470
dolphinfish	0.0150	0.0330		0.0150			0.0410	0.0930	0.0190	0.1650		0.0800
large pelagics				0.0070								0.0350
grunts	0.2690	0.0580		0.0120	0.0910			0.0850	0.0360	0.0470		0.0750
puffers	0.0770			0.0200				0.0880	0.0810	0.0210		0.0880
deep demersals		0.4870		0.0070		0.0100	0.0930				0.0410	0.0540
wrasses												
bigeyes					0.0003			0.0030		0.0004		0.0001
mojarras												
porcupinefishes	0.0060							0.0003	0.0003			0.0006
guitarfishes					0.0010			0.0050	0.0010			0.0020
searobins										0.0870		
toadfishes		0.0830						0.0410				
porgies	0.0320							0.0170	0.0610	0.0050		
cusk-eels	0.0190							0.0330				
lizardfishes		0.0050							0.0020			
croakers								0.0020	0.0020	0.0060	0.0002	0.0040
catfishes									0.0020		0.0002	0.0002

Prey \ Predator	13	14	15	16	17	18	19	20	21	22	23	24
marine birds												
sea lion												
fin whale												
dolphin												
red snapper adults					0.0010							
red snapper juveniles					0.0040							
deep grouper												
sharks												
groupers												
jacks						0.0830						
whitefishes												

Appendix B. Continued.

Prey \ Predator	13	14	15	16	17	18	19	20	21	22	23	24
small shark												
snappers												
triggerfishes	0.0250				0.0070	0.0240						
parrot fish	0.0240				0.0090							
sardines	0.0200				0.5010	0.2480	0.0350	0.0270				
dolphinfish	0.0540				0.0400	0.4160						
large pelagics												
grunts	0.1280				0.0570	0.0040	0.0090					
puffers	0.2930				0.0820	0.0260	0.0070	0.0120				
deep demersals						0.0410						
wrasses												
bigeyes						0.0040						
mojarras												
porcupinefishes												
guitarfishes		0.0020										
searobins												
toadfishes						0.0250						
porgies												
cusk-eels												
lizardfishes					0.0260	0.0020						
croakers	0.0020				0.0030	0.0008						
catfishes												

Prey \ Predator *	25	26	27	28	29	30	31	32	33	34	35	36
marine birds												
sea lion												
fin whale												
dolphin												
red snapper adults												
red snapper juveniles				0.0260			0.0350					
deep grouper												
sharks												
groupers				0.0030			0.0010					
jacks							0.0230					
whitefishes			0.0007	0.0160			0.0100					
small shark												
snappers			0.0005	0.0200			0.0100					
triggerfishes				0.0002								
parrot fish												
sardines							0.1050					0.4500
dolphinfish												
large pelagics												
grunts			0.0007	0.0880	0.1000	0.0030	0.2770	0.0390				
puffers												
deep demersals												0.3600
wrasses			0.0007	0.0530			0.0230					
bigeyes				0.0080								

Appendix B. Continued.

Prey \ Predator *	25	26	27	28	29	30	31	32	33	34	35	36
mojarras		0.0005			0.0020	0.0030	0.1500	0.0120				
porcupinefishes		0.0005										
guitarfishes												
searobins				0.0610		0.0030	0.0790	0.0210				
toadfishes				0.0150								
porgies				0.0480			0.1000					
cusk-eels		0.0005		0.1220								
lizardfishes				0.0020								
croakers												
catfishes		0.0005					0.0260					

* Groups 37 to 44 do not prey on groups 1 to 36.

Prey \ Predator	1	2	3	4	5	6	7	8	9	10	11	12
flounders	0.0020							0.0004				
round rays									0.0090			0.0040
giant squid		0.0320		0.7560		0.4750	0.1500	0.3930		0.0570		0.0060
scallop				0.0410				0.0110				0.0540
brown shrimp	0.0140			0.0320	0.0100		0.0400	0.0130	0.0250			0.0650
clams	0.0090	0.0560		0.0240			0.1540	0.0090	0.0070		0.3520	0.0640
crabs and octopus				0.0160				0.0110	0.2700			0.0880
infauna			0.0350								0.1540	
polychaeta					0.0500	0.0500				0.0220	0.0400	
zooplankton	0.0010		0.5760		0.2090	0.0520					0.3550	
jelly-zooplankton			0.2740		0.4400	0.3550						
phytoplankton			0.0150									
benthic primary producers (large algae)												
benthic primary producers (reefs)												
detritus												

Prey \ Predator	13	14	15	16	17	18	19	20	21	22	23	24
flounders		0.0020										
round rays	0.0004				0.0003		0.0004			0.0020	0.0007	
giant squid					0.1420	0.1100						
scallop	0.0390	0.0180				0.0050	0.0060			0.1020		0.0100
brown shrimp	0.0520	0.0160			0.0160	0.0040	0.0410			0.0400	0.1770	0.1340
clams	0.0540	0.0150			0.0130	0.0040	0.1860	0.0130		0.0530		0.0520
crabs and octopus	0.1150	0.8580	0.0860			0.0050	0.0690	0.3740		0.2730		0.2410
infauna							0.3850			0.1910		0.2660
polychaeta		0.0310								0.3400	0.2240	0.1850
zooplankton	0.1950			0.3020	0.0630		0.0310	0.1240	0.3640			
jelly-zooplankton				0.1090	0.0300		0.0120	0.0450	0.2740			
phytoplankton				0.2570	0.0080		0.0110	0.0800	0.0980			
benthic primary producers (large algae)							0.0650	0.0800				
benthic primary producers (reefs)		0.0580	0.9140				0.0090	0.1750				0.1120
detritus				0.3310			0.1340	0.0700	0.2650		0.5980	

Appendix B. Continued.

Prey \ Predator	25	26	27	28	29	30	31	32	33	34	35	36
flounders		0.0005	0.0020	0.0800			0.1590	0.0290				
round rays				0.0030								
giant squid				0.1690								0.0220
scallop	0.0420	0.0040										
brown shrimp		0.0410	0.0360	0.0300	0.2410			0.0180		0.0570		
clams	0.1510	0.0460										0.0450
crabs and octopus	0.1230	0.8990	0.0360	0.1090	0.1990			0.0560	0.0580	0.1400	0.1570	
infauna	0.6850			0.0820	0.4570	0.3810		0.1700	0.5160	0.3680	0.3980	
polychaeta		0.0080		0.0620		0.0840		0.1210	0.3450	0.4350	0.4450	
zooplankton			0.9240									0.0670
jelly-zooplankton												
phytoplankton												0.0060
benthic primary producers (large algae)									0.0190			
benthic primary producers (reefs)									0.0620			
detritus						0.5270		0.5350				0.0500

Prey \ Predator	37	38	39	40	41	42	43	44
flounders								
round rays								
giant squid								
scallop								
brown shrimp								
clams		0.1690	0.0360					
crabs and octopus				0.0330				
infauna		0.0120		0.0820		0.0170		
polychaeta				0.1450				
zooplankton	0.3700		0.2660	0.0600			0.0860	
jelly-zooplankton							0.0600	
phytoplankton	0.4120	0.1080	0.3260	0.0840			0.4730	0.6030
benthic primary producers (large algae)			0.1000	0.2510				
benthic primary producers (reefs)			0.0890	0.2120				
detritus	0.2180	0.7110	0.1820	0.1330	1.0000	0.9830	0.3820	0.3970

Appendix C. Key indices for La Paz Bay ecosystem, Mexico

Group name	Flow to detr. (t·km^{-2}·year^{-1})	Net efficiency	Omnivory index	Respiration (t·km^{-2}·year^{-1})	Assimilation (t·km^{-2}·year^{-1})	Respiration/ Assimilation	Production/ respiration	Respiration/ Biomass (year^{-1})
marine birds	0.003	0.112	0.121	0.007	0.008	0.888	0.127	7.37
sea lion	0.04	0.1	0.281	0.106	0.118	0.9	0.111	14.184
fin whale	2.001	0.15	0.026	4.254	5.005	0.85	0.176	18.114
dolphin	0.035	0.088	0.102	0.097	0.106	0.912	0.096	13.322
red snapper adults	0.187	0.064	0.079	0.682	0.729	0.936	0.069	6.195
red snapper juveniles	0.141	0.138	0.268	0.436	0.506	0.862	0.16	2.069
deep grouper	0.043	0.091	0.12	0.144	0.158	0.909	0.1	2.11
sharks	0.055	0.135	0.167	0.182	0.21	0.865	0.156	6.71
groupers	0.09	0.134	0.134	0.298	0.344	0.866	0.154	2.703
jacks	0.099	0.189	0.203	0.299	0.368	0.811	0.233	5.84
whitefishes	0.115	0.095	0.021	0.382	0.421	0.905	0.104	2.97
small shark	0.032	0.104	0.394	0.111	0.124	0.896	0.116	3.8
snappers	0.084	0.111	0.15	0.276	0.31	0.889	0.125	3.84
triggerfishes	0.116	0.184	0.105	0.352	0.431	0.816	0.225	3.33
parrot fish	0.324	0.093	0.142	1.015	1.119	0.907	0.102	8.71
sardines	3.141	0.469	0.304	5.568	10.481	0.531	0.882	1.02
dolphinfish	0.4	0.223	0.2	1.141	1.469	0.777	0.288	7.232
large pelagics	0.041	0.059	0.289	0.147	0.156	0.941	0.062	5.12
grunts	1.882	0.136	0.266	5.978	6.922	0.864	0.158	3.8
puffers	2.523	0.08	0.411	8.684	9.436	0.92	0.087	5.89
deep demersals	0.152	0.138	0.279	0.497	0.576	0.863	0.159	8.28
wrasses	0.085	0.132	0.032	0.281	0.323	0.868	0.153	9.37
bigeyes	0.037	0.085	0.306	0.124	0.135	0.915	0.093	6.81
mojarras	0.238	0.154	0.156	0.665	0.786	0.846	0.182	4.94
porcupinefishes	0.088	0.128	0.028	0.282	0.323	0.872	0.146	3.42
guitarfishes	0.04	0.155	0.002	0.109	0.129	0.845	0.184	2.77
searobins	0.617	0.082	0.006	2.081	2.266	0.918	0.089	4.48
toadfishes	0.119	0.095	0.227	0.416	0.46	0.905	0.105	5.43
porgies	0.267	0.1	0.073	0.924	1.028	0.9	0.112	3.67
cusk-eels	0.78	0.038	0.27	2.881	2.994	0.962	0.039	17.86
lizardfishes	0	0.341	0.071	0.219	0.233	0.943	0.361	3.32
croakers	0.079	0.106	0.484	0.243	0.272	0.894	0.118	4.65
catfishes	0.035	0.26	0.085	0.07	0.094	0.74	0.351	4.56
flounders	0	0.313	0.015	0.428	0.442	0.969	0.323	4.03
round rays	0.064	0.065	0.015	0.232	0.248	0.935	0.069	4.49
giant squid	2.218	0.284	0.36	5.7	7.965	0.716	0.397	13.637

Appendix C. Continued.

Group name	Flow to detr. (t·km^{-2}·year^{-1})	Net efficiency	Omnivory index	Respiration (t·km^{-2}·year^{-1})	Assimilation (t·km^{-2}·year^{-1})	Respiration/ Assimilation	Production/ respiration	Respiration/ Biomass (year^{-1})
scallop	0.295	0.25	0.313	0.729	0.972	0.75	0.333	6.362
brown shrimp	2.637	0.198	0.265	6.832	8.514	0.802	0.246	16.518
clams	10.225	0.277	0.296	24.166	33.426	0.723	0.383	6.133
crabs and octopus	8.352	0.312	0.254	20.334	29.546	0.688	0.453	4.68
infauna	9.634	0.376	0	20.007	32.059	0.624	0.602	13.48
polychaeta	5.089	0.453	0.017	9.168	16.748	0.547	0.827	5.08
zooplankton	225.718	0.225	0.15	538.06	694.309	0.775	0.29	74.21
jelly-zooplankton	111.73	0.324	0	198.64	293.842	0.676	0.479	64.056
phytoplankton	2446.261	-	0	0	-	-	-	-
benthic primary producers (large algae)	7.805	-	0	0	-	-	-	-
benthic primary producers (reefs)	1.79	-	0	0	-	-	-	-
detritus	28	-	0.161	0	-	-	-	-

SPATIAL MODELLING OF THE SENEGAMBIAN ECOSYSTEM[1]

Birane Samb
Fishery Biologist
CRODT, Dakar, Sénégal;
Email: bsambe@yahoo.fr

ABSTRACT

An Ecopath and Ecospace model of the Senegambian ecosystem off the coast of west Africa for 2000–2004 is described here. It consists of 21 compartments, including birds, mammals, tuna, sharks, rays, cephalopods, groupers, croakers, seabreams, sardinellas and other fish, zooplankton, meio- and macrobenthos, benthic producers, phytoplankton, discards and detritus. Fisheries include both artisinal and industrial fleets and the ecosystem resembles that of the ecosystem off Peru. Most of the demersal species such as groupers, seabreams and croakers are overexploited. The spatial model includes four habitats: rocky, muddy, muddy sand and sandy areas, and two marine protected areas are included.

INTRODUCTION

The Senegambian ecosystem, influenced by the Canary Islands' current, is subjected to active upwelling that generates a highly productive and diverse marine environment. The extent of exploitation of these biological resources by national and foreign fleets testifies to the economic importance of the fishery sector in the region. Signs of overexploitation of certain resources are generating deep anxieties among stakeholders. It is therefore important to apply a rigorous scientific assessment of these stocks in order to recommend management measures leading to sustainable exploitation.

Besides the classic approaches in stock assessment, the Ecopath trophic modelling approach constitutes a supplementary tool capable of improving the understanding of the ecosystem, by examining spatio-temporal trophic intereactions and simulation. This report describes the development and parameterization of an Ecopath and Ecospace model of the Senegambian ecosystem based on data collected during the period 2000–2004.

ECOPATH MODEL DEVELOPMENT

Definition of the area

The Senegalogambian coast is situated in western Africa, bounded in the north by Mauritania and in the south by Guinea Bissau. The model covers the continental shelf off Senegal and Gambia, extending from the coast to the 200 m isobath. The total surface area is 27,600 km^2. The surface of the Gambian continental shelf represents 14% of the Senegalogambian area. The Senegambian continental shelf is 27 miles wide at its northern limit by Saint Louis, is reduced to 5 miles level with the peninsula of Cape Verde and widens again up to 50 miles at its southern limit.

Definition of functional groups

The model is constructed with 21 functional groups. The functional groups, Ecopath input parameters and data sources used to parameterize the groups are presented in Table 1. A brief description of each functional group is also provided, and the diet composition matrix is presented in Table 2, while sources for the diet composition matrix are listed in individual functional group descriptions. In some cases, the diet composition had to be modified from the original published values to enable model balancing.

---

[1] Cite as: Samb, B. 2007. Spacial modelling of Senegambian ecosystem, p. 161–169 . *In*: Le Quesne, W.J.F., Arreguín-Sánchez, F. and Heymans, S.J.J. (eds.) INCOFISH ecosystem models: transiting from Ecopath to Ecospace. Fisheries Centre Research Reports 15(6). Fisheries Centre, University of British Columbia [ISSN 1198-6727].

Marine birds: The marine birds in the northwest African zone are mainly migratory species present from November to March. The food composition consists mainly of zooplankton, pelagic fish and small hakes (Jarre-Teichmann *et al.,* 1998).

Marine mammals: Several species of dolphin and whale occur along the northwest African coast, of which *Balaenoptera physalus* and *Balaenoptera edeni* (Northridge, 1984) are the most common. Their diet is essentially composed of cephalopods, crustaceans, fish and zooplankton (Northridge, 1984). The P/B value has been kept to 0.047 year^{-1} to take into account accidental captures.

Tuna: Predominantly represented by yellowfin tuna (*Thunnus albacares*), skipjack tuna (*Katsuwonus pelamis*) and big-eye tuna (*Thunnus obesus*), these are large, migratory species and are subject to long-range fishery operations. Their prey consists of fish, crustaceans and mollusks (Cayré *et al.,* 1988).

Coastal tuna and associated species: Representing about 10 species, most important are little thunny (*Euthynnus alletteratus*), Atlantic bonito (*Sarda sarda*), West African Spanish mackerel (*Scomberomorus tritor*) and frisate tuna (*Auxis thazard*). They are present all year and are mainly fished by the artisanal units. Postel (1955) found that their prey is small coastal pelagic fish, crustaceans and cephalopods.

Sharks: This group represents a wide range of species reflecting the area's high shark diversity. The information is based on experimental trawling done in Senegal (Seret, 1981; Caverivière *et al.,* 1985).

Rays: The main species of the group is *Rhinobatos rhinobatos*. The food of the rays is composed of crustaceans and other benthic animals (Caverivière and Andriamirado, 1997).

Cephalopods: These are main target species for important fisheries in Morocco, Mauritania and Senegal. In the central-east Atlantic it is the octopus (*Octopus* spp.) and the cuttlefish (*Sepia* spp.) that dominate in the catch of cephalopods. The squid (*Loligo vulgaris*) is fished especially in Mauritania. The cephalopods in the Senegambian zone are mainly octopus and cuttlefish. Their food mainly consists of fish and zooplankton (Diatta *et al.,* 2001).

The grouper: Also known as white grouper or 'thiof', *Epinephelus aenus* is a symbolic species in Senegal as it is a highly prized fish, though it is now also highly depleted. The food composition of the thiof consists of fish, cephalopods and crustaceans (Levenez, 1993).

Cassava croaker: *Pseudotolithus senegalensis* is a species targeted by some fisheries, and which consumes fish, shrimp and crabs (Diouf, 1996).

Bluespotted seabream: *Sparus caeruleostictus* is carnivorous, predominantly eating mollusks but also crustaceans and fish (Levenez, 1993).

