

COMPLEXITY, COST AND QUALITY OF ECOSYSTEM MODELS AND
THEIR IMPACT ON RESILIENCE:

A COMPARATIVE ANALYSIS, WITH EMPHASIS ON MARINE
MAMMALS AND THE GULF OF ST. LAWRENCE

by

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Abstract

The development of an ecosystem approach is essential to improve understanding of the nature and dynamics of exploited marine ecosystems and the complexity of species interactions. A database of 393 *Ecopath* models was compiled to investigate questions pertaining to 1) the uncertainty in model parameters, 2) the relationship between ecosystem complexity and stability, 3) the effect of marine mammals on ecosystem productivity, and 4) the lack of recovery of commercially caught predatory fish species. Reviewing the strengths and weaknesses of *Ecopath* methods showed that few published models have addressed uncertainty even when the tools were provided with the software. Estimating uncertainty (with confidence intervals for parameters) was improved by combining the *Ecopath* approach with other modelling techniques. The second analyses, using 50 ecosystem models, showed that quality of input data affects conclusions concerning the relationship between complexity and stability in ecosystems. Findings further support the notion that stability also increases as community complexity (expressed as ascendancy and omnivory) increases. The third analyses used seven ecosystem models to explore whether the presence of marine mammals and their overlap with fisheries for food resources affects overall ecosystem productivity, and whether their extirpation could decrease productivity. Simulation results were equivocal about whether extirpation of marine mammals from ecosystems would benefit fisheries, while mixed trophic impact analyses suggested that beneficial predation does occur in these ecosystems. Finally, a case-study of four *Ecopath* models from the Gulf of St. Lawrence addressed the collapse in biomass of predatory fish and the potential causes of the lack of recovery of these species. Analyses revealed that the ecosystem structure shifted from one previously dominated by piscivorous groundfish during the mid-1980s to one dominated by small-bodied pelagic species during the mid-1990s. Part of the total mortality of groundfish was accounted for by seal predation when fishing mortality was reduced. These analyses collectively demonstrate the value of investigating ecological questions applicable to marine ecosystems using a multi-model comparative approach.

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List of acronyms

4RS	NAFO zones for the northern Gulf of St. Lawrence
4T	NAFO zone for the southern Gulf of St. Lawrence
A	Ascendency, from network analysis
AE	Assimilation efficiency
AVAS	Additive and Variance Stabilizing transformation in the S-Plus 6 software
B	Biomass density (in $t \cdot km^{-2}$) parameter in <i>EwE</i>
BorMiCon	Boreal Migration and Consumption model
BUM	Best Unbalanced Model (in <i>EwE</i>)
C	Catch (in tonnes)
Ca	Capacity, from network analysis
CDEENA	Comparative Dynamics of Exploited Ecosystems in the Northwest Atlantic, research program from DFO Canada
CSIRO	Commonwealth Scientific and Industrial Research Organisation, in Australia
DC	Diet composition
DFO	Department of Fisheries and Oceans, Canada
Dynumes	Dynamic Numerical Marine Ecosystem model
EE	Ecotrophic efficiency parameter in <i>EwE</i>
ERSEM	European Regional Seas Ecosystem model
EwE	Ecopath with Ecosim
F	Fishing effort
FAO	Food and Agriculture Organization of the United Nations
FISHCODE	Special programme of global partnerships for responsible fisheries established by the FAO Fisheries department
Gadget	Globally Applicable Area-Disaggregated General Ecosystem Toolbox
GE	Gross Efficiency parameter in <i>EwE</i>
IPN	Instituto Politécnico Nacional, Mexico
M0	Unexplained mortality, in <i>EwE</i>
M2	Predation mortality, in <i>EwE</i>
MPA	Marine Protected Area
MSVPA	Multispecies virtual population analysis
MULTSPEC	Area-structured modelling approach developed to simulate interaction between commercially important fish and marine mammals in the Barents Sea
NATO	North Atlantic Treaty Organisation
NGSL	Northern Gulf of St. Lawrence
NMFS	National Marine Fisheries Service in NOAA
NOAA	National Oceanic & Atmospheric Administration
O	Overhead, from network analysis
OI	Omnivory index
P/B	Production per unit of biomass parameter (equivalent to <i>Z</i>) in <i>EwE</i>

PPR	Primary production required, in <i>EwE</i>
Q/B	Consumption per unit of biomass parameter in <i>EwE</i>
SGSL	Southern Gulf of St. Lawrence
SOI	Systems' Omnivory Index, in <i>EwE</i>
TL	Trophic Level
TL _c	Trophic Level of the catch
TL _Q	Trophic Level of the consumption of a particular trophic group
Y	Fisheries Catch
Z	Instantaneous total mortality rate (in year ⁻¹)