Other demersal fish: This group represents several species, including the sparids, such as the red pandora (*Pagellus bellottii*). The food composition of these species is variable; studies of the stomach contents show their diet consists of crustaceans, zooplankton, pelagic fish, cephalopods, benthos and detritus (Franqueville, 1983; Fischer *et al.,* 1981).

Round and **flat sardinella:** These coastal pelagic fish constitute, in landed tonnage, the most important marine resource of the study area. The stocks are widely shared because of their migration. The clupeids are mainly the two species of sardinella, the round (*Sardinella aurita*) and the flat (*S. maderensis*). The food composition of both species consists of zooplankton and phytoplankton (Nieland, 1982; Medina-Gaertner, 1985).

Other coastal pelagic fish: This group includes the carangids exploited in the area. The group includes the Cunene horse mackerel (*Trachurus trecae*) and the false scad (*Caranx rhonchus*). Chub mackerel (*Scomber japonicus*) also occurs on all West African coasts, but only provides a small catch. The food composition of horse mackerel in general consists of zooplankton, phytoplankton and other small pelagic fish (Kompowski and Slosarczyk, 1976).

Table 1. Biomass values, P/B and Q/B used in the Senegambian model; values of TL, EE and P/Q obtained from Ecopath and references

Name of group	Trophic level	Biomass ($t \cdot km^{-2}$)	Prod./biom. ($year^{-1}$)	Cons./ biom. ($year^{-1}$)	EE	Prod./cons.	References
Marine birds	3.59	0.118	0.120	118.000	0.000	0.001	Crawford *et al.* (1991); Jarre-Teichmann *et al.* (1998)
Marine mammals	3.34	0.039	0.047	17.265	0.000	0.003	Northridge (1984)
Tuna	3.23	2.540	1.600	4.769	0.073	0.336	C.R.O.D.T. (1997); Iccat (1999)
Coastal tuna	3.16	2.890	0.800	9.500	0.100	0.084	Diouf (1980); Pauly and Munro (1984); Pauly (1979); Postel (1955); Gouriou (1993)
Sharks	3.37	0.230	0.905	3.516	0.615	0.257	Seret (1981); Pauly (1980); Bransletter (1987)
Rays	2.71	0.131	1.000	6.000	0.763	0.167	Schneider (1990); Brander and Palmer (1985); Opitz (1993)
Cephalopods	3.15	1.087	1.900	11.700	0.834	0.162	Opitz (1993)
Grouper	3.53	0.018	0.720	4.010	0.914	0.180	Laurans, Gascuel and Barry (2003); CRODT/JICA (2006); Levenez (1993)
Cassava croakers	3.32	0.073	0.800	4.500	0.863	0.178	Diouf (1996); CRODT/JICA (2006)
Bluespotted seabream	3.58	0.072	0.710	4.000	0.998	0.178	Levenez (1993)
Other demersal fish	2.30	5.600	1.200	6.000	0.506	0.200	Franqueville (1983); Pauly (1980); Dah *et al.* (1991); Palomares and Pauly (1998); Fischer *et al.* (1981)
Round sardinella	2.70	7.065	1.560	20.200	0.993	0.077	FAO (2005); Toresen *et al.* (2001); Toresen *et al.* (2002); Krakstad *et al.* (2003); Krakstad *et al.* (2004)**;** Camarena (1986); Samb (1988); Nieland (1982); Medina-Gaertner (1985); Samb (1997)
Flat sardinella	2.80	17.934	0.760	13.900	0.961	0.055	FAO (2005); Toresen *et al.* (2001); Toresen *et al.* (2002); Krakstad *et al.* (2003); Krakstad *et al.* (2004); Camarena (1986); Samb (1988); Nieland (1982); Medina-Gaertner (1985); Samb (1997)
Other coastal pelagic fish	2.80	12.228	1.100	10.635	0.900	0.103	Saetersdal *et al.* (1995); Toresen (1996 à 1998); Toresen and Kolding (1999); Maxim (1995)
Zooplankton	2.00	20.636	58.356	274.805	0.369	0.212	Touré (1983)
Meiobenthos	2.06	19.600	4.000	30.000	0.961	0.133	Olivieri *et al.* (1993)
Macrobenthos	2.17	93.000	1.200	10.000	0.908	0.120	Olivieri *et al.* (1993)
Benthic producers	1.00	10.500	15.000	-	0.564	-	Jarre-Teichmann *et al.* (1998)
Phytoplankton	1.00	82.014	138.189	-	0.511	-	Voituriez and Herbland (1982)
Discards	1.00	0.001	-	-	0.000	-	
Detritus	1.00	10.000	-	-	0.161	-	

Table 2. Diet composition of the groups making up the Senegambian Ecopath model.

Prey \ Predator	**Marine birds**	**Marine mammals**	**Tuna**	**Coastal tuna**	**Sharks**	**Rays**	**Cephalopods**	**Grouper**	**Cassava croaker**	**Bluespotted seabream**	**Other demersal fish**	**Round sardinella**	**Flat sardinella**	**Other coastal pelagic fish**	Zoo plankton	Meio- benthos	Macro- benthos
Marine birds																	
Marine mammals																	
Tuna					0.1												
Coastal tuna																	
Sharks																	
Rays																	
Cephalopods		0.1	0.05	0.03				0.2		0.2	0						
Grouper									0	0							
Cassava croaker								0.05		0.1							
Bluespotted seabream								0.01	0.01								
Other demersal fish		0.05			0.1	0.14	0.04	0.74	0.99	0.7							
Round sardinella	0.3	0.1	0.03	0.03	0.03		0.03				0						
Flat sardinella	0.25	0.2	0.1	0.1	0.15		0.05				0						
Other coastal pelagic fish	0.35	0.1	0.15	0.08	0.1		0.05				0.01						
Zooplankton		0.35	0.63	0.75	0.53		0.58				0.14	0.7	0.8	0.8			
Meiobenthos						0.09					0.03						0.08
Macrobenthos						0.38	0.25				0.1					0.05	0.07
Benthic producers						0.4					0.38					0.05	0.05
Phytoplankton											0.16	0.3	0.2	0.2	1		
Discards	0.1	0.1	0.05	0.03													
Detritus											0.2					0.9	0.8

Zooplankton: Studies of secondary production, achieved solely near the Cape Verde peninsula, indicate a strong relation between the abundance of the zooplankton and the intensity of the upwelling (Touré, 1983). The zooplankton consumes exclusively phytoplankton.

Benthos: The macrobenthos is important for the food of demersal fish, but there is limited information available for this group.

Phytoplankton: Primary production has been studied in the study area by several authors (Voiturier and Herbland, 1982).

Fisheries

The fishery in the area consists of an artisanal sector in perpetual 'development' and an industrial sector made up of flotilla boats operating within the framework of fishing agreements (Table 3). Due to depletion of the resources, the co-existence of these fisheries raises difficulties in management. The landed value of the groups in the fisheries is presented in Table 4.

Table 3. Mean Senegalese landings (in tonnes) for the years 2000–2004. Data from CRODT.

Group/catch	Artisanal	Industrial	Total catch
Tuna		5,714	5,714
Coastal tuna	6,168		6,168
Sharks	1,335	2,083	3,418
Rays	2,403	267	2,670
Cephalopods	3,925	2,056	5,981
Grouper	134	134	267
Cassava croaker	481		481
Bluespotted seabream	1,255		1,255
Other demersal fish	42,800	13,937	56,738
Round sardinella	134,915	7,209	142,124
Flat sardinella	122,019	4,379	126,398
Other coastal pelagic fish	55,216	8,918	64,133
Total catch	366,725	42,640	409,364

Table 4. Value of landings in Euros per kg for catches from Senegalese waters. Data from CRODT.

Group/value	Artisanal	Industrial
Tuna	-	1.10
Coastal tuna	0.76	-
Sharks	0.43	1.00
Rays	0.64	0.74
Cephalopods	2.73	2.73
Grouper	6.73	6.73
Cassava croaker	1.20	-
Bluespotted seabream	2.22	-
Other demersal fish	1.45	1.45
Round sardinella	0.25	0.25
Flat sardinella	0.21	0.21
Other coastal pelagic fish	0.67	-

ECOSPACE MODEL DEVELOPMENT

Habitat definition and associations

The benthic habitat of the Senegambian continental shelf is mainly made up of four different sediment types: rocky bottom, sandy bottom, muddy muddy and muddy sand (Domain, 1980). On the north coast the rocky bottom predominates between 10 and 20 m. On the central south coast the rocky bottom mainly occurs at depths of 30–60 m. The sand occupies the main part of the southern shallow waters down to 40 m. Following the sedimentary classification of Domain (1980) four types of habitat were defined in the Ecospace model (Figure 1).

The habitat map (16°03'N and 12°20'N**)** is based on a grid of 40 rows and 20 columns. The length of the cell sides is 5 km. The functional groups are assigned to the different habitats following Domain (1976); the habitat associations are presented in Table 5. In general the pelagic species occur across the whole shelf, whereas some of the demersal species are restricted to specific sediment types.

Due to a lack of specific information on dispersal rates the general base dispersal rates for different types of organisms used by Zeller and Reinert (2004) are used in this model (Table 5). The dispersal rates of functional groups were set according to their general type using the following scheme: marine mammals, 300 km·year^{-1}; sea birds, 300 km·year^{-1}; pelagic fish, 300 km·year^{-1}; demersal fish, 30 km·year^{-1}, benthic invertebrates, 3 km·year^{-1}; plankton, 300 km·year^{-1}; detritus, 3 km·year^{-1}; turtles, 300 km·year^{-1}; and pelagic invertebrates, 300 km·year^{-1}.

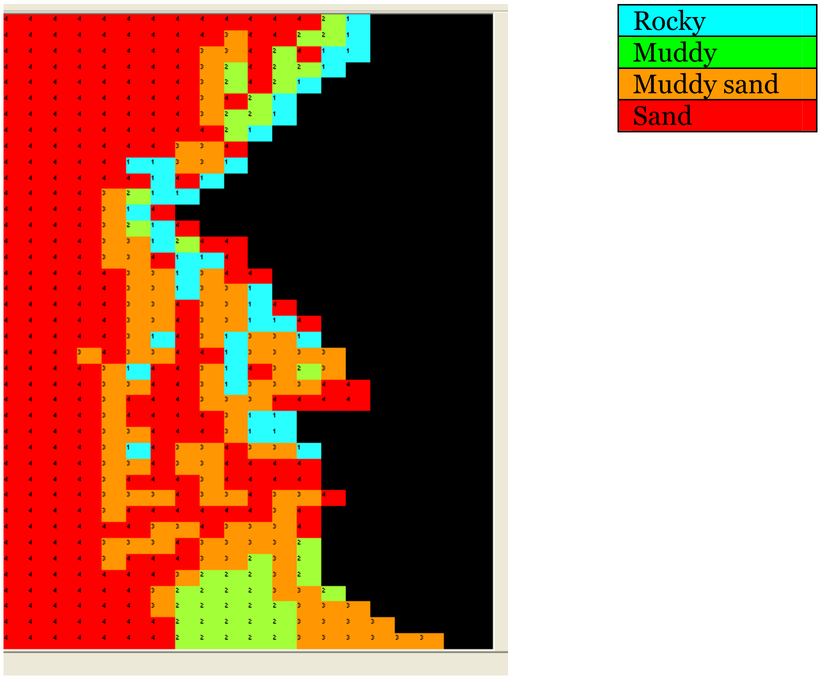


Figure 1. The habitat map of the Senegambian Ecospace model.

Table 5. Habitat associations and dispersal rates of the functional groups within the Senegambian Ecospace model.

Group / Habitat	All	Rocky	Muddy	Muddy sand	Sand	Ecospace area	Ecopath area	Dispersal rate (km·year^{-1})
Marine birds	+					1.000	1.000	300
Marine mammals	+					1.000	1.000	300
Thonids	+					1.000	1.000	300
Coastal thonids	+					1.000	1.000	300
Sharks	+					1.000	1.000	300
Rays			+	+	+	0.920	1.000	30
Cephalopods	+					1.000	1.000	300
Grouper		+	+			0.167	1.000	30
Cassava croaker			+	+	+	0.920	1.000	30
Bluespotted seabream		+				0.080	1.000	30
Other demersal fish	+			`		1.000	1.000	30
Round sardinella	+					1.000	1.000	300
Flat sardinella	+					1.000	1.000	300
Other coastal pelagic fish	+					1.000	1.000	300
Zooplankton	+					1.000	1.000	300
Meiobenthos	+					1.000	1.000	30
Macrobenthos	+					1.000	1.000	30
Benthic producers	+					1.000	1.000	30
Phytoplankton	+					1.000	1.000	300
Discards	+					1.000	1.000	
Detritus	+					1.000	1.000	3
Habitat area	1.000	0.080	0.088	0.235	0.598	-	-	

Map with MPAs

Four MPAs occur within the area covered by the model (Figure 2). These MPAs are represented on the base map. Two MPAs are located north of Dakar and two others are in the south of Dakar. The protected areas include the Saint-Louis Marine Protected Area near the northern border of Mauritania (476 km²), the Kayar MPA north of Dakar (171 km²), the Joal-Fadiouth MPA (174 km²) and the Abene MPA in the coastal waters south of The Gambia (119 km²). The four MPAs together include habitats such as islands, mangroves and a marine canyon, as well as open waters and the seafloor. The MPAs will also protect more than 700 fish species and important nesting and feeding areas. The MPAs are year round and, in theory, the fleets cannot operate within their limits.

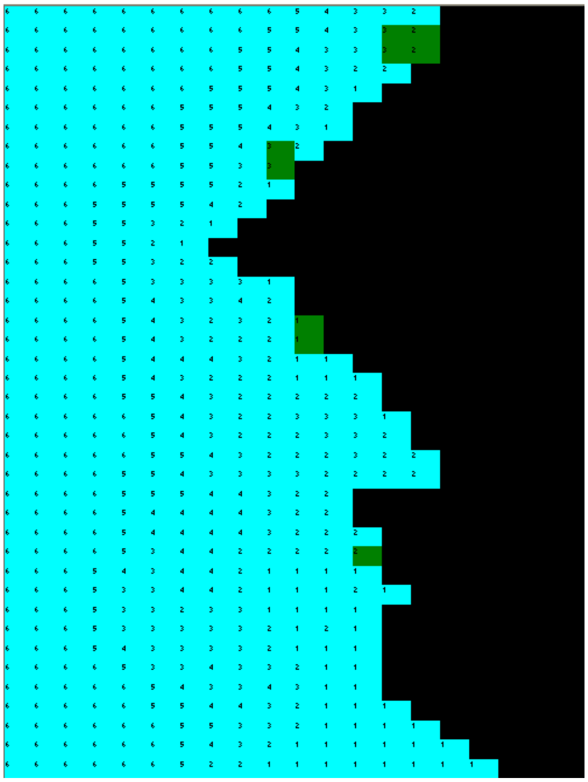


Figure 2. Basemap of the model region indicating the location of the four MPAs.

CONCLUSIONS

The developed model shows certain strong resemblances with that of Peru (Jarre-Teichmann, 1998). The phytoplankton and detritus groups are, by definition, at trophic level 1. At the level 2.0–2.5 is the zooplankton. As in the ecosystem of Peru, the coastal pelagics occupy the trophic level 2.5–3.0. On the other hand, with regard to Peru, only the deepwater species for the level 3.5; the coastal demersal species are at level 3.0. The tunas and cephalopods are found at a level between 3.5 and 4.0.

The mean trophic level of the catches of the model is 2.72, which is low with regard to comparable ecosystems.

As in other upwelling ecosystems already described, the pelagic zone is the main area for production and biomass. The most important flux is determined in the interactions between the phytoplankton, the zooplankton and the coastal pelagics. Thus, the Senegambian ecosystem is strongly impacted by the state of the sardinella stocks.

Table 6 presents a statistical summary characterizing the Senegambian ecosystem. The total biomass excluding the detritus is 275 t·km⁻² with sardinella comprising the bulk of the biomass. The Senegambian ecosystem exhibits a high productivity, with a ratio total primary production on respiration estimated at 2.39 and a ratio primary production on biomass estimated at 41.66; this high production of phytoplankton and zooplankton sustains the high abundance of sardinella.

Table 6. Statistic summary characterizing the Senegambian ecosystem model

Parameter	Value	Units
Sum of all consumption	7,813.683	$t \cdot km^{-2} \cdot year^{-1}$
Sum of all exports	6,737.864	$t \cdot km^{-2} \cdot year^{-1}$
Sum of all respiratory flows	4,803.118	$t \cdot km^{-2} \cdot year^{-1}$
Sum of all flows into detritus	8,052.094	$t \cdot km^{-2} \cdot year^{-1}$
Total system throughput	27,407	$t \cdot km^{-2} \cdot year^{-1}$
Sum of all production	12,937	$t \cdot km^{-2} \cdot year^{-1}$
Mean trophic level of the catch	2.72	
Gross efficiency (catch/net p.p.)	0.001354	
Calculated total net primary production	11,490.93	$t \cdot km^{-2} \cdot year^{-1}$
Total primary prod./total respiration	2.392	
Net system production	6,687.815	$t \cdot km^{-2} \cdot year^{-1}$
Total primary prod./total biomass	41.668	
Total biomass/total throughput	0.01	
Total biomass (excluding detritus)	275.775	$t \cdot km^{-2}$
Total catches	15.556	$t \cdot km^{-2} \cdot year^{-1}$
Connectance Index	0.205	

The study area is a part of the African northwest ecosystem under the influence of the current of the Canary Islands. The works of Jarre-Teichmann (1998) on trophic modelling of the whole zone has already displayed the importance and the role of pelagic fishes in the trophic structure within the region, and especially the role of sardinelles as well as prey as the target of fisheries.

The current situation of the stocks is one of overexploitation for most of the demersal species, particularly the grouper, seabream and croaker. On the other hand, the pelagic species are less exploited. The scenarios to be examined with the model will allow a study of the impact of the different exploitation regimes on the ecosystem.

REFERENCES

Brander, K. and Palmer, D. 1985. Growth rate of *Raja clavata* in the north east Irish Sea. J. Cons. CIEM 42:125-128.