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Lyne

26 March 2007

*Accuse not Nature, she hath don her part
Do thou but thine, and be not diffident
Of Wisdom, she deserts thee not, if thou
Dismiss not her, when most thou needst her nigh,
By attributing overmuch to things
Less excellent, as thou thy self perceav'st.*

John Milton
Paradise Lost, 1667

Co-authorship statement

A version of chapter 5 has been submitted for publication to Deep Sea Research II. The paper was co-authored with Department of Fisheries and Oceans scientists Martin Castonguay, Claude Savenkoff, Doug Swain, Denis Chabot, Hugo Bourdages, Mike O. Hammill, and Mark Hanson. This project was realized under the DFO program Comparative Dynamics of Exploited Ecosystems in the Northwest Atlantic. Overall guidance and directions for the research was provided by Dr. Castonguay, my co-supervisor. The modelling and data analysis conducted to explore the structure of the two ecosystems were primarily conducted by myself. Preparation of the manuscript, mainly for discussion, involved significant inputs from all co-authors. Initial writing and development work was carried out by myself.

Introductory chapter

The role of ecosystem models, particularly *Ecopath* with *Ecosim*, as a transition to ecosystem based management.

Introduction

1.1.1 Studying marine ecosystems

The world's ocean covers 70% of our planet, and marine ecosystems play a critical role in maintaining many species (including humans) health and well being. Relative to terrestrial systems, our knowledge of marine ecosystems is often restricted by the difficulty of direct observation. Indeed, despite their obvious richness, marine ecosystems have largely been left out of most discussions about biodiversity. The knowledge on abundance of organisms or the interactions they have within food webs is also fragmentary (Mooney 1998). What is established, however, is that, globally, many fish populations have been declining in abundance over the past 50 years (Christensen *et al.* 2003; Myers and Worm, 2003), with many large-scale fisheries around the world collapsing (Pauly *et al.* 2002; Worm *et al.* 2006). What was perceived for a long time as an inexhaustible resource all of a sudden seems quite limited (Rosenberg *et al.* 1993). The most important pressures being exerted on the ocean ecosystem are overfishing, destruction of coastal ecosystems, pollution through oil spills and illicit disposal, land-based contamination, and climate change (Costanza *et al.* 1998).

Throughout all oceans of the world, intensive exploitation has led to dramatic changes in the structure and productivity of marine ecosystems (Fogarty and Murawski 1998), directly (fisheries catches) or indirectly (changes in the foodweb structure, habitat disturbance). Overfishing has become more important, and simultaneously, more difficult to manage (Ludwig *et al.* 1993). Overfishing diminishes the catches, and the genetic diversity and ecological resilience of exploited populations (Botsford *et al.* 1997; Pauly *et al.* 1998). As a result, the long-term sustainability of many fish stocks and the stability of

large marine ecosystems appear threatened. It is essential to focus on that issue not only to preserve the biodiversity of our planet, but also because more than one billion people now rely on fish as their main source of animal protein, making it the fifth largest food commodity in the world (FAO 2002).

For many years, marine systems have been studied and managed from a single-species point of view. However, there is awareness in scientific and general communication that this traditional way of managing fisheries is not sufficient (Hofmann and Powell 1998). With the necessity to understand in detail the nature and dynamics of exploited marine ecosystems, and more precisely the complexity of species interactions, the development of the ecosystem approach for management of marine systems is becoming more and more important (Sissenwine and Daan 1991; Kröger and Law 2005, Choi *et al.* 2005). The science of marine management evolved rapidly from compartmentalized programs around distinct species to a more global view encompassed by the phrase “ecosystem approach” (Kröger and Law 2005).

To address the world's ever-growing environmental problems, a comprehensive understanding of the structure, function and regulation of major ecosystems is essential (Mann 1988; Pahl-Wostl 1993; McCann 2000). Constructing models to examine the behavior of ecosystems is therefore the focus of much contemporary research.

1.1.2 Ecosystem modelling

Marine ecosystems are often very complex systems that are heavily influenced by humans. In most cases, it is impossible to directly experiment with the ecosystems to understand how they work. Computer models and simulations can however improve our understanding of these systems. Ecosystem models allow for a better understanding of how species are influenced by each other and by human activities. They can be used both to quantitatively describe the functioning of marine ecosystems, and to provide indications of how these are likely to change in response to different ecological perturbations. Thus, ecosystem modelling is a useful tool for investigating a wide range of scientific questions in the world's oceans. Moreover, when many ecosystem models of the same type are

available, it becomes possible to perform global scale analyses and quantification of important marine ecological processes.