Bransletter, S. 1987. Age and growth validation of newborn sharks in laboratory aquaria with comments on the life story of the Atlantic sharpnose shark. Copeia 2: 291-299.

Camarena-Luhrs, T. 1986. Les principales espèces de pélagiques côtiers au Sénégal: Biologie et évaluation des ressources. Thèse, Université de la Bretagne Occidentale. 188 p.

Caverivière, A. and Andriamirado, G.A.R. 1997. Minimal fish predation for the pink shrimp *Penaeus notalis* in Senegal (West Africa). Bull. Mar. Sci. 61(3): 685-695.

Caverivière, A. *et al.* 1985. Prospection et évaluation des ressources halieutiques profondes au Sénégal. Document scientifique du CRODT. Janvier 1985.

Cayré P., Kothias, J.M., Stretta, M. and Diouf, T. 1988. La biologie des thonidés de l'Atlantique tropical est, p 157-264. In: A. Fonteneau and J. Marcille (eds.) Ressources, pêche et biologie des thonidés tropicaux de l'Atlantique tropicale Centre Est. FAO. Doc. Tech. Pêches (292).

Crawford, R.J.M., Ryan, P.G. and Williams, A.J. 1991. Seabird consumption and production in the Benguela and Western Agulhas ecosystems. S. Afr. J. Mar. Sci. 11: 357-375.

CRODT/JICA, 2006. Etude de l'évaluation et de la gestion des ressources halieutiques. Rapport final (Provisoire). Overseas Agro-Fisheries Consultants Co., Ltd. Mai 2006.

Dah, A., Girardin, M. and Vall, M. 1991. Les poissons de la communauté à sparidés, p. 99-116. In: P. Chavance and M. Girardin (eds.) L'environnement, les ressources et les pêcheries de la ZEE Mauritanienne. CRNOP, Nouadhibou.

De la Cruz-Aguero, G. 1993. A preliminary model of Mandinga lagoon, Veracruz, Mexico, p. 193-196. In: V. Christensen and D. Pauly (eds.) Trophic models of aquatic ecosystems. ICLARM Conf. Proc. 26.

Dème, M. 2000. Exploitation, gestion et conservation des stocks de requins: état des lieux au Sénégal. Document de la Commission sous régionale des pêches, Dakar Thiaroye.

de Paula e Silva, R., Sousa, M.I. and Caramelo, A.M. 1993. The Maputo Bay ecosystem (Mozambique), p. 214-223. In: V. Christensen and D. Pauly (eds.) Trophic models of aquatic ecosystems. ICLARM Conf. Proc. 26. ICLARM, Manila, Philippines.

Diatta, Y., Ba, F. L. and Capape, C. 2001. Rôle trophique du poulpe commun, *Octopus vulgaris*, chez les élasmobranches de la côte du Sénégal (Atlantique oriental tropical) Comparaison avec les espèces des côtes Tunisiennes (Méditerranée centrale). ACTA ADRIAT., 42 (1): 77-88, 2001.

Diouf, P.S. 1996 Les peuplements de poissons des milieux estuariens de l'Afrique de l'Ouest : L'exemple de l'estuaire hyperhalin du Sine-Saloum. Université de Montpellier II. Thèses et Documents Microfiches No.156. ORSTOM, Paris. 267 p.

Diouf, T. 1980. Pêche et biologie de trois scombridae exploités au Sénégal: *Euthynnus alletteratus, Sarda sarda* et *Scomberomorus tritor*. Thèse de Doctorat 3ème cycle, Université de Bretagne Occidentale, France. 159 p.

FAO, 2005. Rapport du Groupe de Travail de la FAO sur l'évaluation des petits pélagiques au large de l'Afrique nord occidentale. Nouadhibou, Mauritanie, 26 avril au 5 mai 2005. Sous presse.

Domain F. 1980.- Contribution à la connaissance de l'écologie des espèces démersales du plateau continental sénégalo-mauritanien. Les ressources démersales dans le contexte du Golfe de Guinée. Thèse doct. D'état, Univ. Paris VI Mus. Nat. Hist.Nat., 342 p.

Fischer , W., Bianchi, G. and Scott, W.B. 1981. Fiches FAO d'identification des espèces pour les besoins de la pêche. Atlantique centre-est ; zones de pêches 34, 47 (en partie). Canada Fonds de dépôts. Ottawa, Ministère des Pêcheries et Océans, en accord avec la FAO, Vols. 1-7.

Franqueville, C. 1983. Biologie et dynamique de population des daurades (*Pagellus bellottii,* Steindacher, 1982) le long des côtes Sénégalaises. Thèse Doc. D.Etat. Université d.Aix-Marseille II. 276 p.

Fréon, P. 1988. Réponses et adaptation des stocks de clupéidés d'Afrique de l'Ouest à la variabilité du milieu ; analyse et réflexion à partir de l'exemple du Sénégal. Études et thèses, ORSTOM, Paris.

Gouriou. 1993. The environment in the Eastern Tropical Atlantic, p. 11-30. In: A. Fonteneau and J. Marcille (eds.) Resources, fishing and biology of the tropical tuna in the Eastern Central Atlantic. FAO Fish. Rech. Pap. 292, FAO, Rome. 354 p.

ICCAT. 1999a. Rapport de la période biennale 1998-1999. 1ère partie (1998)-Vol. 1. Version Française. Madrid, Espagne.

ICCAT. 1999b. Rapport de la période biennale 1998-1999. 1ère partie (1998)-Vol. 2. Version Française. Madrid, Espagne.

Jarre-Teichmann, A. and Christensen, V. 1998. Comparative modeling of trophic flows in four large upwelling ecosystems, p. 423-443. In: M.H. Durand, P. Cury, R. Mendelssohn, C. Roy, A. Bakun and D. Pauly (eds.) Global versus Local Changes in Upwelling Systems. Éditions de l.Orstom, Collection Colloques et séminaires, Paris.

Kompowski, A. and Slosarczyk, W. 1976. Some investigations on horse mackerel (*Trachurus trachurus*) in the ICSEAF area in 1973. Colln. Scient. Pap. int. Commn. SE Atl. Fish. 3: 27-38.

Krakstad, J.O., Olsen, M. and Sarre, A. 2003. Survey of the pelagic fish resources off northwest Africa. 29 oct. 2002 - 15 nov. 2003.

Krakstad, J.O., Sylla, M., Mbye, E.M. and Olsen, M. 2004. Survey of the pelagic fish resources off northwest Africa. Part I SENEGAL-THE GAMBIA; 25 octobre - 3 novembre 2004.

Laurans, M., Gascuel, D. and Barry, M. 2003. Revue des connaissances sur la biologie du thiof (*Epinephelus aenus*) et diagnostic de l'état du stock au Sénégal in Evaluations des stocks démersaux en Afrique du nord-ouest, Travaux du Groupe "Analyses monospécifiques" du projet SIAP COPACE/PACE Séries 03/65.

Levenez, J.J. 1993. Synthèse bibliographique des connaissances sur la biologie de quelques espèces de poissons concernant le symposium. In. L'évaluation des ressources exploitables par la pêche artisanale. Symposium Dakar, 8 au 13 Février 1993. Sénégal. Tome 2. Ed. M. Barry, T. Diouf et A. Fonteneau. ORSTOM éditions.

Medina-Gaertner, M. 1985. Etude du zooplancton côtier de la Baie de Dakar et de son utilisation par les poissons comme source de nourriture. Thèse, Uni. Bret. Occident. 141 p.

Nieland, H. 1982. The food of *Sardinella aurita* (Val.) and *Sardinella eba* (Val.) off the coast Senegal Rapp. P,-V, Réun. Cons. Int. Explor. Mer 180: 369-373.

Northridge, S.P. 1984. World review of interactions between marine mammals and fisheries. FAO Fish. Tech. Pap. 251. Rome. 190 p.

Olivieri, R.A., Cohen, A. and Chavez, F.P. 1993. An ecosystem model of Monterey Bay, California, P. 315-322. In: V. Christensen and D. Pauly (eds.) Trophic models of aquatic ecosystems. ICLARM Conf. Proc.26.

Opitz, S. 1993. A quantitative model of the trophic interactions. in a Caribbean coral reef ecosystem, p. 259-268. In: V. Christensen and D. Pauly (eds.) Trophic models of aquatic ecosystems. ICLARM Conf. Proc. 26.

Palomares, M.L.D. and Pauly, D. 2000. Trophic ecology, p. 176-178. In: R. Froese and D. Pauly (eds.) FishBase 2000: Concepts, design and data sources. ICLARM, Los Baños, Philippines.

Pauly, D. 1979. Gill size and temperature as governing factors in fish growth: a generalization of von Bertalanffy.s growth formula. Ber. Inst. Meereskd. Christian-Albrechts Univ. Kiel 63. 156 p.

Pauly, D. 1980. On the interrelationships between natural mortality, growth parameters, and mean environmental temperature in 175 fish stocks. J. Cons. Int. Explor. Mer 39(2): 175-192.

Pauly, D. and Munro, J. 1984. Once more on growth comparison in fish and invertebrates. Fishbyte 2(1):21.

Pauly, D., 1978. A preliminary compilation of fish length growth parameters. Ber. Inst. Meereskd. Christian-Albrechts-Univ. Kiel (55):1-200.

Postel, E. 1955. Résumé des connaissances acquises sur les Clupéidés de l'Ouest Africain. Rapp. Cons. int. Explor. Mer 137: 14-17.

Samb, B. 1988. Seasonal growth, mortality, recruitment pattern of *Sardinella maderensis* off Senegal, p. 257-271. In:: S.C. Venema, J.M. Christensen and D. Pauly (eds.) Contributions to tropical fisheries biology. FAO/DANIDA Follow-up Training Course on Fish Stock Assessment in the Tropics, Denmark 1986, Philippines, 1987. FAO Fisheries Report n° 389. Rome.

Samb, B. 1997. Synthèse des évaluations récentes sur l'état des stocks de sardinelles, chinchards et maquereaux dans la zone nord COPACE. Document COPACE/FAO. 11th Session du COPACE/FAO sur l'Evaluation des Stocks.24 au 26 Septembre 1997, Accra, Ghana.

Schneider, W. 1990. FAO species identification sheets for fishery purposes. Field guide to the commercial marine resources of the Gulf of Guinea. Prepared and published with the support of the FAO Regional Office for Africa. FAO, Rome. 26 p.

Seret, B. 1981. Poissons de mer de l.Ouest africain. Initiation et documentation technique n° 49. ORSTOM, Paris.

Toresen, R., Sarre, A. and Olsen, M. 2001. Survey of the pelagic fish resources off north west Africa . Part I SENEGAL-THE GAMBIA-29oct-08 Nov 2001.

Toresen, R., Sarre, A. and Olsen, M. 2002. Survey of the pelagic fish resources off northwest Africa. 29 oct. 2002 - 16 nov. 2002.

Touré, D. 1983. Contribution à l'étude de l'upwelling de la baie de Gorée (Dakar Sénégal) et de ses conséquences sur le développement de la biomasse phytoplanctonique. Doc. Sci. CRODT n° 93.

Voituriez, B. and Herbland, A. 1982. Comparaison des systèmes productifs de l'Atlantique Tropical est: dômes thermiques, upwellings côtiers et upwellings équatorial. rapp. P.-V. Réun. CIEM, 180: 114-30.

Zeller, D. and Reinert, J. 2004 . Modelling spatial closures and fishing effort restrictions in the Faroe Island marine ecosystem. Ecological Modelling 172 403-42.

A BENTHIC ECOSYSTEM MODEL OF THE SINALOA CONTINENTAL SHELF, MEXICO [1]

L. A. Salcido-Guevara and F. Arreguín-Sánchez
Centro Interdisciplinario de Ciencias Marinas del IPN,
Apartado postal 592, La Paz 23000, Baja California Sur, Mexico;
Email: salcidog@gmail.com

ABSTRACT

The trophic network of the southern Sinaloa benthonic ecosystem was reconstructed for the period 1994–1997, using Ecopath with Ecosim version 5.1. The ecosystem is a resource for finfish and shrimp fisheries. The majority of the 37 functional groups were determined from the makeup of captures taken by commercial trawls similar to those used by the shrimp fishery. Incidental captures represented approximately 91% of the total and consisted mainly of fish from the families Sciaenidae, Haemulidae, and Serranidae, followed by macrocrustaceans (Portunidae) and invertebrates (Echinodermata). The trophic model obtained had a pedigree index of 0.57, which represents an acceptable quality from the data used. The ecosystem is represented by 4 discreet trophic levels; medium-level carnivores, including Pleuronectiformes, birds, Sciaenidae, Serranidae, and Centropomidae, contribute the majority of energy transfer in the third level. The mixed trophic impacts show that detritus positively affects the majority of functional groups, mainly the primary consumers (TL=2). The shrimp fleet also uses the Penaeidae as a resource. Primary producers exert a positive impact on groups taken by the finfish fleet, although to a lesser extent. The ecosystem is in a low state of maturity or development according to system attributes, which indicate an overhead of 2.3 times the ascendance.

INTRODUCTION

The Pacific coast contributes 70% of Mexico's fishery landings and the state of Sinaloa contributes 14%, of which tuna and sardines make up the majority. Shrimp occupies third place but has greater value than other species, and since it contributes the largest proportion of captures (70%) of demersal species, it occupies first place in generating revenues in Mexico (CONAPESCA, 2003). For more than two decades, studies dedicated to shrimp fishing have revealed the enormous disproportion of incidental captures, comprising mainly fish and crustaceans. This is the source of some difficulty in making good decisions in managing the resource in Sinaloa.

In recent years, the Mexican federal government has promoted the reduction of fishing effort through the purchase of trawlers (a financial mechanism to reduce the fleet size). Before this type of measure, the recovery of all or part of the ecosystem would have been possible to an extent, but how can changes in the ecosystem and its consequences on the future be identified in a timely manner? To start with, we hope that later analysis of the ecosystem described by our trophic model constructed using Ecopath with Ecosim (Christensen and Pauly, 1992) will identify changes in ecosystem attributes resulting from incidental captures and variation in fishing intensity, as well as contributing proposals for optimal management solutions based on ecological, social, and economic criteria.

This report presents the data sources and calculations used to parameterize an Ecopath model of the southern Sinaloa continental shelf.

---

[1] Cite as: Salcido-Guevara, L. A. and Arreguín-Sánchez, F. 2007. A benthic ecosystem model of the Sinaloa continental shelf, Mexico, p. 170–188. *In*: Le Quesne, W.J.F., Arreguín-Sánchez, F. and Heymans, S.J.J. (eds.) INCOFISH ecosystem models: transiting from Ecopath to Ecospace. Fisheries Centre Research Reports 15(6). Fisheries Centre, University of British Columbia [ISSN 1198-6727].

MATERIALS AND METHODS

The study area was located on the continental shelf of southern Sinaloa, from the mouth of the river San Lorenzo (24°10'N, -107°27'W) to the mouth of Teacapán (22°22'N, -105°50'W), with depths between 20 and 140 meters and covering an area of approximately 6,250 km^2 (Figure 1). Incidental capture data came from 148 trawls using shrimp nets during the period from September 1994 to January 1997, in BIOCAPESS tours of 'The Puma' of the Autonomous National University of Mexico. Data were registered by Manjarrez-Acosta (2001).

The balanced biomass trophic model was constructed with 'Ecopath with Ecosim' softward package version 5.1.0.17, modified by Christensen and Pauly (1992), and consists of a series of linear equations that represent each functional group quantitatively as

$$B_i\left(\frac{P}{B}\right)_i EE_i = \sum_{j=1}^{n} B_j\left(\frac{Q}{B}\right)_j DC_{ji} + Y_i + E_i + BA_i \qquad \textbf{\textit{Eq. 1}}$$

in which B_i is the biomass of group i; $(P/B)_i$ and $(Q/B)_i$ are the ratios of production to biomass and consumption to biomass of i respectively; EE_i is the ecotrophic efficiency and describes the production used in the system; DC_{ji} is the average fraction of prey i in the diet of predator j; and E_i, Y_i, and BA_i are the net migration, total captures, and accumulated biomass of i.

Model structure

Considering the commercial and ecological importance of organisms captured in the trawls, our model was based on 37 functional groups, represented mainly by fish and followed by crustaceans, mollusks and other invertebrates (Table 1). We considered 13 functional groups of commercial interest, taking into account commercial capture data, consisting of 8 groups of fish, 3 crustaceans, and 2 mollusk groups. The remaining groups were chosen according to ecological criteria, selecting those of greatest abundance by weight or importance in the diet of other groups, such as bivalves, macrophytes, zooplankton, phytoplankton and detritus. From the capture data the landings of the functional groups is made up as follows: Portunidae by *Callinectes* spp. (99%) and *Euphilax* spp. (1%); Penaeidae by *Litopenaeus* spp. (59%), *Trachypenaeus* spp. (15%), *Sicyonia* spp. (8%) and *Xiphopenaeus riveti* (17%) (according to Hendrickx, 1996); and other macrocrustaceans by *Calappidae* (44%), *Maiopsis panamensis* (21%) (according to Hendrickx *et al.*, 1992), *Pleuroncodes* spp. (27%), Paguridae (2%) and other crabs (6%); cephalopoda mainly by *Loligo* spp. and Palinura by *Scyllarides* spp.