Different types of models are available, that focus on different levels of interactions in a studied ecosystem (see Whipple *et al.* [2000] for an exhaustive review). The model of Andersen and Ursin (1977) used a mass-balance approach to describe the North Sea ecosystem. It included a complete suite of ecosystem compartments (from nutrients to predatory fish), but also required a lot of data, making it costly and difficult to use (Whipple *et al.* 2000; Pauly and Christensen 2002). Its major merits were to demonstrate that modeling an entire sea was feasible, and to inspire Multispecies Virtual Population Analysis (MSVPA; Sparre 1991).

Models using Gadget (Globally Applicable Area-Disaggregated General Ecosystem Toolbox), an environment for statistical multispecies modeling (Begley and Howell 2004), have been developed as a forward simulation model using statistical estimation through weighted combinations of several log-likelihood criteria (Stefansson and Pálsson 1998). The BorMiCon model (Boreal Migration and Consumption; Stefansson and Pálsson 1997) uses the Gadget approach to represent temporal and spatial differences in the interaction of organisms around Iceland. They have the advantage of being multispecies-multiarea-multifleet simulation models. MULTSPEC (Bogstad *et al.* 1997) is also an area-structured modelling approach developed to simulate interaction between commercially important fish and marine mammals in the Barents Sea. These models share the characteristics of being system-specific, modelling only a small component of the ecosystem for a specific purpose. Also, primary and secondary productions are poorly represented.

The ERSEM model (European Regional Seas Ecosystem Model) was developed to simulate ecosystem dynamics of the North Sea (Baretta *et al.* 1995). This model simulates the annual cycles of carbon, nitrogen, phosphorus and silicate in the pelagic and benthic food webs. This interlinked set of biological data is useful to describe the biological and chemical interactions between trophic groups of the ecosystem, but the higher trophic groups are not well represented.

On the other hand, ecosystem models such as Dynumes (Dynamic Numerical Marine Ecosystem model; Laevastu and Larkin 1981) include a wide range of trophic

groups, from phytoplankton to marine mammals. They also have a spatial component which represents fish movements among habitat types. However, this modelling approach has large data requirements for biological and fisheries parameters, and applications are thus time-consuming and costly to construct (Whipple *et al.* 2000).

The common problem with the models presented above is that they are usually constructed for a specific area or ecological issue, and because very few different applications are available, neither comparison nor validation is feasible.

Size-spectra models (Sheldon *et al.* 1977; Moloney and Field 1985; Shin and Cury 2004) constitute an alternative to species or guild-based models, and place species or guilds in size classes for analyzing ecological relationships within ecosystems. This is a potentially useful approach for coarse predictions of fish production and potential catch in data-sparse situations, though the method still needs refining. However, this is a steady-state model that cannot make multiyear projections (Whipple *et al.* 2000).

Another method to estimate the parameters of a food web is known as inverse modelling. This approach aims to compute the solution that minimizes the imbalances between inputs and outputs. The inverse approach provides a global criterion for an optimal (balanced) solution. When the system of equations is strongly underdetermined, additional constraints must be added to limit the range of possible solutions and thus to obtain a meaningful solution (Vézina and Platt 1988; Savenkoff *et al.* 2001). Models built with inverse approach are very robust in terms of uncertainty. However, this model is also steady-state and cannot make multiyear projections. In addition, few models are available, so global inferences based on inverse models are not presently possible.

Agent-based modelling (ABM) is mainly used in evolutionary ecology, archaeology, economics and social sciences. However, this modelling approach has great potential for increasing the breadth of resource management questions that may be considered (see Fulton *et al.* 2007 for a review). Early ABMs were often tightly focused on only a small portion of the ecosystem, but newer hybrid models incorporate more trophic groups and use differential equations, with decision based agents. *InVitro* (Gray *et al.* 2006) is an example of such a hybrid model. It has been built for management strategy evaluation. It has the potential to simulate the effects of a wide range of human activities

on a regional ecosystem, including fisheries, tourism, oil and gas or salt production, and to forecast system response to different management regimes.

Atlantis (Fulton et al. 2004; Fulton *et al.* 2007) is an biogeochemical, spatially explicit, 3D, ecosystem models intended for management strategy evaluation that has been applied in 13 marine systems around the world, primarily in Australia and the US. It contains sub-models to represent each step in the management strategy and adaptive management cycles.