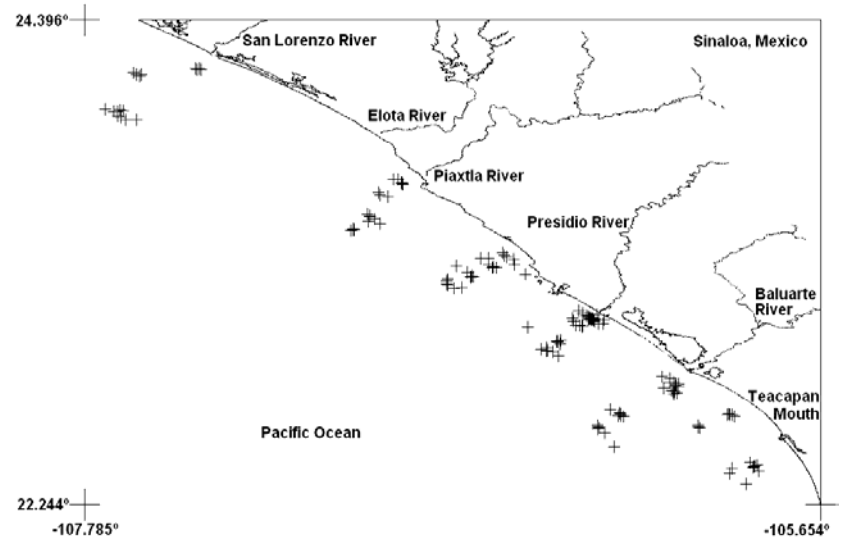


Figure 1. Study area on the continental shelf in southern Sinaloa, showing sampling stations from which shrimp trawling data were taken.

Input data

Two separate fleets, an industrial shrimp trawl fleet and a finfish fleet, were designated in the model to represent the dynamics of the fishery that occur in the study region. Fleet capture data came from official registries (SEMARNAP, 1995, 1996, 1997). A 90% discard rate reported for the zone was considered for the respective groups (Rodriguez-Cagica, 1996).

The initial biomass of the majority of functional groups was estimated from trawl data. A relationship between the capture per effort unit (CPUE) and stock abundance was assumed in order to use the

Table 1. Structure of incidental capture (wet weight) represented by the relative abundance of fish and other groups in southern Sinaloa, Mexico.

Group and species	t·km^{-2}	Group and species	t·km^{-2}	Group and species	t·km^{-2}	Group and species	t·km^{-2}
1. Sciaenidae	0.3233	7. Pleuronectiformes	0.1276	13. Clupeidae	0.0196	Balistidae	0.0071
Menticirrhus nasus	0.0843	Bothidae	0.1037	Clupeidae	0.0143	*Balistes polylepis*	0.0071
Micropogonias ectenes	0.0541	*Bothus constellatus*	0.1037	*Lile stolifera*	0.0124	Ophichthidae	0.0055
Larimus argenteus	0.0455	Paralichthyidae	0.0192	*Ophistonema libertate*	0.0019	*Ophichthus zophochir*	0.0055
Cynoscion stolzmanni	0.0332	*Etropus crossotus*	0.0139	Engraulidae	0.0053	Malacanthidae	0.0044
Cynoscion reticulatus	0.0254	*Paralichthys* spp.	0.0030	*Anchoa lucida*	0.0053	*Caulolatilus affinnis*	0.0044
Larimus acclivis	0.0241	*Cyclopsetta querna*	0.0023	14. Scombridae	0.0180	Priacanthidae	0.0028
Umbrina xanti	0.0198	Achiridae	0.0047	*Scomberomorus sierra*	0.0114	*Pristigenys serrula*	0.0028
Cynoscion xanthulus	0.0178	*Achirus mazatlanus*	0.0045	*Scomber japonicus*	0.0066	Ogcocephalidae	0.0026
Stellifer illecebrosus	0.0094	*Achirus panamensis*	0.0002	15. Tetraodontidae	0.0148	*Zalieutes elater*	0.0026
Ophioscion imiceps	0.0069	8. Scorpaenidae/Triglidae	0.0971	*Sphoeroides lobatus*	0.0084	Lophiidae	0.0022
Cynoscion spp.	0.0025	Scorpaenidae	0.0147	*Sphoeroides annulatus*	0.0054	*Lophiodes caulinaris*	0.0022
Stellifer furthii	0.0003	*Pontinus sierra*	0.0108	*Sphoeroides* spp.	0.0011	Atennaridae	0.0019
2. Haemulidae	0.2431	*Scorpaena russula*	0.0038	16. Lutjanidae	0.0138	*Antennarius avalonis*	0.0019
Haemulopsis leuciscus	0.0998	Triglidae	0.0691	*Lutjanus guttatus*	0.0125	Trichiuridae	0.0018
Pomadasys panamensis	0.0833	*Prionotus stephanophrys*	0.0634	*Lutjanus colorado*	0.0008	*Trichiurus leptururs*	0.0018
Orthopristis spp.	0.0397	*Bellator loxias*	0.0370	*Lutjanus argentiventris*	0.0005	Apogonidae	0.0016
Orthopristis chalceus	0.0164	*Prionotus ruscarius*	0.0001	17. Coryphaenidae	0.0054	*Apogon retrosella*	0.0016
Conodon serrifer	0.0019	9. Centropomidae	0.0691	*Coryphaena hippurus*	0.0054	Pristigasteridae	0.0011
Pomadasys spp.	0.0015	*Centropomus robalito*	0.0691	18. Mugilidae	0.0005	*Pliosteostoma lutipinnis*	0.0011
Pomadasys bayanus	0.0005	10. Rajiformes	0.0634	*Mugil cephalus*	0.0005	Nematistiidae	0.0008
3. Polynaemidae/Mullidae	0.2070	Rhinobatidae	0.0370	19. Other fish	0.2520	*Nematistius pectoralis*	0.0008
Polynemidae	0.1096	*Rhinobatos glaucostigma*	0.0370	Stromateidae	0.1128	Muraenidae	0.0008
Polydactylus approximans	0.1060	Urolophidae	0.0264	*Peprilus medius*	0.0846	*Muraena lentiginosa*	0.0008
Polydactylus opercularis	0.0036	*Urotrygon munda*	0.0153	*Peprilus snyderi*	0.0282	Other groups (non-fish)	-
Mullidae	0.0974	*Urotrygon chilensis*	0.0111	Sphyraenidae	0.0385	20. Portunidae	0.4207
Mulloidichthys dentatus	0.0928	11. Carangidae	0.0582	*Sphyraena ensis*	0.0385	21. Penaeidae	0.2970
Pseudupeneus grandisquamis	0.0046	*Chloroscombrus orqueta*	0.0423	Batrachoididae	0.0320	22. Echinodermata	0.2061
4. Synodontidae	0.1873	*Selene peruviana*	0.0132	*Porichthys analis*	0.0320	23. Other macrocrustaceans	0.0702
Synodus scituliceps	0.1873	*Selar crumenophthalmus*	0.0014	Brotulidae	0.0167	24. Coelenterata	0.0482
5. Gerreidae	0.1729	*Selene brevoorti*	0.0014	*Brotula clarkae*	0.0167	25. Cephalopoda	0.0482
Eucinostomus dowii	0.1488	12. Ariidae	0.0275	Ephippidae	0.0120	26. Stomatopoda	0.0140
Diapterus peruvianus	0.0241	*Arius seemanni*	0.0214	*Chaetodipterus zonatus*	0.0120	27. Cheloniidae	0.0064
6. Serranidae	0.1673	*Bagre panamensis*	0.0037	Cynoglossidae	0.0074	28. Porifera	0.0061
Diplectrum pacificum	0.1640	*Bagre* spp.	0.0023	*Symphurus elongatus*	0.0074	29. Gastropoda	0.0050
Diplectrum maximun	0.0019	-	-	-	-	30. Polychaeta	0.0013
Epinephelus acanthistius	0.0011	-	-	-	-	31. Palinura	0.0001
Hemanthias peruanus	0.0003	-	-	-	-	-	-

coefficients of capturability from the model of Leslie and Davies (1939). Bivalve incidental capture was reported as frequency of individuals, but it was necessary to consider this group since it is important in the diet of other groups. The biomass of bivalves was obtained in agreement with the capture proportions of the bivalve *Chione kellettii* (1.6 t·km^{-2}) and the gastropod *Solenosteira gatesi* (0.65 t·km^{-2}), these being the most abundant mollusk species in southern Sinaloa during 1984 (Hendrickx, 1985).

Table 2. References for the values used to estimate Q/B and P/B in Table 3.

Species	Equation		*L*∞	a	b	*W*∞	*K*	*A*	*D*	*P*
	Q/B	*P/B*								
Arius seemanni	28	-	29; 25	26	26	26	19	5	-	-
Calappa convexa	-	32	-	-	-	-	23	-	-	-
Callinectes spp.	-	32	-	-	-	-	21	-	-	-
Chloroscombrus orqueta	28	-	26	26	26	5	-	5	-	-
Coryphaena hippurus	27	-	25; 15	15	15	26	16	29; 17	29; 17	29; 17
Cyclopsetta querna	27	30	9	26	26	26	9	29; 3	29; 3	29; 3
Cynoscion reticulatus	28	-	1	2	2	26	1	29; 3	29; 3	29; 3
Diplectrum pacificum	24	-	8	26	26	26	8	5	-	-
Eucinostomus dowii	28	-	29; 25	26	26	26	6	5	-	-
Haemulopsis leuciscus	-	-	-	2	2	-	-	-	-	-
Isostichopus fuscus	-	32	-	-	-	-	20	-	-	-
Lile stolifera	24	-	29; 25	26	26	26	-	5	-	-
Litopenaeus vannamei		33	22	-	-	-	22	-	-	-
Lutjanus guttatus	27	31	14	-	-	14	14	3	29;3	29; 3
Menticirrhus nasus	-	30	25; 29	-	-	-	6	-	-	-
Mugil cephalus	24	-	18	-	-	18	18	5	-	-
Peprilus medius	28	-	29; 25	26	26	26	6	5	-	-
Polydactylus approximans	28	-	29; 25	26	26	26	6	29; 3	29;3	29; 3
Pomadasys panamensis	24	31	4	-	-	26	4	5	-	-
Prionotus stephanophrys	28	31	4	26	26	26	4	5	-	-
Rhinobatos glaucostigma	28	-	29; 25	26	26	26	10	29; 28; 5	-	-
Scomberomorus sierra	24	31	11	11	11	26	11	12	-	-
Sphoeroides annulatus	28	30	29; 25; 13	13	13	26	6	29; 13	29; 13	29; 13
Synodus scituliceps	24	-	25; 7	26	26	26	29; 7	5	-	-

1: Mendoza-López *et al.* (1992); 2: IGFA (2001); 3: Amezcua-Linares (1996); 4: Pérez-González (1995); 5: García and Duarte (2002); 6: Froese and Pauly (2005); 7: Morales-Nin (1996); 8: Pauly and Binohlan (1996); 9: Mendoza-López *et al.* (1997); 10: Pauly (1978); 11: Medina-Gómez (pers. com.); 12: Arreguín-Sánchez *et al.* (2002); 13: Sánchez-Cárdenas (2005); 14: Soto-Avila (2004): 15: Madrid and Beltrán-Pimienta (2001); 16: González-Ramos *et al.* (1997); 17: Morán-Angulo (pers. com.); 18: Rodríguez-Gerrero *et al.* (1986); 19: Waburton (1978); 20: Reyes-Bonilla (1997); 21: Gil and Sarmiento (2001); 22: Rojas-Zepeda *et al.* (1993); 23: Ayon-Parente (2000); 24: Palomares and Pauly (1998); 25: Pauly (1983); 26: This work with $W=aL^b$; 27: Jarre *et al.* (1991); 28: Palomares and Pauly (1989); 29: This work; 30: Beverton and Holt (1957); 31: Hoenig (1983); 32: Rainer (1982); 33: Baranov (1918). All values of Q/B were estimated at a temperature of 20.79°C (Manjarrez-Acosta, 2001). $L\infty$, $W\infty$ and K are parameters of VBGE.

Zooplankton biomass was obtained as annual average dry weight (0.0643 g·m^{-3}) reported for the Bay of Mazatlán (Alvarez-Chain, 1985). The conversion factor to wet weight (15%) proposed by Jørgensen (1979) was used. Phytoplankton biomass was based on the annual chlorophyll concentration (5.14 mg·m^{-3}) reported for the Bay of Mazatlán (Cruz-Martinez, 1995). In order to obtain this biomass, the reported proportions of carbon/chlorophyll (44.9), dry phytoplankton/carbon (5.4) (Durbin and Durbin, 1998) and wet weight/dry organic matter (5) (Parsons *et al.*, 1977) were replaced in a single expression as follows:

$$B = 1212.3[Cla]z \qquad \textbf{Eq. 2}$$

in which B is wet weight of phytoplankton biomass (t·km^{-2}); Cla is chlorophyll-a concentration (g·m^{-3}); and z is euphotic depth (m). Annual phytoplankton production for the southern Gulf of California was 98.55 gC·m^{-2}·year^{-1} (Penié-Rodriguez *et al.*, 2002). Phytoplankton and zooplankton biomass were estimated at an average 20 m euphotic depth. Macrophyte biomass was assumed equal to that reported for the Bay of Mazatlán (Garza-Osuna, 1999). For the birds group, the biomass reported for the Sonora continental shelf was taken (Arreguín-Sánchez *et al.*, 2002). The biomasses of the 8 remaining groups were calculated during model balancing by assuming EE values from EE values reported for similar groups in other models (Christensen and Pauly, 1993). Detritus biomass was calculated by the Ecoempire routine in Ecopath, at primary production of 0.27 gC·m^{-2}·dia^{-1}, as reported for the southern Gulf of California (Penié-Rodríguez *et al.*, 2002).

Because P/B is equivalent to the instantaneous rate of total mortality Z (year^{-1}) in equilibrium conditions (Allen, 1971), the input values for the model were calculated by different methods depending on availability of information and similarities with other published estimates (Tables 2 and 3). The first estimate for fish was taken from the model of Beverton and Holt (1957), based on size and parameters of the von Bertalanffy growth equation (VBGE). In some cases, where $L\infty$ was unknown the maximum registered length for the region was used (Pauly, 1983).

The second estimate of P/B was from the model of Hoenig (1983), with Z based on fish longevity. In some cases a relationship between K (VBGE) and longevity was assumed (Pauly, 1980). The third estimate was made knowing Q/B and the gross food conversion efficiency P/Q (=GE) to get P/B from $GE=(P/B)/(Q/B)$. Values of Q/B for fish were obtained from three different equations (Palomares and Pauly, 1989;

Table 3. Data for estimating proportions of consumption/biomass (Q/B) and production/biomass (P/B). The references are in Table 2.

Functional Group and Species	$L\infty$ (cm)	a	b	$W\infty$ (g)	K (year^{-1})	*A*	*D*	*P*	*HD*	*h*	*d*
Sciaenidae											
Cynoscion reticulatus	57.71	0.0087	3	1,672	0.252	2.13	4.48	0.3	0	-	-
Menticirrhus nasus	52.63	-	-	-	0.42	-	-	-	-	-	-
Haemulidae											
Pomadasys panamensis	33.5	-	-	617	0.61	2.5	-	-	-	0	0
Haemulopsis leuciscus	-	0.0164	3	-	-	-	-	-	-	-	-
Polynemidae/Mullidae											
Polynemidae											
Polydactylus approximans	32.63	0.0099	2.9967	340	0.6	2.71	3.1	0.46	0	-	-
Synodontidae											
Synodus scituliceps	45.26	0.0041	3.1097	578	0.333	2.2	-	-	-	0	0
Gerreidae											
Eucinostomus dowii	21.47	0.0292	2.7097	119	0.8	2.7	-	-	0	-	-
Serranidae											
Diplectrum pacificum	36.4	0.0088	3.1361	692	0.247	1.5	-	-	-	0	0
Pleuronectiformes											
Paralichthyidae											
Cyclopsetta querna	20.82	0.0015	3.659	100	0.66	1.09	2	0.2	-	-	-
Scorpaenidae/Triglidae											
Triglidae											
Prionotus stephanophrys	33.5	0.0369	2.3788	157	0.505	1.2	-	-	0	-	-
Rajiformes											
Rhinobatidae											
Rhinobatos glaucostigma	73.68	0.0031	3.0173	1,336	0.15	2.89	-	-	0	-	-
Carangidae											
Chloroscombrus orqueta	36.54	0.0133	2.8575	388	-	4.1	-	-	0	-	-
Ariidae											
Arius seemanni	42.11	0.0021	3.3933	682	0.1	1.8	-	-	0	-	-
Clupeidae											
Lile stolifera	15.68	0.0132	2.8043	30	-	2.4	-	-	-	0	0
Scombridae											
Scomberomorus sierra	119.2	0.0134	2.8388	10,501	0.07	3.6	-	-	-	0	0
Tetraodontidae											
Sphoeroides annulatus	46.32	0.0376	2.8958	2,505	0.28	2.3	3.14	0.31	0	-	-
Lutjanidae											
Lutjanus guttatus	85.82	-	-	7,273	0.087	2.16	2.62	0.3	-	-	-
Coryphaenidae											
Coryphaena hippurus	135.79	0.028	2.706	16,546	0.16	5.64	4.08	0.21	-	-	-
Mugilidae											
Mugil cephalus	42.74	-	-	667	0.345	1.4	-	-	-	0	1
Other fish											
Stromateidae											
Peprilus medius	28.42	0.0025	3.5075	314	0.54	2.6	-	-	0	-	-
Echinodermata											
Isostichopus fuscus	-	-	-	-	0.43	-	-	-	-	-	-
Portunidae											
Callinectes spp.	-	-	-	-	2.1	-	-	-	-	-	-
Penaeidae											
Litopenaeus vannamei	16.35	-	-	-	2.5	-	-	-	-	-	-
Other macrocrustaceans											
Calappa convexa	-	-	-	-	0.52	-	-	-	-	-	-

$L\infty$, $W\infty$ and K are parameters of VBGE; a and b are intercept and slope of the potential equation $W=aL^b$; A is the radial aspect of the caudal fin of a fish; D and P are morphometric variables of a fish, D= standard length/maximum body height, and P=height of caudal peduncle/maximum body height; HD is feeding type of a fish (0=carnivorous; 1=herbivorous & detritivorous); h and d are feeding types: h=1 (herbivorous), h=0 (carnivorous & detritivorous), d=1 (detritivorous) and d=0 (herbivorous & carnivorous).