Finally, *Ecopath* models are very inclusive, based on the full range of organisms in an ecosystem, and can be used for long-range simulations. These models have been applied to many ecosystems, making comparisons possible. As a result, *Ecopath* models represent the best option for the present analysis.

The *Ecopath with Ecosim* (*EwE*) modelling approach indeed allows the construction of ecosystem models (Christensen and Pauly 1992). In addition to making ecosystem analyses possible, this approach requires to collect and use the available biological information for species of a given ecosystem and to verify that it is compatible with information on other species.

The principal objection often raised against multispecies models is that they generally require excessive amounts of data. The ecosystem analysis used here is relatively easy to use, allows the estimation of a number of missing parameters, and has already been used on many ecosystems. *Ecopath with Ecosim* is an ecological software suite that was developed at the University of British Columbia's Fisheries Centre, with applications widespread throughout the world. The *Ecopath* approach was developed in the early 1980s by J.J. Polovina and co-workers at the NMFS Laboratory in Honolulu. It was first applied to a coral reef system, as a tool to allow quantitative analyses of biological interactions within aquatic systems (Polovina 1984). The method was expanded to integrate a wide range of analytic routines (Christensen and Pauly 1992). This was further developed into *Ecopath with Ecosim*, which provides a dynamic modeling capability for exploring past and future impacts of fishing and environmental disturbances as well as for exploring optimal fishing policies (Walters et al. 1997; 1999).

In 2007, the *EwE* modelling approach has been recognized as one of the top 10 breakthroughs in marine science by the NOAA, in a special Web site celebrating 200

years of science, service, and stewardship (<http://www.celebrating200years.noaa.gov>). NOAA recognized *Ecopath* modeling as the first to apply a type of statistics called “path analysis” to the field of marine ecology. The model’s simplicity and its ability to accurately identify ecological relationships, it is stated, “have revolutionized scientists’ ability worldwide to understand complex marine ecosystems” (NOAA 2007).

1.1.3 Census of *Ecopath* models

In order to compile many comparable marine ecosystem models in a database, this thesis focused on *Ecopath* models. This modeling approach was chosen because its software (*Ecopath with Ecosim*) was easily available (and free to download from the website <http://www.ecopath.org>), and has been used by a wide range of research groups all over the world, thus providing coverage of a good number of the marine ecosystems of the planet. In summary: while good modelling techniques exist, only *Ecopath* could provide enough models for the kind of comparative analyses envisaged here.

The database of *Ecopath* models used here was started by Dr. Villy Christensen assisted by Mr. Sherman Lai (see <http://www.ecopath.org>). I completed this database through an exhaustive questionnaire sent to all the *Ecopath* users who downloaded the software. Doing so, I made sure that, in the present study, as many existing *Ecopath* models were taken into account. Each *Ecopath* user who received the questionnaire (by email) was invited to give a series of information on their models (see the complete questionnaire in Appendix 1).

Results: the models database

The use of ecosystem modelling for research in fisheries and aquatic sciences has increased rapidly in the last decade. According to *Google scholar*, a search engine covering peer-reviewed papers, theses, books, abstracts, and other scholarly literature from all broad areas of research, there was an total of 201 publications in the 1980s containing the term “ecosystem modelling” or “ecosystem modeling” in either the title or the text of the publications, while during the 1990s this number increased to 1966 publications (Figure 1.1). In the years 2000s, this number reached 3593 publications. The

same thing is observed for the use of the term “*Ecopath*”, which increased from 17 publications in the 1980s period, to 370 in the 1990s, and 968 in the years 2000s (Figure 1.2).

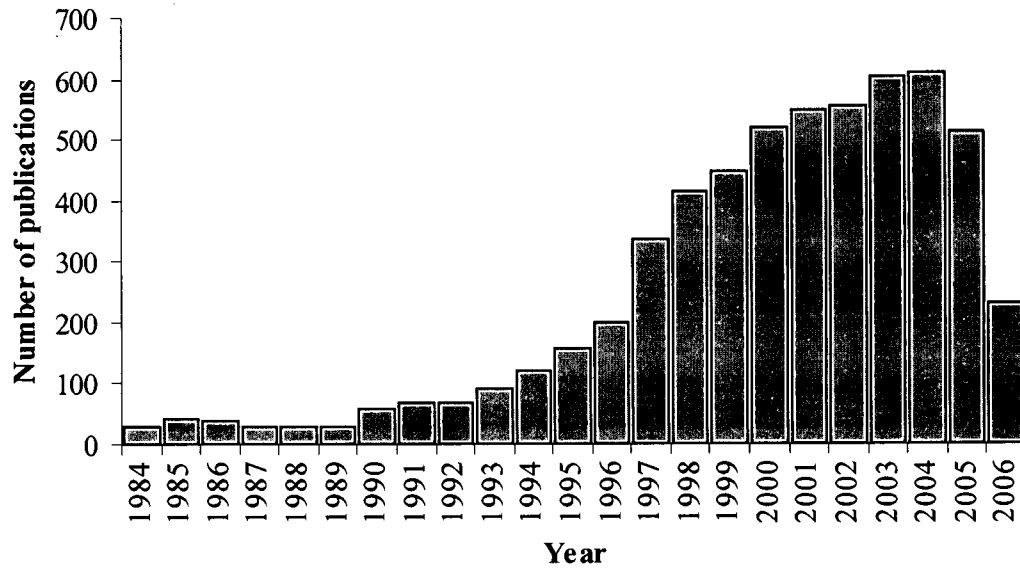


Figure 1.1. Occurrence of the word ‘ecosystem modelling’ or ‘ecosystem modeling’ in the title or abstract of publications, according to *Google Scholar*.

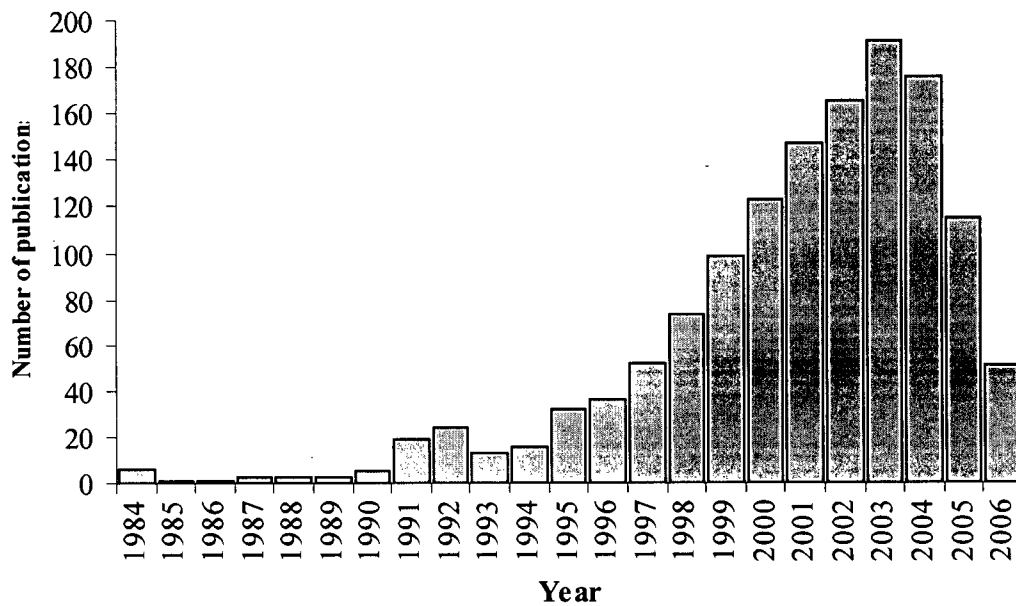


Figure 1.2. Occurrence of the word “Ecopath” in the title or abstract of publications, according to Google Scholar.

1.2.1 Geographical coverage

The *Ecopath with Ecosim* software has more than 2800 registered users from approximately 120 countries. In May 2006, of all the users contacted, 347 had replied to my questionnaire. With additional information taken from an in-depth literature search, a total of 393 *EwE* models had been constructed and were available for different ecosystems of the world (Figure 1.3; Appendix 2).

The great majority (80%) of *EwE* models described were constructed for marine habitats (Table 1.1). Another 18% of models describe lakes, rivers or other freshwater habitats. Finally, six models are constructed so far for terrestrial ecosystems.

Interestingly, there is also an online game called the ‘Meru Park wildlife game’, simulating the management of a wildlife park in the Serengeti, constructed by *Agence Française de Développement* and the *Fonds Français pour l’Environnement Mondiale*, in collaboration with *France 5 TV*, built mainly from an *Ecopath* model constructed by M. Villanueva (INP/ENSAT, Castanet Tolosan, France, pers. comm.).

Table 1.1. Number of *Ecopath* models constructed for different habitat types.