Table 4. References for the predator-prey matrix of the benthonic ecosystem model of southern Sinaloa, Mexico. *Data from the study area.

Group and species	Reference
Vertebrates	-
Birds	1; 5
Sciaenidae	1; 6
Cynoscion reticulatus	*3
Larimus acclivis	*3
Cynoscion xanthulus	*4; *2
Haemulidae	1; 6
Pomadasys panamensis	*7
Pomadasys macracanthus	*3; *4
Anisotremus interruptus	*2
Polynemidae/Mullidae	20
Polydactylus opercularis	*3
Pseudupeneus grandisquamis	24
Synodontidae	-
Synodus sechurae	24
Gerreidae	-
Diapterus peruvianus	25; 26; 14
Gerres cinereus	25
Eucinostomus entomelas	26
Eugerres axillaris	26
Serranidae	6; 16; 29; 30
Paralabrax maculatofasciatus	27; 28; 31
Pleuronectiformes	*2
Cyclopsetta querna	*17
C. panamensis	*17
Scorpaenidae/Triglidae	1
Scorpaena russula	24
Prionotus stephanophrys	*7
Centropomidae	-
Centropomus robalito	*3; *2; *8; *9; *10
Centropomus nigrescens	*4; *10
Rajiformes	29
Rhinobatos productus	27
Urobatis halleri	28; 32
Urobatis maculatus	28
Carangidae	1; 16; 19; 20
Carangidae	29; 33; 34; 35
Caranx hippos	*3; *2
Ariidae	16
Arius seemanni	*3
Arius guatemalensis	*2
Clupeidae	-
Ophistonema libertate	31
Scombridae	19; 20; 21; 22
Scomberomorus sierra	*18
Tetraodontidae	-
Sphoeroides annulatus	31
Sphoeroides lobatus	28
Lutjanidae	15; 16
Lutjanus argentiventris	*9; *11
Lutjanus colorado	*11; 13
Lutjanus guttatus	12; 14
Coryphaenidae	-
Coryphaena hippurus	*23
Mugilidae	-
Mugil cephalus	*2
Other fish	-
Sphyraena ensis	36
Chaetodipterus zonatus	36
Trichiurus nitens	36
Balistes polylepis	36
Ophichthus zophochir	36
Zalieutes elater	36
Lophiodes caulinaris	36
Antennarius avalonis	36
Apogon retrosella	36
Pristigenys serrula	36
Nematistius pectoralis	36
Muraena lentiginosa	36
Cheloniidae	45
Lepidochelys olivacea	44; 47
Careta careta	46
Invertebrates	-
Portunidae	-
Callinectes arcuatus	*2; 37
Callinectes bellicosus	37
Penaeidae	1
Litopenaeus spp.	*2
Echinodermata	38
Coelenterata	22
Aurelia aurita	39; 40; 41; 42
Stomolophus meleagris	43
Cephalopoda	1; 22
Stomatopoda	1; 6
Porifera	38
Gastropoda	*2
Polychaeta	1; *2
Palinura	-
Panulirus inflatus	48
Panulirus gracilis	48
Panulirus interruptus	49
Other macrocrustaceans	-
Pleuroncodes planipes	50
Plankton	-
Zooplankton	1; *2

1: Arreguín-Sánchez *et al.* (2002); 2: Zetina-Rejón *et al.* (2003); 3: Arriaga-Haro *et al.* (1989); 4: Espinoza-Flores *et al.* (1990); 5: Chávez-Garibay (pers. com.); 6: Morales-Zárate *et al.* (2004); 7: Pérez-González (1995); 8: De La Garza-De Los Santos *et al.* (1985); 9: García-Telles *et al.* (1989); 10: Ramírez-Zavala *et al.* (1991); 11: Santamaría-Miranda *et al.* (2005); 12: Saucedo-Lozano (2000); 13: Rodrigo-Rojas (1997); 14: López-Peralta and Arcila (2002); 15: Abitia-Cárdenas *et al.* (1990); 16: Wineken *et al.* (2000); 17: Portillo-Cruz (2004); 18: Pérez-Ramos (1994); 19: Olson and Watters (2003); 20: Silvestre *et al.* (1993); 21: Mendoza (1993); 22: Sánchez and Olaso (2004); 23: Tripp-Valdez (2005); 24: Raymundo-Huizar (2000); 25: Chávez-Comparán and Gregory-Hammann (1989); 26: Varela-Romero (1990); 27: Cruz-Escalona (1998); 28: Bocanegra-Castillo (1998); 29: Gorostieta-Monjaraz (2001); 30: Manickchand-Heileman *et al.* (2004); 31: Maeda-Martínez (1981); 32: Valadez-González *et al.* (2001); 33: Arreguín-Sánchez *et al.* (1993); 34: Salini *et al.* (1994); 35: Nellis and Henke (2000); 36: Froese and Pauly (2005); 37: Rodríguez-Rojero (2004); 38: Opitz (1993); 39: Okey and Mahmoudi (2002); 40: Yi-Ling Chen (2001); 41: Schneider and Behrends (1994); 42: Barz and Hirche (2003); 43: Larson (1991); 44: Montenegro *et al.* (1984); 45: Sparre and Venema (1997); 46: Youngkin and Wyneken (2004); 47: Márquez *et al.* (1976); 48: Aramoni-Serrano (1982); 49: Díaz-Arredondo and Guzmán-Del-Próo (1995); 50: Perez-Flores (1991).

Palomares and Pauly, 1998; Jarre *et al.*, 1991). To estimate Q/B for Rajiformes the radial aspect (A) of the equation of Palomares and Pauly (1989) was obtained with data on *Rhinobatos glaucostigma* (García and Duarte, 2002). The Q/B of Synodontidae was estimated assuming a relationship between the K parameter (VBGE) and longevity (Pauly, 1980), using a longevity of 9 years for *Synodus scituliceps* from the study area (Morales-Nin, 1996). Values for the remaining groups were taken from the literature.

Due to a shortage of information, the diet of a functional group in some cases was based on that of one of its dominant species. In other cases, it was necessary to consider data on species from bordering areas not covered by the model (Table 4). So as not to lose connections within the trophic network, consumption was assumed for some groups according to stomach content studies, expressed as frequency of appearance. For example, the Cheloniidae group was considered prey of birds, Lutjanidae, Carangidae, Serranidae, Ariidae and the other fish category (Nellis and Henke, 2000; Wineken *et al.*, 2000). Values <1% were assumed in the respective diet of each group mentioned. For other groups such as Coelenterata, Rajiformes, Ariidae, Pleuronectiformes, and Polynemidae/Mullidae, cannibalism <5% of the diet was assumed (Silvestre *et al.*, 1993; Zetina-Rejón *et al.*, 2003; Sánchez and Olaso, 2004).

MODEL BALANCING

Parameters P/B and Q/B proposed for the Ecopath model showed trends similar to those published for models in other areas (Christensen and Pauly, 1993). The pedigree index had a value of 0.57, indicating an average input data certainty. The model was optimized with Ecoranger, for which a variation of 10% in the parameters of the model was allowed, except for biomass accumulation, which was not considered. Later a series of iterations with resampling options was made using the least squares criterion, to obtain the best adjusted model from 1000 successful runs (Table 5). The predator-prey matrix appears in Appendix A.

Table 5. Input parameters to the balanced Ecopath model of the southern Sinaloa ecosystem.

Group	*Biomass*	*P/B*	*Q/B*	*EE*	Catch ($t\cdot km^{-2}$)		Discard ($t\cdot km^{-2}$)
	($t\cdot km^{-2}$)	($year^{-1}$)	($year^{-1}$)		Industrial	Finfish fleet	Industrial
Birds	0.021	0.406	87.542	*0.765*	-	-	-
Sciaenidae	1.379	0.865	6.882	*0.717*	*0.021	0.0626	0.0189
Haemulidae	1.304	2.105	9.627	*0.697*	*0.0158	-	0.0142
Centropomidae	1.398	0.707	2.473	*0.888*	*0.0045	0.0106	0.0041
Lutjanidae	0.678	0.744	3.2	*0.738*	*0.0009	0.072	0.0008
Pleuronectiformes	2.601	1.488	5.038	*0.83*	*0.0083	-	0.0075
Scombridae	1.381	0.896	5.453	*0.82*	*0.0012	0.2209	0.0011
Coryphaenidae	0.347	0.833	7.268	*0.781*	*0.0003	-	0.0003
Carangidae	1.022	2.877	12.001	*0.816*	*0.0038	-	0.0034
Scorpaenidae/Triglidae	0.564	1.189	8.748	*0.117*	*0.0063	-	0.0057
Serranidae	2.794	1.132	5.834	*0.61*	*0.0109	-	0.0098
Rajiformes	1.021	1.139	6.398	*0.845*	*0.0054	-	0.0049
Ariidae	0.96	1.987	6.192	*0.917*	*0.0018	0.0191	0.0016
Polynemidae/Mullidae	0.718	2.097	11.03	*0.865*	*0.0135	-	0.0122
Tetraodontidae	0.726	2.2	6.031	*0.878*	*0.001	-	0.0009
Synodontidae	0.561	1.728	6.74	*0.899*	*0.0122	-	0.011
Cheloniidae	*0.84*	0.104	2.788	0.534	*0.0007	-	0.0007
Gerreidae	2.004	3.636	12.281	*0.813*	*0.0112	0.2028	0.0101
Clupeidae	*10.477*	3.484	16.03	0.92	*0.0013	4.7668	0.0012
Mugilidae	*1.029*	1.02	16.388	0.958	*3.6×10^{-5}	0.2536	3.2×10^{-5}
Other fish	5.827	3.259	10.836	*0.881*	*0.0164	-	0.0148
Coelenterata	0.71	3.147	11.046	*0.815*	*0.0031	-	0.0031
Cephalopoda	2.959	3.277	18.09	*0.906*	*0.0035	0.303	0.0032
Gastropoda	*3.846*	3.557	15.712	0.773	*0.0004	0.0044	0.0003
Bivalvia	6.68	2.442	10.908	*0.645*	-	0.2049	-
Echinodermata	8.228	0.948	3.184	*0.901*	*0.0139	-	0.0125
Porifera	*4.29*	1.846	4.735	0.732	*0.0004	-	0.0004
Palinura	*3.723*	1.145	7.929	0.946	*6.6×10^{-6}	0.0096	6×10^{-6}
Portunidae	1.205	3.108	9.133	*0.852*	*0.0225	0.8645	-
Stomatopoda	0.814	2.302	8.591	*0.877*	*0.0008	-	0.0008
Penaeidae	1.005	5.483	21.059	*0.986*	1.6883	1.3581	-
Polychaeta	*6.306*	6.1	25.093	0.75	*0.0003	-	0.0003
Other macrocrustaceans	*6.76*	1.276	6.612	0.893	*0.0047	-	0.0042
Zooplankton	25.397	19.054	86.506	*0.839*	-	-	-
Phytoplankton	124.624	21.351	-	*0.674*	-	-	-
Macrophytes	109.321	7.612	-	*0.148*	-	-	-
Detritus	4.119	-	-	*0.267*	-	-	-

Numbers in italics = Model estimate; * = Bycatch; P/B = production/biomass ratio; Q/B = consumption/ biomass ratio; EE = ecotrophic efficiency.

Biological consistency tests of functional groups were conducted to test whether the balanced model could be considered biologically plausible. To test for biological plausibility the following proportions were examined: the gross food conversion efficiency was greater in the lower trophic levels, with a rank of $0.005 \le P/Q \le 0.39$. Because respiration (R) cannot exceed assimilation (A), a value of $0 < R/A < 1$ was required for all functional groups, with larger values towards the upper trophic levels, which have lower production than lower ones. The production/respiration (P/R) ratio, like the respiration/biomass (R/B), had a value between 0 and 1 with higher values towards the lower trophic levels (Table 6).

Table 6. Balanced and optimized Ecopath model parameters corresponding to the benthonic ecosystem of southern Sinaloa, Mexico.

Group	Trophic level	Omnivory index	Consumption	Production	Respiration	Assimilation
Birds	3.74	0.210	1.828	0.009	1.454	1.462
Sciaenidae	3.60	0.280	9.491	1.190	6.400	7.592
Haemulidae	3.13	0.169	12.551	2.744	7.297	10.041
Centropomidae	3.54	0.193	3.456	0.989	1.776	2.765
Lutjanidae	3.40	0.130	2.170	0.504	1.232	1.736
Pleuronectiformes	3.91	0.214	13.102	3.868	6.612	10.481
Scombridae	4.04	0.209	7.528	1.239	4.785	6.022
Coryphaenidae	4.16	0.094	2.520	0.288	1.727	2.016
Carangidae	3.40	0.242	12.268	2.942	6.873	9.815
Scorpaenidae/Triglidae	3.24	0.110	4.933	0.672	3.276	3.946
Serranidae	3.60	0.301	16.298	3.161	9.877	13.039
Rajiformes	3.05	0.534	6.532	1.162	4.063	5.226
Ariidae	2.81	0.446	5.942	1.907	2.847	4.754
Polynemidae/Mullidae	3.16	0.101	7.923	1.508	4.832	6.339
Tetraodontidae	2.97	0.207	4.377	1.596	1.905	3.502
Synodontidae	4.10	0.312	3.780	0.970	2.055	3.024
Cheloniidae	3.23	0.171	2.342	0.088	1.786	1.873
Gerreidae	2.34	0.272	24.609	7.279	12.401	19.687
Clupeidae	2.78	0.242	167.939	36.497	97.846	134.351
Mugilidae	2.26	0.199	16.856	1.045	12.436	13.485
Other fish	2.74	0.563	63.136	18.976	31.521	50.509
Coelenterata	2.99	0.171	7.844	2.234	4.040	6.275
Cephalopoda	3.20	0.089	53.533	9.707	33.128	42.826
Gastropoda	2.00	0.000	60.433	13.693	34.665	48.346
Bivalvia	2.31	0.242	72.862	16.328	41.975	58.289
Echinodermata	2.34	0.269	26.196	7.803	13.159	20.957
Porifera	2.03	0.028	20.313	7.917	8.334	16.250
Palinura	2.65	0.563	29.518	4.258	19.353	23.614
Portunidae	2.40	0.332	11.004	3.743	5.058	8.803
Stomatopoda	2.05	0.096	6.994	1.875	3.721	5.595
Penaeidae	2.02	0.021	21.163	5.516	11.420	16.930
Polychaeta	2.01	0.006	158.236	38.423	88.125	126.589
Other macrocrustaceans	2.00	0.005	44.692	8.626	27.126	35.754
Zooplankton	2.09	0.090	2,197.002	484.002	1,273.690	1,757.602
Phytoplankton	1.00	-	-	2,660.85	-	-
Macrophytes	1.00	-	-	832.151	-	-
Detritus	1.00	0.362	2,312.474	-	-	-

Consumption, production, respiration, and assimilation in $t \cdot km^{-2} \cdot year^{-1}$

Trophic properties of functional groups

The benthonic ecosystem is divided into 4 discreet trophic levels. Coryphaenidae occupies the highest trophic level (TL=4.16), which, together with Scombridae (TL=4.04) and Synodontidae (TL=4.1), is considered a top predator of the ecosystem. The remaining fish and invertebrate groups are located in the second and third trophic levels (Figure 2).

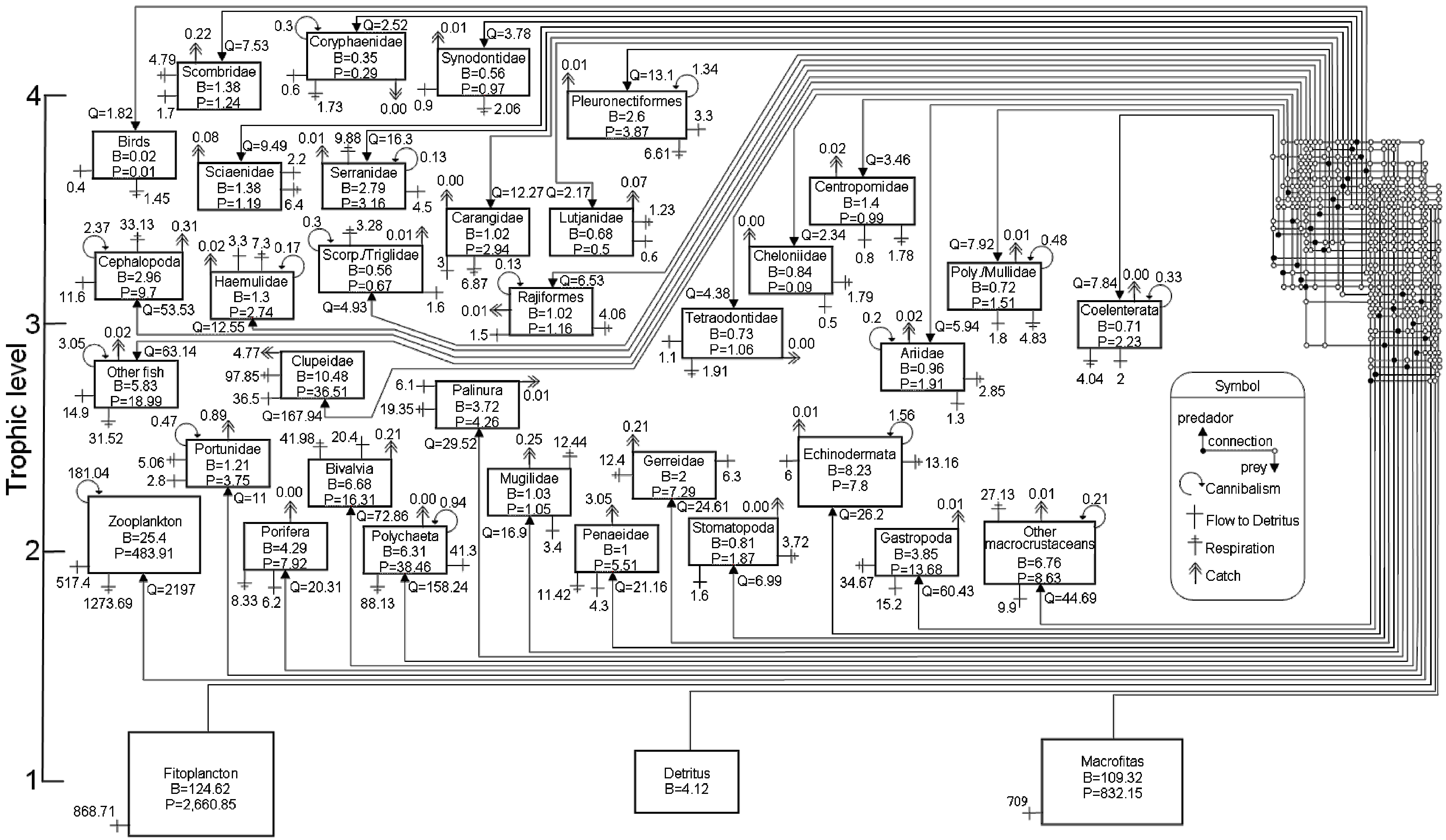


Figure 2. Biomass flows in the southern Sinaloa benthonic ecosystem. B = biomass (t·km^{-2}); P = production (t·km^{-2}·year^{-1}); Q = Consumption (t·km^{-2}·year^{-1}); all other flows expressed in t·km^{-2}·year^{-1}.