Environment modeled	Number of <i>EwE</i> models	%
Marine	316	80.4
Freshwater	71	18.1
Terrestrial	6	1.5
TOTAL	393	100.0

Out of the 393 models covering over 80 countries, half were constructed in only eleven countries, for which eight or more *EwE* models are available. The most important country in terms of *EwE* models available are the USA, followed by Mexico, and Canada (Table 1.2).

Table 1.2. The eleven most important regions in terms of *Ecopath* models constructed.

Country	Number of <i>EwE</i> models	% of all models
USA	59*	15.0
Mexico	32	8.1
Canada	26*	6.9
Australia	11	2.8
France	11	2.8
Philippines	11	2.8
Brazil	10	2.5
Chile	9	2.3
Italy	9	2.3
China	8	2.0
South Africa	8	2.0
TOTAL	194	49.5

* USA and Canada share an additional 9 models representing the Great Lakes.

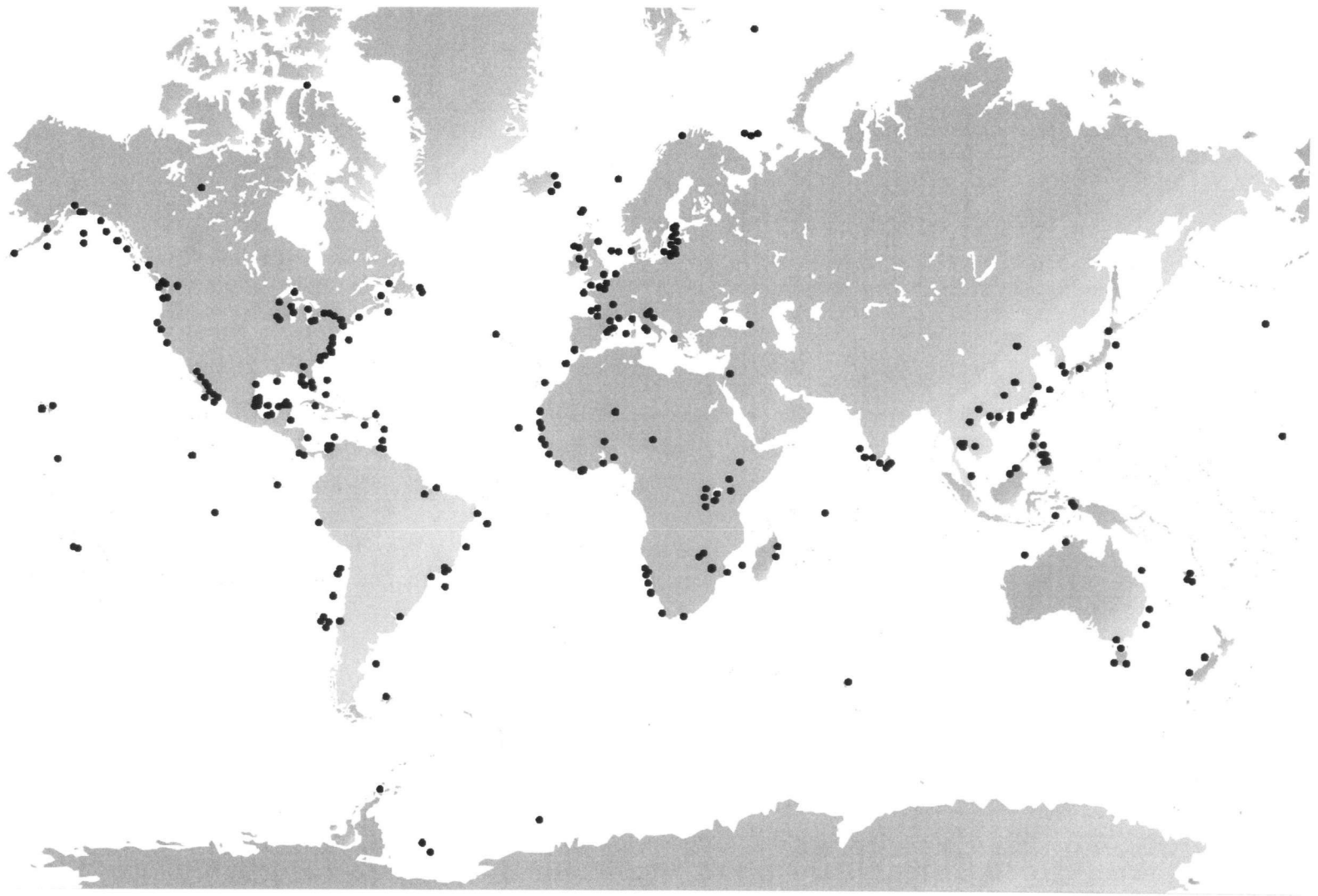


Figure 1.3. Ecosystem models constructed from 1984 to 2007 with *Ecopath*. A total of 393 models are shown on the map, 316 in marine habitats, 71 in rivers, lakes or reservoirs, and 6 terrestrial ecosystems.

1.2.2 Structure and quality of Ecopath models

For a sub-sample of 50 models, more details were collected about the size and quality (see Chapter 3 of this thesis for more details). In terms of size, most *Ecopath* models (42%) have less than 20 trophic groups. Models with twenty to forty trophic groups represent 30%, while 28% of *Ecopath* models have more than 40 trophic groups (Table 1.3). Occurrence of larger models tend to continue to increase, as we with newer models (not part of in this sub sample) such as English Channel (Stanford and Pitcher 2004; 50 groups), Northern British Columbia coast (Ainsworth *et al.* 2002; 53 groups), Norwegian Sea (Skaret and Pitcher (in press.); 58 groups), and Raja Ampat (Ainsworth *et al.* 2007; 96 groups).

Table 1.3. Number of *Ecopath* models for different size categories, in terms of trophic groups.

Number of trophic groups	Number of <i>EwE</i> models	%
Less than 20	21	42
20 to 40	15	30
More than 40	14	28
TOTAL	50	100

The overall quality of *EwE* models was calculated for a sub-sample of 50 models, and expressed as a fraction ranging from zero to one, i.e. their “pedigree” (see Chapter 3 of this thesis for complete methodology and analysis). My results show that few models show a very low pedigree (2% have a pedigree lower than 0.2), or a very high pedigree (10% have a pedigree higher than 0.6). Forty percent of *EwE* models have an intermediate pedigree from 0.200 to 0.399, and 48% of the models fall into the higher range with pedigree from 0.400 to 0.599 (Table 1.4).

Table 1.4. Number of *Ecopath* for different levels of quality (pedigree).

Overall pedigree	Number of <i>EwE</i> models	%
< 0.200	1	2.0
0.200 – 0.399	20	40.0
0.400 – 0.599	24	48.0
≥ 0.600	5	10.0
TOTAL	50	100.0

1.2.3 Rationale of Ecopath modelling projects

Few ecosystem models appear to have been developed in response to specific questions. Most models (42%) were constructed to describe the structure of ecosystems, from the simplest foodweb (e.g., the model developed by Palomares *et al.* [1993] to describe a littoral lagoon in the French Mediterranean with its 10 functional groups) to the most elaborate (e.g., the model developed by Ainsworth *et al.* [2007] to analyze the ecology and economics of Bird's Head seascape, Papua, in Indonesia, which has 96 functional groups). Another 30% of the models were used to deal with fisheries management issues such as in the Ebrié Lagoon of Ivory Coast (McNamara 2004). Eleven percent addressed explicit theoretical ecology questions (e.g., trophic networks and carbon flows in south eastern Baltic coastal ecosystems by Tomczak *et al.* 2005), while 9% concentrate on policy matters, as was the case for the Batabanó ecosystem in Cuba (Wolff *et al.*, in prep.). Finally, 6% of the models were constructed to assist in the creation or management of marine protected areas (e.g., the model developed by Libralato *et al.* [2006] for the Miramare MPA in Italy).

Of the *Ecopath* models constructed to date, 32% were for Ph.D. projects (e.g., chapter 5 of this thesis), 9% for M. Sc. projects (e.g., Nsiku's [1999] model of Lake Malawi), and 7% for post-doctoral projects (e.g., Bundy [2001] model of the Newfoundland shelf ecosystem). Research scientists constructed 19% of *Ecopath* models, followed with 17% by faculty members, 5% by research assistants, and 11% by graduate students (without specification of their degree).

In 55% of cases, models were constructed under university research projects (as is the case, for example, for the models developed at the Fisheries Centre, University of British Columbia by Ainsworth *et al.* [2002] for Northern British Columbia ecosystems). In 37% of the cases, models were constructed as part of governmental projects (for example, the Gulf of St. Lawrence model presented in this thesis was constructed under the *Comparative Dynamics of Exploited Ecosystems of the Northwest Atlantic – CDEENA* program from Department of Fisheries and Oceans of Canada). Finally, models were constructed by independent research institutions (neither university nor government) in 8% of the cases.

1.2.4 Publishing Ecopath models

In terms of publications, of the 314 models published in some way, close to 60% are published in peer-reviewed journals; 15% in reports; 11% in book chapters; 9% are available as M.Sc. or Ph.D. theses, and about 5% were published in conference proceedings (Table 1.5).