The ecosystem omnivory index was 0.2, and the most specialized groups were Cephalopoda (*OI*=0.089) and Coryphaenidae (*OI*=0.094). Gastropoda had a null index (*OI*=0) since it preys only on primary producers (macrophytes and detritus). The index was larger and more varied in the middle trophic levels (0.33≤*OI*≤0.56), assuming a general trend for the area, which has been observed by other authors (Arreguín-Sánchez *et al.*, 2002; Zetina-Rejón *et al.*, 2003; Galván-Piña, 2005; Cruz-Escalona, 2005). On the other hand, greater competetion is observed in the middle trophic levels, due to trophic superposition among Cheloniidae, Haemulidae, Ariidae, Tetraodontidae, Rajiformes, Palinura, Gerreidae, and Carangidae (0.6≤*O*ij≤0.99). Nevertheless, the average omnivory of these groups is above the ecosystem average (*OI*=0.33).

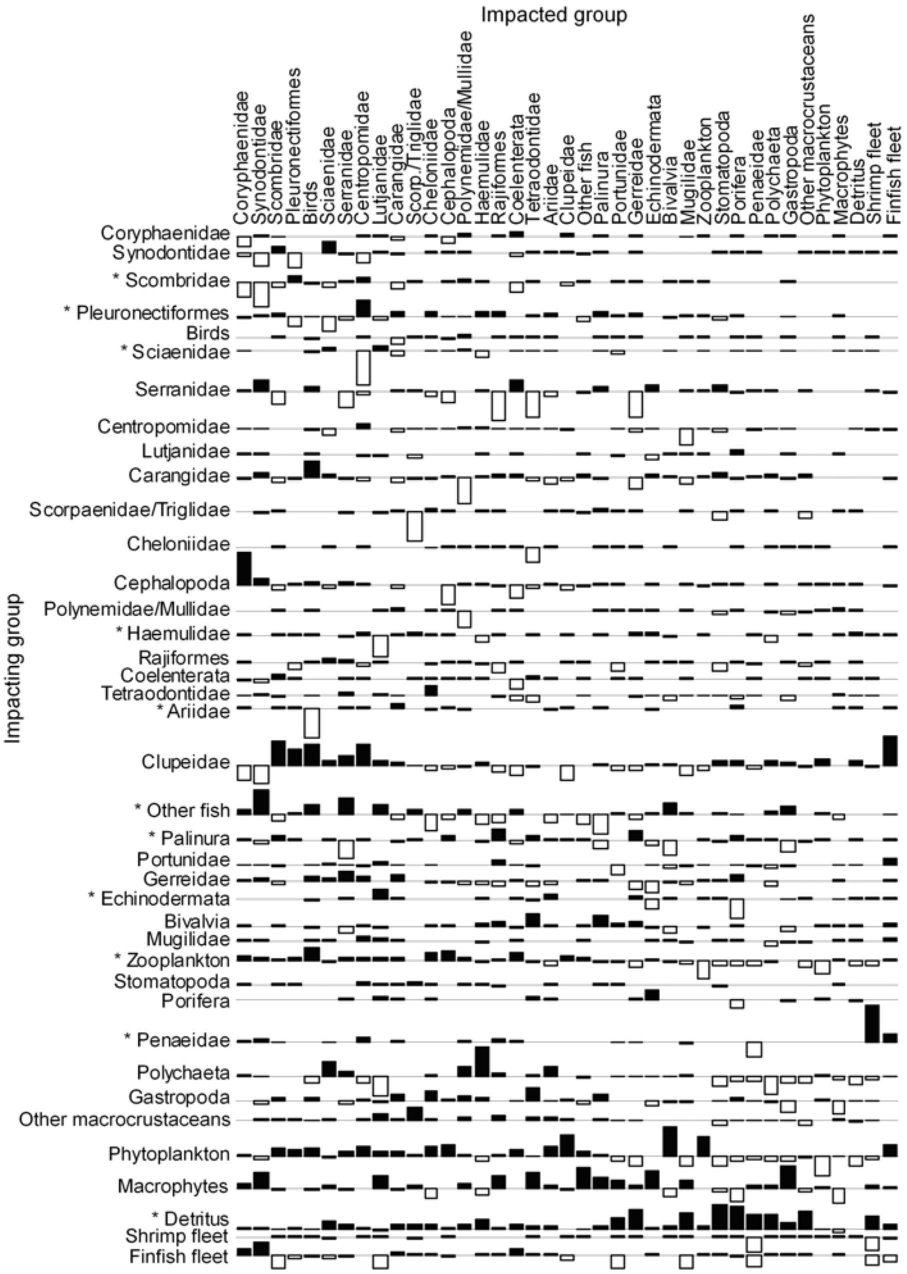


Figure 3. Trophic impacts among functional groups of the benthonic ecosystem of southern Sinaloa, Mexico. Groups are ordered by trophic level and include impacts of the industrial shrimp and finfish fleet. *Greater impact (-1≤*TI*≤0.85) than other groups (-0.45≤*TI*≤0.46).

The mixed trophic impacts show greater positive influence on the lower part of the trophic network, where detritus is more frequently important (Figure 3). This impact is also apparent on the shrimp fleet, which depends on the Penaeidae resource. While the positive impact of primary producers is generally lower, it happens more often, as, for example, on the finfish fleet, which uses the Clupeidae, Bivalvia, Gastropoda, and Cephalopoda groups. The middle and lower trophic levels are more often negatively affected, and the finfish fleet causes more impact than the shrimp fleet. Nonetheless, the impact of both fleets is less than that of natural predation. Specifically, Centropomidae is affected more by Sciaenidae (*TI*=-0.996) than by fishing (*TI*=-0.017).

On the other hand, trophic cascade effects appear when a predator impacts negatively on another and its prey thus benefits indirectly. An example is Pleuronectiformes, which impacts Sciaenidae (*TI*=-0.51) negatively to the benefit of Centropomidae (*TI*=0.46). It is important to mention that the result of the impacts is based on group biomass. Otherwise an analysis considering an occurrence, *e.g.*, the number of juveniles captured incidentally, could give different results in the case of fishing impacts.

Trophic properties of the ecosystem

Statistics for the ecosystem are given in Table 7. The total flow is near 9,000 t·km^{-2}·year^{-1}, with 35% total consumption, 26% flow to detritus, and 20% respiration flows. Of the flow to detritus, 91% is contributed by phytoplankton (38%), macrophytes (31%) and zooplankton (22%), with an increase toward the lower trophic levels. The net production of the system was 1,706 t·km^{-2}·year^{-1}, and the ratios of total primary production/total respiration and total primary production/total biomass were >1. The connectance of the system indicates 24% of possible trophic connections. Generally, production and respiration tended to diminish towards the higher trophic levels, with a larger decrement in production than that of respiration ($b_{production}>b_{respiration}$) (Figure 4). This suggests a greater energy cost in the upper trophic levels and greater contributions from the birds, Coryphaenidae, Sciaenidae, and Cheloniidae groups.

Table 7. Summary of statistics for the benthonic ecosystem of southern Sinaloa, Mexico.

Parameter	Value
Total consumption*	3099
Total exports*	1706
Total respiratory flows*	1787
Total flows to detritus*	2312
Total system throughput*	8905
Net system production*	1706
Calculated total net primary prod.*	3493
Total production*	4188
Total biomass (excluding detritus)**	344
Total catches*	10.2
Mean trophic level of the catch	2.54
Gross efficiency (catch/net p.p.)	0.0029
Total primary prod./total respiration	1.96
Total primary prod./total biomass***	10.17
Total biomass/total throughput***	0.04
Connectance Index	0.24
System Omnivory Index	0.197

* t·km^{-2}·year^{-1}; ** t·km^{-2}; *** year^{-1}.

The ecosystem has an average transference efficiency of 14.8%, with greater transference in trophic level III (Figure 5), in which the ratios of consumption flows to respiratory flows and detritus flows are 1.69 and 4.24 respectively. The energy (biomass) that flows in the ecosystem comes mainly from the primary producers: phytoplankton and macrophytes (2,185 t·km^{-2}·year^{-1}), which amount to 3 times the other source of energy, detritus (721 t·km^{-2}·year^{-1}). It is important to indicate that each trophic level receives more energy from detritus than it returns, taking a net energy gain. However, the primary consumers (II) lose more energy (646 t·km^{-2}·year^{-1}) than they receive (617 t·km^{-2}·year^{-1}). On top of the losses through respiration (1,565 t·km^{-2}·year^{-1}), it has the lowest energy transfer. Generally, 92% of the total energy that flows to detritus is contributed by primary producers.

The flow indices show ascendancy of 10,769 flow bits (t·km^{-2}·year^{-1}·bits), overhead of 25,286 flow bits, and capacity of 35,065 flow bits (Table 8). This suggests the ecosystem has low development, and high resilience to disturbances (Ulanowicz, 1986).

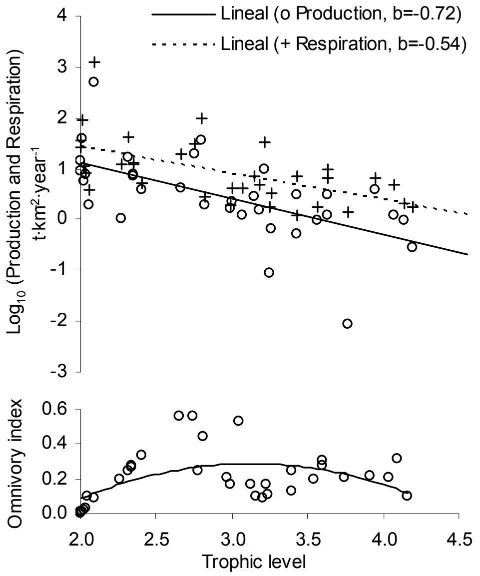


Figure 4. Production, respiration and omnivory index variation versus trophic level.

DISCUSSION

The functional groups included in the Ecopath model represent the greater part of the benthonic ecosystem of southern Sinaloa, according to the literature (Chávez and Arvizu, 1972; Chapa-Saldaña, 1976; Rosales-Juárez, 1976; Hendrickx, 1985; Valenzuela-Tanori, 1988; Plascencia-González, 1993; Rodríguez-Cagica, 1996). The diet matrix used in the model is predominantly based on information of the eating habits from studies conducted in the study area. This is important, since feeding is considered one of the most important parameters for reconstructing a trophic network of an ecosystem, and thus is important in understanding its dynamics (Christensen *et al.*, 2005).

The biomasses of some groups in the initial Ecopath model (unbalanced) obtained with capturability and those of the final model (balanced and optimized) had differences >100%. In the case of the Penaeidae group, which is the object of the shrimp fishery, Ecopath underestimated by 84% (1.01 t·km^{-2}) that obtained with capturability (6.23 t·km^{-2}). This difference might indicate that while the Ecopath model biomass reflects the system average, the estimates from capturability correspond to a precise biomass for a certain time and space during the fishing season. This suggests that trawls that target highly productive fishing grounds, such as near river mouths, could cause overestimation of total ecosystem biomass. It is important to mention that the differences between the two methods does not indicate the robustness of estimates, since it is difficult to confirm their fidelity to reality. Nevertheless, the shrimp biomass obtained by Ecopath model balancing is a conservative estimate, and corresponds well with alternative estimates of 1.6 t·km^{-2} for the same area and time of study (INP, 2000).

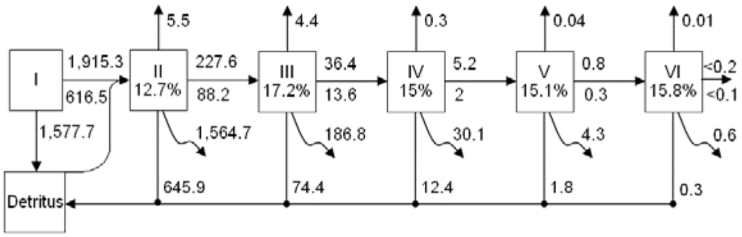


Figure 5. Trophic structure by discreet trophic levels. Transference efficiency (%); flows expressed in t·km^{-2}·year^{-1} (arrows); biomass flow consumed from primary producers (value above the horizontal-right arrow) and from detritus (below arrow); flow to detritus (horizontal-left); export due to the fishing (vertical-up); respiration (curved-down).

Several methodologies were used to estimate *P*/*B*. Capture size frequency, as proposed by Beverton and Holt (1957), was used preferentially for commercially exploited groups. Failing this, a value was obtained from the bibliography, or the empirical equation of Hoenig (1983) which assumes a relationship between longevity and total mortality. This was also used for noncommercial groups, for which an additional relationship among longevity, biomass, and production was assumed (Rainer, 1982). For the exploited shrimp group (Penaeidae), the Ecopath model used a fishing mortality (F=3.03) close to that obtained individually with the capture model of Baranov (1918) (F=3.25), and to those from bordering areas in the Gulf of California (2.49<F<3.12) (Lluch, 1976; Arreguín-Sanchez *et al.*, 2002). Using three equations to obtain *Q*/*B* allows one to select the best fit to the *Q*/*B* distribution of similar groups in several models (Christensen and Pauly, 1993).

Table 8. Flow indices for the benthonic ecosystem of southern Sinaloa, Mexico

Source	Ascendancy		Overhead		Capacity	
	flowbits	%	flowbits	%	flowbits	%
Internal flow	4,784	13	19,331	54	24,114	67
Respiration	2,724	8	5,036	14	7,760	22
Export	3,262	9	919	3	4,180	12
Totals	10,769	29.9	25,286	70.1	36,054	100

The biological consistency of the functional groups as revealed by ratios *P*/*Q, R*/*A, P*/*R,* and *R*/*B* (Christensen *et al.*, 2005), and the pedigree index of the model (0.57) does not differ much from those obtained in other models of Mexican ecosystems (Zetina-Rejón *et al.*, 2003; Galván-Piña, 2005; Cruz-Escalona, 2005). The model consistency obtained and the data quality and origin, satisfy the requisites for this type of work, and provide a reasonable image of energy flows and the effects of biomass exploitation in the southern Sinaloa ecosystem during the 1990s.

Ecosystem energy (biomass) flows through consumption cost more, are dissipated to the biotope accordingly, and are transferred to the higher trophic levels with a transference efficiency (14.8%) above that established by the ecological tithe (≈10%) (Lindeman, 1942). Carnivores of the third level trophic are key elements in ecosystem productivity, since they have the highest transference efficiency, allowing them to take energy at least cost from bottom to top of the trophic network. On the other hand, although the majority of groups at this level have low omnivory, indicating higher specialization, the trophic overlap is very low, resulting in low competition for resources. This allows a coexistence that results from niche differentiation according to Gause' principle of competitive exclusion, which states that two species related by the same ecological needs cannot live together unless they compete.

The mixed trophic impacts show the importance of detritus for several ecosystem groups, mainly for the primary consumers (II). Work describing the importance for nearby ecosystems like Huizache-Caimanero has indicated that detritus is a primary energy source that modulates the impacts among ecosystem groups (Zetina-Rejón *et al.*, 2003). Incidental capture evidently has positive and negative effects on an ecosystem, but most of these effects are small compared with those of predation. Most positive impacts of incidental capture take place through trophic cascade (*TI*=0.11), but have much less effect than the negative impacts (*TI*=-0.6). The greatest negative ecosystem impact is the finfish fleet, which has greater impact than incidental capture of the shrimp fleet.

The flow statistics and indices suggest that the ecosystem is in a state of low development, characterized by the following attributes: a high entropy according to the ratio of total respiration flows to total system biomass (*R*/*B*=5.2) (Odum, 1985); an energetic community indicated by total primary production greater than total respiration (PP/R=1.96), and greater than total system biomass (P/B=10.17); an ascendancy at 30% of capacity, and high resilience to disturbance (Ulanowicz, 1986). This indicates that the ecosystem has high growth potential.

ACKNOWLEDGEMENTS

Thanks to Instituto Politécnico Nacional (CICIMAR) and CONACYT for scholarships, to the Universidad Autónoma de México (ICMandL) and Universidad Autónoma de Sinaloa (FACIMAR) for contributions and support, and to projects of SEMARNAP and CONACYT (SEMARNAP-CONACYT 2002-C01-1231), of SPI-IPN (20040641, 20050686, 20060579), CONACYT-SAGARPA 2003-02-157, and of the European Commission (INCOFISH contract 003739) for economic support. Thanks also to N. Gudiño-González for providing data. The text was translated from the original Spanish by Taylor Morey.

REFERENCES

Abitia-Cárdenas, L.A., Rodríguez-Romero, J. and Galván-Magaña, F. 1990. Observaciones tróficas de tres especies de peces de importancia comercial de bahía Concepción, Baja California Sur, México. Inv. Mar. CICIMAR. 5 (1), 55-61.

Allen, K.R. 1971. Relation between production and biomass. J. Fish. Res. Borrad Can. 28, 1573-1581.

Álvarez-Cadena, J.N. 1985. Composición y abundancia de los copépodos planctónicos de la bahía de Mazatlán, Sin. México (1979-1980). An. Inst. Biol. Univ. Nal. Autón. México, 12 (1), 1-29.

Amezcua-Linares, F. 1996. Peces demersales de la plataforma continental del Pacifico central de México. ICMyL. UNAM. Comisión Nacional para el conocimiento y uso de la biodiversidad. México, D. F. 184 p.

Aramoni-Serrano, G.P. 1982. Alimentación de las langostas *Panulirus inflatus* (Bouvier) y *P. gracilis* Streets en Zihuatanejo, Guerrero y su relación con el bentos. Tesis de licenciatura. Facultad de Ciencias, UNAM. México. 438 p.

Arreguín-Sánchez, F., Arcos, E. and Chávez, E. 2002. Flows of biomass and structure in an exploited benthic ecosystem in the gulf of California, Mexico. Ecol. Model. 156, 167-183.

Arreguín-Sánchez, F., Valero-Pacheco, E. and Chávez, E.A. 1993. A trophic box model of the coastal fish communities of the southwestern Gulf of Mexico. *In*: Christensen, V., Pauly, D. (Eds.), Trophic models of acuatic ecosystems. ICLARAM Conf. Proc., pp. 197-205.

Arriaga-Haro, V.M., Ocegueda-Carvajal, M.T., Ojeda-Cardenas, E. and Gonzalez-Felix, J.E. 1989. Análisis del contenido estomacal y determinación de la madurez gonádica de algunos especies de peces que ocurren en la bahía de Mazatlán, Sinaloa. Memoria. FACIMAR, UAS. México. 71 p.

Ayon-Parente, M. 2000. Aspectos biológicos pesqueros del cangrejo tanque *Calappa convexa* de Saussure (Crustacea:Brachyura: Calappidae) en el sur de Sinaloa. Tesis de maestría. Facultad de Medicina Veterinaria Zootecnia, Universidad de Colima. México. 79 p.

Baranov, F.I. 1918. On the question of the biological basis of fisheries. *In*: Edwards, E.F., Megrey, B.A. (Eds.), Mathematical analysis of fish stock dynamics. American Fisheries Society. U. S. A, pp. 81-128.

Barz, K. and Hirche, H.J. 2003. Seasonal distribution and prey of *Aurelia aurita* in the Bornholm Basin (central Baltic). Alfred Wegener-Institute for Polar and Marine Research. Germany. World Wide Web electronic publication. (http://www.ifm.uni-hamburg.de/globec/gg_ publications.html)

Beverton, R.J.H. and Holt, S.J. 1957. On the dynamics of exploited fish populations. Fish. Invest., London. 19, 533.

Bocanegra-Castillo, N. 1998. Interacciones tróficas de la ictiofauna más abundante en Laguna Ojo de Liebre, Baja California Sur, México. Tesis de maestría. CICIMAR, IPN. México. 70 p.

Chapa-Saldaña, H. 1976. La fauna acompañante del camarón como un índice de monopesca. *In*: Symposium sobre biología y dinámica poblacional del camarón. Memorias. Guaymas, Sonora, pp. 447-450.

Chávez-Comparán, J.C. and Gregory-Hammann, M. 1989. Dieta de las mojarras, *Gerres cinereus* y *Diapterus peruvianus* (Pisces: Gerreidae) en la Laguna de Cuyutlán, Colima, México, durante verano. Ciencias Marinas. 15 (3), 71-80.

Chávez, H. and Arvizu-Martínez, J. 1972. Estudio de los recursos pesqueros demersales del Golfo de California, 1968-1969. *In*: Carranza, J. (Ed.), Mem. IV Cong. Nal. Ocean. México, pp. 361-378.

Christensen, V., Walters, C.J. and Pauly, D. 2005. Ecopath with Ecosim: a User's Guide. Fisheries Centre, University of British Columbia. Vancouver.

Christensen, V. and Pauly, D. 1992. ECOPATH II – a software for balancing steady-state ecosystem models and calculating network characteristics. Ecol. Model. 61, 169-185.

Christensen, V. and Pauly, D. 1993. Flow characteristics of aquatic ecosystems. *In*: Christensen, V., Pauly, D. (Eds.), Trophic models of aquatic ecosystems. ICLARM Conf. Proc., pp. 338-352.

CONAPESCA. 2003. Anuario Estadístico de Acuacultura y Pesca 2003. Comisión Nacional de Acuacultura y Pesca. SAGARPA. México. 400 p.

Cruz-Escalona, V.H. 1998. Análisis trophic de la ictiofauna de Laguna San Ignacio, B.C.S. Tesis de maestría. CICIMAR, IPN. México. 128 p.

Cruz-Escalona, V.H. 2005. Interdependencia ecotrófica entre Laguna de Alvarado, Veracruz y la plataforma continental adyacente. Tesis de doctorado. CICIMAR, IPN. México. 136 p.

Cruz-Martínez, A. 1995. Productividad primaria acuática en la Bahía de Mazatlán. Tesis de licenciatura. ICMyL, UNAM. México. 56 p.

De La Garza-De Los Santos, R., Macías-Martínez, A., Pérez-Y-Pérez, R. and Sánchez-Mendez, M.A. 1985. Algunos aspectos ecológicos de la ictiofauna del estero "El Sábalo" con un estudio sobre la alimentación de *Centropomus robalito* Jordan y Gilbert. Memoria. FACIMAR, UAS. México. 110 p.

Díaz-Arredondo, M.A. and Guzmán-Del-Próo, S. 1995. Hábitos alimentarios de la langosta roja (*Panulirus interruptus* Randall, 1840) en Bahía Tortugas, Baja California Sur. Ciencias Marinas. 21 (4), 439-462.

Durbin, A.G. and Durbin, E.G. 1998. Effects of menhaden predation on plankton populations in Narragansett Bay, Rhode Island. Estauries. 21 (3), 449-465.

Espinoza-Flores, A., Arana-Murrieta, J.A., Mayoral-Lechuga, A., Ramos-Gonzalez, R.J. and Virgen-Barajas, A.C. 1990. Tasa de digestión del camarón por el Chihuil *Arius liropus* y aspectos trophic de otros peces depredadores. Memoria. FACIMAR, UAS. México. 52 p.

Froese, R. and Pauly, D. 2005. FishBase. World Wide Web electronic publication. (www.fishbase.org, version 02/2005).

Galván-Piña, V.H. 2005. Impacto de la pesca en la estructura, función y productividad del ecosistema de la plataforma continental de las costas de Jalisco y Colima, México. Tesis de doctorado. CICIMAR, IPN. México. 106 p.

García, C.B. and Duarte, L.O. 2002. Consumption to biomass (Q/B) ratio and estimates of Q/B-predictor parameters for caribbean fishes. NAGA, ICLARM Quaterly. 25 (2), 19-31.

García-Telles, B., Leon-Peraza, M.D.J., Velazquez-Ayon, J.G. and Rivera-Naranjo, O.O. 1989. Estudio trophic de *Centropomus robalito* y *Lutjanus argentiventris* en el estero La Sirena, Mazatlán, Sinaloa. FACIMAR, UAS. México. 76 p.

Garza-Osuna, T.E. 1999. Características estructurales de las comunidades de macroalgas de la bahía de Mazatlán durante 'El Niño 1997-98'. Tesis de licenciatura. ICMyL, UNAM. México. 51 p.

Gil, L.H. and Sarmiento, S. 2001. Algunos aspectos biológicos y pesqueros de las jaibas (*Callinectes* spp.) en el sistema lagunar Mar Muerto, Oaxaca-Chiapas. *In*: Ramírez-Félix, E., Singh-Cabanillas, J. (Eds.), La pesquería de Jaiba (*Callinectes* spp.) en el Pacífico Mexicano: Diagnóstico y Propuesta de Regulación. Instituto Nacional de la Pesca, México, pp. 41.

González-Ramos, O., Mendizábal-Y-Oriza, D., Vélez-Marín, R. and Fajardo, J. 1997. Edad y crecimiento del dorado *Coryphaena hippurus* en la zona oceánica del Pacífico mexicano. Memorias. V Congreso Nacional de Ictiología. FACIMAR, UAS. México. 63 p.

Gorostieta-Monjaraz, M. 2001. Dinámica de la estructura trófica del ecosistema de bahía Concepción, B. C. S. México. Tesis de maestría. CICIMAR, IPN. México. 75 p.

Hendrickx, M.E., Pérez-González, R. and Flores-Campaña, L.M. 1992. Identificación y colectas del cangrejo araña *Maiopsis panamensis* Faxon, 1895 (Brachyura: Majidae) en el Pacífico este tropical. Ciencias del Mar. 1 (12), 31-34.

Hendrickx, M.E. 1985. Diversidad de los macroinvertebrados bentónicos acompañantes del camarón en el área del Golfo de California y su importancia como recurso potencial. *In*: Yáñez-Arancibia, A. (Ed.), Recursos Pesqueros Potenciales de México: La pesca acompañante del camarón. México, D. F., pp. 95-148.

Hendrickx, M.E. 1996. Los camarones Penaeoidea bentónicos (Crustacea: Decapoda: Dendrobranchiata) del Pacífico mexicano. CONABIO. UNAM. México. 151 p.

Hoenig, J.M. 1983. Empirical use of longevity data to estimate mortality rates. US Fish. Bull. 81 (4), 898-903.

IGFA. 2001. Database of IGFA angling records until 2001. *In*: Froese, R., Pauly, D., 2005. FishBase. World Wide Web electronic publication (www.fishbase.org, version 02/2005).

INP. 2000. Sustentabilidad y pesca responsable en México: evaluación y manejo 1999-2000. Instituto Nacional de la Pesca. México. 1111 p.

Jarre, A., Palomares, M.L., Soriano, M.L., Sambilay, V.C. and Pauly, D. 1991. Some a new analytical and comparative methods for estimating the food consumption of fish. ICES Mar. Sci. Symp. 193, 99-108.

Jørgensen, S.E. 1979. Handbook of environmental data and ecological parameters. International Society for Ecological Modelling, Copenhagen. 1162 p.

Larson, R.J. 1991. Diet, prey selection and daily ration of *Stomolophus meleagris*, a filter-feeding scyphomedusa from the NE Gulf of Mexico. Est. Coast. And Shelf Sci. 32 (5), 511-525.

Leslie, P.H. and Davies, H.S. 1939. An attempt to determine the absolute number of rats on a given area. J. Anim. Ecol. 8, 94-113.

Lindeman, R.L. 1942. The trophic dinamic aspect of ecology. Ecology. 23, 399-418.

Lluch-Belda, D. 1976. Aplicación de modelos poblacionales en la pesquería del camarón: una evaluación resumida. Memorias del Simposio sobre Biología y Dinámica Poblacional de Camarones, Vol. 2. Instituto Nacional de Pesca, México. pp. 127-168.

López-Peralta, R.H. and Arcila, C.C.A.T. 2002. Diet composition of fish species from the southern continental shelf of Colombia. NAGA, WorldFish Center Quarterly, 25 (3 & 4), 23-29.

Madrid, V.J. and Beltrán-Pimienta, R. 2001. Longitud, peso y sexo del dorado *Coryphaena hippurus* (Perciformes: Coryphaenidae), del litoral de Sinaloa, Nayarit y Baja California Sur, México. Rev. Biol. Trop. 49, 916-931.

Maeda-Martinez, A.N. 1981. Composición, abundancia, diversidad y alimentación de la ictiofauna, en tres lagunas costeras del Golfo de California. Tesis de licenciatura. Facultad de Ciencias Biológicas, UANL. Nuevo León. México. 140 p.

Manjarrez-Acosta, C. 2001. Variación estacional de la comunidad de peces de fondos blandos del área costera del sur de Sinaloa. Tesis de maestría. CICIMAR, IPN. México. 134 p.

Manickchand-Heileman, S., Mendoza-Hill, J., Lum-Kong, A. and Arocha, F. 2004. A trophic model for exploring possible ecosystem impacts of fishing in the Gulf of Paria, between Venezuela and Trinidad. Ecol. Model. 172, 307–322.

Márquez, R., Villanueva, A. and Peña-Flores, C. 1976. Sinopsis de datos biológicos sobre la tortuga golfina, *Lepidochelys olivacea* (Eschscholtz 1829) en México. INP Sinopsis sobre la Pesca No. 2. Instituto Nacional de Pesca, México. 61 p.

Mendoza, J.J. 1993. A preliminary biomass budget for the northeastern Venezuela shelf ecosystem. *In*: Christensen, V., Pauly, D. (Eds.), Trophic models of acuatic ecosystems. ICLARAM Conf. Proc., pp. 285-297.

Mendoza-López, J., Osuna, P.E., Manjarrez, A.C. and Audelo, J.M. 1992. Crecimiento individual de la corvina graniza (*Cynoscion reticulatus*; Günther, 1864). Resúmenes. IX Simp. Int. Biol. Mar. UABCS. México. 66 p.

Mendoza-López, J., Monarrez-Burgos, R., Tello-Alcantar, E. and Montes-Verdugo, A. 1997. Aspectos biológicos pesqueros de *Cycloseptta querna* (Jordan y Bollman 1986-1900). Memorias. V Congreso Nacional de Ictiología. FACIMAR, UAS. México. 59 p.

Montenegro-Silva, B.D.C., Bernal-González, N.G. and Guerrero, A.M. 1984. Estudio del contenido estomacal de la tortuga marina *Lepidochelys olivacea*, en la costa de Oaxaca, México. Anal. Inst. Cienc. Mar y Limnol. UNAM. México. 20 p.

Morales-Nin, B. 1996. Abundance, distribution and growth of *Synodus evermanni* Jordan and Ballman, 1890 and *Synodus scituliceps* Jordan and Gilbert, 1882 (Pisces: Synodontidae) from the Mexican Pacific shelf. Publicaciones Especiales. Instituto Español de Oceanografía. 21, 253-262.

Morales-Zárate, M.V., Arreguín-Sánchez, F., López-Martínez, J. and Lluch-Cota, S.E. 2004. Ecosystem trophic structure and energy flux in the Northern Gulf of California, Mexico. Ecol. Model. 174, 331–345.

Nellis, D.W. and Henke, S.E. 2000. Predation of Leatherback turtle hatchlings by near shore aquatic predators. *In*: Kalb, H.J., Wibbels, T. (Eds.), Proceedings of the Nineteenth Annual Symposium on Sea Turtle Biology and Conservation. U.S. Dept. Commerce. NOAA Tech. Memo. NMFS-SEFSC-443. pp. 168.

Odum, E.P. 1985. Fundamentos de ecología. Interamericana, México.

Okey, T.A. and Mahmoudi, B. 2002. An ecosystem model of the west Florida shelf for use in fisheries management and ecological research: Volume II. Model Construction. Florida Marine Research Institute. 153 p.

Olson, R.J. and Watters, G.M. 2003. A model of the pelagic ecosystem in the eastern tropical pacific ocean. Inter-Am. Trop. Tuna Comm. Bulletin. 22 (3), 90.

Opitz, S. 1993. A quantitative model of the trophic interactions in a Caribbean coral reef ecosystem. *In*: Christensen, V., Pauly, D. (Eds.) Trophic models of acuatic ecosystems. ICLARAM Conf. Proc., pp. 259-267.

Opitz, S. 1996. Trophic interactions in caribbean coral reefs. ICLARM Tech. Rep. 43, 341.

Palomares, M.L. and Pauly, D. 1989. A multiple regression model for predicting the food consumption of marine fish populations. Aust. J. Mar. Freshwat. Res. 40, 259-273.

Palomares, M.L. and Pauly, D. 1998. Predicting food consumption of fish populations as functions of mortality, food type, morphometrics, temperature and salinity. Aust. J. Mar. Freshwat. Res. 49, 447-453.

Parsons, T.R., Takahashi, M. and Hargrave, B. 1977. Biological oceanographic processes. Permagon Press, New York.

Pauly, D. 1978. A preliminary compilation of fish length growth parameters. Berichte des Institut für Meerekunde an der Christian-Albrechts Universität Kiel. 55, 200.

Pauly, D. 1980. A selection of simple methods for the assessment of tropical fish stocks. FAO Fish. Circ. 729. 54.

Pauly, D. 1983. Algunos métodos simples para la evaluación de recursos pesqueros tropicales. FAO Doc. Tec. Pesq. 234, 49.

Pauly, D. and Binohlan, C. 1996. Fish base and auxim as tools for comparing the life-history patterns growth and natural mortality of fish: applications to snappers and groupers. *In*: Arreguín-Sánchez, F., Munro, J.L., Balgos, M.C., Pauly, D. (Eds.), Biology, Fisheries and Culture of Tropical Groupers and Snappers. ICLARM Conf. Proc., pp. 218-243.

Penié-Rodriguez, I., Blanco-Parra, M.P. and Estradas-Romero, A. 2002. Métodos de investigación oceanográfica. Informe de campaña oceanográfica MAZCAB-IV. UNAM. México. 89 p.

Perez-Flores, R. 1991. Alimentación de la langostilla *Pleuroncodes planipes* (Stimpson, 1860) durante el periodo de reproducción (Marzo, 1990) en la costa occidental de Baja California Sur. Tesis profesional. Escuela Nacional de Estudios Profesionales Zaragoza, UNAM. México. 64 p.

Pérez-González, R. 1995. Crecimiento, alimentación y desarrollo gonadal de dos especies de peces demersales dominantes en la plataforma continental del sur de Sinaloa, México: *Prionotus stephanophrys* (Triglidae) y *Pomadasys panamensis* (Haemulidae). Tesis de maestría. ICMyL, UNAM. México. 174 p.

Pérez-Ramos, V.H. 1994. Maduración sexual, hábitos alimenticios, estructura poblacional, variación temporal del esfuerzo y captura de la pesquería de la sierra del Pacífico (*Scomberomorus sierra*, Jordan y Starks, 1895) en la bahía Mazatlán, Sinaloa. Durante el periodo 1988-1989. Memoria. FACIMAR, UAS. México. 59 p.

Plascencia-González, H.G. 1993. Contribución al conocimiento de las comunidades de peces asociados a los fondos blandos del sur de Sinaloa (Proyecto SIPCO). Tesis de maestría. ICMyL. UNAM. 200 p.

Portillo-Cruz, A. 2004. Interacción trófica entre dos especies de lenguados *Cyclopsetta querna* (Jordan y Bollman, 1890) y *Cyclopsetta panamensis* (Steindachner, 1876) de la zona centro-sur de la costa de Sinaloa, México. Tesis profesional. FACIMAR, UAS. México. 46 p.

Rainer, F.S. 1982. Trophic structure and production in the macrobenthos of a temperate australian estuary. Estuar. Coast. Shelf. S. 5, 423-441.

Ramírez-Zavala, J.R., Acedo-Navarro, A., Valdenebro-Ruíz, O. and Bojorquez-López, A. 1991. Espectro trophic de peces depredadores de camarón en el estero "El Ostial" del sistema lagunar Huizache-Caimanero. Memoria. FACIMAR, UAS. México. 74 p.

Raymundo-Huizar, A.R. 2000. Análisis de la dieta de los peces demersales de fondos blandos en la plataforma continental de Jalisco y Colima, México. Tesis de maestría. Facultad de Medicina Veterinaria y Zootecnia, Universidad de Colima. México. 89 p.

Reyes-Bonilla, H. 1997. Biología poblacional de *Isostichopus fuscus* (Ludwig, 1875) (Echinodertmata: Holothuroidea) en el sur del Golfo de California. Proyecto CONABIO. México. 83 p.

Rodrigo-Rojas, J. 1997. Dieta del "pargo colorado" *Lutjanus colorado* (Pisces: Lutjanidae) en el Golfo de Nicoya, Costa Rica. Instituto de Zoología, Universidad Austral de Chile. Chile. World Wide Web electronic publication. (www.ots.duke.edu/ tropibiojnl/claris/45-3/SANCHEZ.HTM)

Rodríguez-Cajica, S.R. 1996. Contribución al conocimiento de la fauna de acompañamiento del camarón frente a la costa de Sinaloa, México. Tesis de maestría. ICMyL. UNAM. México. 124 p.

Rodríguez-Gerrero, M.D.L.A., Zamudio-Vásquez, R.I., Cazesuz-Sánchez, H.M. and Carvajal-García, H.E. 1986. Aspectos de crecimiento y madurez gonadal en la lisa (*Mugil cephalus* Linaeus 1758), en el estero "El Sábalo" en Mazatlán, Sin., México. Ciclo 1983-1984. Memoria. FACIMAR, UAS. México. 84 p.

Rodríguez-Rojero, A. 2004. Hábitos alimenticios de las jaibas *Callinectes bellicosus* Stimpson y *C. arcuatus* Ordway (Brachyura: Portunidae) en Bahía Magdalena, Baja California Sur, México. Tesis de maestría. CICIMAR, IPN. México. 111 p.

Rojas-Zepeda, P.G., Castro, R., Anaya-Cota, M. and Sakoda-Correa, J.D. 1993. Algunos parámetros ecológicos que influyen en el crecimiento, distribución y abundancia del camarón blanco *Penaeus vannamei* Boone, en el estero de Las Escopamas, Mazatlán, Sinaloa. (1985-1986). Memoria. FACIMAR, UAS. México. 76 p.

Rosales-Juárez, F. 1976. Contribución al conocimiento de la fauna de acompañamiento del camarón en altamar frente a las costas de Sinaloa, México. Memorias de la Reunión sobre los Recursos de la Pesca Costera en México. Instituto Nacional de Pesca, pp. 25-80.

Salini, J.P., Blaber, S.J. and Brewer, D.T. 1994. Diets of trawled predatory fish of the Gulf of Carpentaria, Australia, with particular reference to predation on prawns. Aust. J. Mar. Freshwat. Res. 45, 397-411.

Sánchez-Cárdenas, R. 2005. Aspectos reproductivos del botete diana *Sphoeroides annulatus* (Jenyns, 1842) (Pisces: Tetraodontidae), en la bahía de Mazatlán, Sinaloa, México. Tesis de licenciatura. FACIMAR, UAS. México. 86 p.

Sánchez, F. and Olaso, I. 2004. Effects of fisheries on the Cantabrian Sea shelf ecosystem. Ecol. Model. 172, 151–174.

Santamaría-Miranda, A., Saucedo-Lozano, M., Herrera-Moreno, M.N. and Apún-Molina, J.P. 2005. Hábitos alimenticios del pargo amarillo *Lutjanus argentiventris* y del pargo rojo *Lutjanus colorado* (Pisces: Lutjanidae) en el norte de Sinaloa, México. Rev. Biol. Mar. y Ocean. 40 (1), 33–44.

Saucedo-Lozano, M. 2000. Alimentación natural de juveniles de *Lutjanus peru* (Nichols y Murphy, 1922) y *Lutjanus guttatus* (Steindachner, 1869) (Lutjanidae: Perciformes) en la costa de Jalisco y Colima, México. Tesis de maestría. Facultad de Medicina Veterinaria y Zootecnia, Universidad de Colima. México. 68 p.

Schneider, G. and Behrends, G. 1994. Population dynamics and the trophic role of *Aurelia aurita* medusae in the Kiel Bight and western Baltic. ICES J. Mar. Sci. 51, 359-367.

SEMARNAP, 1995. Anuario Estadístico de Pesca 1995, SEMARNAP, México.

SEMARNAP, 1996. Anuario Estadístico de Pesca 1996, SEMARNAP, México.

SEMARNAP, 1997. Anuario Estadístico de Pesca 1997, SEMARNAP, México.

Silvestre, G., Selvanathan, S. and Salleh, A.H.M. 1993. Preliminary trophic model of the coastal fisheries resources of Brunei Darussalam, South China Sea. *In*: Christensen, V., Pauly, D. (Eds.) , Trophic models of acuatic ecosystems. ICLARAM Conf. Proc., pp. 300-306.

Soto-Avila, C. 2004. Determinación de la edad y el crecimiento del pargo lunarejo *Lutjanus guttatus* (Steindachner, 1869) en la bahía de Mazatlán, Sinaloa, México. Tesis de licenciatura. FACIMAR, UAS. México. 51 p.

Sparre, P. and Venema, S.C. 1997. Introducción a la evaluación de recursos pesqueros tropicales. Parte 1. Manual. FAO Documento Técnico de Pesca. N°. 306.1 Rev. 2. 420 p.

Tripp-Valdez, A. 2005. Ecología trófica del dorado *Coryphaena hippurus* (Linnaeus, 1758) en dos áreas del sur del Golfo de California. Tesis de maestría. CICIMAR, IPN. 125 p.

Ulanowicz, R.E. 1986. Growth and development: ecosystems phenomenology. Springer-Verlag, New York.

Valadez-González, C., Aguilar-Palomino, B. and Hernández-Vázquez, S. 2001. Hábitos alimentarios de la raya *Urobatis halleri* (Cooper, 1863) (Chondrichthyes: Urolophidae) capturada en la plataforma continental de Jalisco y Colima, México. Ciencias Marinas, 27 (1), 91-104.

Valenzuela-Tanori, M. 1988. Evaluación de la fauna que acompaña al camarón en arrastres comerciales de las costas de Sonora y Sinaloa, México. Tesis de licenciatura. FACIMAR, UAS. México. 38 p.

Varela-Romero, A. 1990. Aspectos trophic de las mojarras (Pisces:Gerreidae) en tres sistemas costeros de Sonora. Tesis profesional. UABCS. México. 66 p.

Wineken, J., Fisher, L., Salmon, M. and Weege, S. 2000. Managing Relocated Sea Turtle Nests in Open-Beach Hatcheries. Lessons in Hatchery Design and Implementation in Hillsboro Beach, Broward County, Florida. *In*: Kalb, H.J., Wibbels, T. (Eds.), Proceedings of the Nineteenth Annual Symposium on Sea Turtle Biology and Conservation. U.S. Dept. Commerce. NOAA Tech. Memo. NMFS-SEFSC-443, pp. 193.

Waburton, K. 1978. Community structure, abundance and diversity of the fish of a Mexican coastal lagoon. Estuar. Coast. Mar. Sci. 7, 497-519.

Yi-Ling, C. 2001. Population dynamics and feeding of the moon jellyfish (*Aurelia aurita*) in Tapeng Bay, southwestern Taiwan. Master's thesis. World Wide Web electronic publication. (http://etd.lib.nsysu.edu.tw/ETD-db/)

Youngkin, D. and Wyneken, J. 2004. A long-term dietary analysis of loggerhead sea turtles (*Caretta caretta*) from Cumberland, Island Georgia. *In*: Coyne, M.S., Clark, R.D. (Eds.), Proceedings of the Twenty-First Annual Symposium on Sea Turtle Biology and Conservation. NOAA Technical Memoramdum NMFS-SEFSC-528, pp. 363.

Zetina-Rejón, M.J., Arreguín-Sánchez, F. and Chávez, E.A. 2003. Trophic structure and flows of energy in the Huizache-Caimanero lagoon complex on the Pacific coast of Mexico. Estuar. Coast. Shelf S. 57, 803-815.

Appendix A. Predator-prey matrix for the benthonic ecosystem trophic model of southern Sinaloa, Mexico.

Prey \ Predator		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
1	Birds	-	-	-	-	-	-	-	-	-	-	-	-	0.001	-	-	-	-
2	Sciaenidae	-	-	-	0.045	-	0.046	-	0.006	-	-	-	-	-	-	-	-	-
3	Haemulidae	-	0.039	0.014	-	-	0.006	-	0.019	-	-	-	-	-	-	-	-	-
4	Centropomidae	-	0.087	-	-	0.016	-	-	-	-	-	-	-	-	-	-	-	-
5	Lutjanidae	-	-	0.024	-	-	-	-	-	-	-	-	-	-	-	-	-	-
6	Pleuronectiformes	-	0.021	-	-	-	0.102	-	-	-	-	-	0.077	-	-	-	0.308	-
7	Scombridae	-	-	-	-	-	-	-	0.031	0.013	-	0.019	-	-	-	-	-	-
8	Coryphaenidae	-	-	-	-	-	-	0.02	0.011	0.004	-	-	-	-	-	-	-	-
9	Carangidae	0.146	0.037	-	0.029	-	-	0.098	0.096	-	-	-	-	-	-	-	-	-
10	Scorpaenidae/Triglidae	-	-	-	-	0.004	-	-	0.0001	0.00062	0.011	-	-	-	-	-	-	-
11	Serranidae	-	-	0.012	-	-	-	-	0.002	-	-	0.008	-	-	-	-	-	-
12	Rajiformes	-	0.002	0.002	-	-	-	0.005	-	-	-	0.041	0.02	-	-	-	-	-
13	Ariidae	-	-	-	-	-	-	0.009	0.02	0.022	-	0.018	-	0.034	-	-	-	-
14	Polynemidae/Mullidae	-	-	-	-	0.011	-	-	-	0.064	-	-	-	-	0.061	-	-	-
15	Tetraodontidae	-	-	-	-	0.02	-	-	0.017	0.012	-	0.048	-	-	-	-	-	0.163
16	Synodontidae	-	-	-	-	-	-	0.112	-	0.001	-	-	-	-	-	-	-	-
17	Cheloniidae	0.0001	-	-	-	0.0001	-	-	-	0.00011	-	0.0002	-	0.00041	-	-	-	-
18	Gerreidae	-	0.074	-	0.137	0.019	-	-	0.006	0.11	-	0.191	-	-	-	-	-	-
19	Clupeidae	0.411	0.316	-	0.458	0.203	0.237	0.667	0.032	0.27	-	0.229	-	-	-	-	-	-
20	Mugilidae	-	0.032	-	0.079	-	-	-	0.015	0.011	-	-	-	-	-	-	-	-
21	Other fish	0.033	0.04	0.085	0.006	0.02	0.408	0.0001	0.096	0.005	0.272	0.04	0.02	0.115	0.077	-	0.632	0.061
22	Coelenterata	-	-	-	-	-	-	0.088	-	-	-	-	-	-	-	0.042	-	0.0001
23	Cephalopoda	0.138	-	-	-	0.01	0.117	0.002	0.64	-	-	0.156	0.002	-	-	-	0.034	-
24	Gastropoda	-	-	0.031	-	-	-	-	-	0.095	-	0.016	0.004	-	0.146	0.262	-	0.044
25	Bivalvia	-	-	0.053	0.008	0.004	0.002	-	-	0.015	-	0.013	0.014	0.018	-	0.195	-	0.006
26	Echinodermata	-	-	-	-	0.358	-	-	-	-	-	0.002	-	0.152	-	-	-	-
27	Porifera	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.074	-	-
28	Palinura	-	-	-	-	0.003	-	-	-	-	-	-	-	-	-	-	-	-
29	Portunidae	-	0.033	0.021	-	0.063	-	-	0.00041	0.004	-	0.026	0.09	-	-	-	-	0.0001
30	Stomatopoda	-	0.009	0.009	0.017	0.025	0.02	-	0.006	-	0.088	0.0004	0.046	0.015	0.024	-	0.005	0.006
31	Penaeidae	-	0.023	0.005	0.057	0.024	0.016	-	0.00042	0.012	0.051	0.011	0.039	0.006	0.03	-	0.006	0.0001
32	Polychaeta	-	0.247	0.681	0.09	0.093	0.005	-	-	-	0.034	0.104	0.143	0.182	0.251	0.115	-	-
33	Other macrocrustaceans	-	0.04	0.012	0.049	0.099	0.035	-	0.001	0.008	0.347	0.008	0.078	0.038	0.048	0.042	0.014	0.002
34	Zooplankton	0.272	-	0.017	0.017	0.019	0.005	-	-	0.325	0.197	0.029	0.264	0.064	0.364	0.124	-	0.684
35	Phytoplankton	-	-	-	-	-	-	-	-	0.00063	-	-	-	0.264	-	-	-	-
36	Macrophytes	-	-	0.034	0.009	0.008	-	-	-	0.007	-	0.04	0.202	0.11	-	0.147	-	0.033
37	Detritus	-	-	-	-	-	-	-	-	0.021	-	-	-	-	-	-	-	-
	Import	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

Appendix A. Continued.

Prey \ Predator	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34
1 Birds	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
2 Sciaenidae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
3 Haemulidae	-	-	-	0.019	-	-	-	-	-	-	-	-	-	-	-	-	-
4 Centropomidae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
5 Lutjanidae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
6 Pleuronectiformes	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
7 Scombridae	-	-	-	0.004	-	-	-	-	-	-	-	-	-	-	-	-	-
8 Coryphaenidae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
9 Carangidae	-	-	-	0.011	-	-	-	-	-	-	-	-	-	-	-	-	-
10 Scorpaenidae/Triglidae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
11 Serranidae	-	-	-	-	-	-	-	-	-	-	0.055	-	-	-	-	-	-
12 Rajiformes	-	-	-	-	-	-	-	-	-	-	-	-	0.013	-	-	-	-
13 Ariidae	-	-	-	0.013	-	-	-	-	-	-	-	-	-	-	-	-	-
14 Polynemidae/Mullidae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
15 Tetraodontidae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
16 Synodontidae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
17 Cheloniidae	-	-	-	0.00061	-	-	-	-	-	-	-	-	-	-	-	-	-
18 Gerreidae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
19 Clupeidae	-	-	-	0.056	-	0.079	-	-	-	-	-	-	-	-	-	-	-
20 Mugilidae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
21 Other fish	-	-	-	0.048	-	-	-	-	-	-	-	0.035	0.014	-	-	-	-
22 Coelenterata	-	-	-	-	0.042	0.012	-	-	-	-	-	-	-	-	-	-	-
23 Cephalopoda	-	-	-	-	-	0.044	-	-	-	-	-	-	-	-	-	-	-
24 Gastropoda	0.014	-	0.019	-	-	-	-	-	0.017	-	0.16	0.046	-	-	-	-	-
25 Bivalvia	0.016	-	0.002	0.015	-	-	-	-	0.003	-	0.206	0.056	-	-	-	-	-
26 Echinodermata	0.075	-	-	0.008	-	-	-	-	0.059	-	0.047	-	-	-	-	-	-
27 Porifera	0.015	-	-	-	-	-	-	-	0.194	-	-	-	-	-	-	-	-
28 Palinura	-	-	-	0.06	-	-	-	-	0.008	-	-	-	-	-	-	-	-
29 Portunidae	-	-	-	0.001	-	-	-	-	-	-	-	0.043	-	-	-	-	-
30 Stomatopoda	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
31 Penaeidae	-	-	-	0.003	-	0.003	-	-	0.001	-	-	0.01	-	-	-	-	-
32 Polychaeta	0.14	0.003	0.171	0.014	-	-	-	-	0.016	-	-	0.137	-	0.021	0.006	-	-
33 Other macrocrustaceans	0.009	0.007	0.019	0.004	-	-	-	-	0.001	-	0.013	0.006	-	0.00081	0.00029	0.005	0.00013
34 Zooplankton	0.037	0.704	0.044	0.274	0.836	0.862	-	0.284	0.011	0.024	-	-	-	-	-	-	0.082
35 Phytoplankton	-	0.286	-	-	-	-	-	0.54	0.003	0.01	-	-	-	0.139	-	0.2	0.77
36 Macrophytes	-	-	0.118	0.459	-	-	0.566	-	0.553	0.082	0.519	0.203	-	0.116	0.113	-	-
37 Detritus	0.693	-	0.626	0.009	0.122	-	0.434	0.176	0.132	0.883	-	0.463	0.972	0.724	0.881	0.795	0.148
Import	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-