Table 1.5. Number of *Ecopath* models published by type of publication.

Type of publication	Number of <i>EwE</i> models	%
Book chapter	34	10.8
Report	47	15.0
Conference proceedings	18	5.7
Thesis	28	8.9
Peer-reviewed journal	187	59.6
TOTAL	314	100.0

While most authors stated that they constructed only one *Ecopath* model, some others are very notable in terms of the number of models they constructed and published (Table 1.6). These authors are mainly from one of the top-ten countries listed in Table 1.2, but also from Spain and Germany.

Table 1.6. Most notable authors in terms of *Ecopath* models constructed, according to the survey*.

Author	Institution	Number of <i>EwE</i> models
Jacques Moreau	École Nationale Supérieure Agronomique de Toulouse, France	17
Sheila Heymans	Fisheries Centre, University of British Columbia, Canada	14
Thomas A. Okey	Commonwealth Scientific and Industrial Research Organisation, Australia	7
Francisco Arreguín- Sánchez	Centro Interdisciplinario de Ciencias Marinas del IPN, Mexico	6
Marta Coll	Institut de Ciències del Mar, Spain.	6
Lyne Morissette	Fisheries Centre, University of British Columbia, Canada	6
Matthias Wolff	Center für Tropical Marine Ecology, Germany	6
Beth Fulton	Commonwealth Scientific and Industrial Research Organisation, Australia	5
Cathy Bulman	Commonwealth Scientific and Industrial Research Organisation, Australia	4
Alida Bundy	Bedford Institute of Oceanography, Canada	4
James Hagy	University of Maryland, USA	4
Simone Libralato	Universita Ca' Foscari - Dipartimento di Scienze Ambientali, Italy	4
TOTAL		83

* These numbers do not account for the inputs of Dr Villy Christensen, who advised on the construction of many, if not most of these models, of Dr. Tony Pitcher, who constructed many models with his research team, and of Dr Daniel Pauly, who inspired and assisted in the construction and documentation of many *EwE* models.

Discussion & Conclusions

Ecosystem modelling is definitely an active research field. It is clear from the many responses that I received that this represents a popular way to address management, conservation, and ecological issues for marine ecosystems. The use of *Ecopath with Ecosim* as an approach to address such issues is extensive, and widespread around the globe.

The *Ecopath* representation of a naturally dynamic system helps to identify major shortcomings in the data and provides important reference points for more specific research on ecosystems. Such an ecosystem point of view allows an understanding of the inter-connections between the species groups of an ecosystem. From a management point of view, knowing that impacting one group will cause changes in another can provide tools for long-term and multispecies management. The strengths of *Ecopath* modelling are also to identify knowledge gaps, and to allow a universal format for comparing different ecosystem models.

Over the past years, we have seen a transition from single species approach to an ecosystem-based approach. Because the *Ecopath with Ecosim* software package is free and relatively easy to use, its increasing application in many countries certainly accelerated this transition to ecosystem-based approach.

At first, aquatic ecosystem models were constructed with focus on a particular species, for which we were describing the ecosystem. Most of the time, these models had a small number of trophic groups, principally describing species that were commercially important for the fishery. However, it was then considered that species (not only the ones of interest for a given study) are interacting with each other within a foodweb and that the effects of predation or competition are generating multiple indirect effects that need to be analyzed. *Ecopath with Ecosim* offered a fairly simple way to address this issue and became one of the important modelling tools to conduct ecosystem-based analyses.

My results show that more models are constructed for marine ecosystems than for freshwater ones. The fishing industry and the species caught are much more important in marine habitats, where commercial fishing plays an important role, than in freshwater ecosystems, where there is less commercial and more sports fishing.

The top-ten countries generating the largest numbers of *EwE* model all tend to have large aquatic areas (coasts, rivers, or lakes), and their *EwE* models are mainly constructed for marine systems. All these countries depend on an important fishery industry, and most of them have governmental agencies starting to show interest towards ecosystem-based management. This is the case, for example, for CEFAS and SAMS in the UK, CSIRO in Australia, DFO in Canada, and NOAA in USA.

Because *Ecopath with Ecosim* is a software project that is being developed at UBC Fisheries Centre, it is not surprising to see that the most productive authors in terms of *EwE* models are current and past members or collaborators of this research institution. UBC Fisheries Centre is indeed a place where ecosystem modelers can share knowledge and new ideas about this modelling technique, and apply it to their ecosystem of interest.

Moreover, these models can be used for more purposes than they were built for, as they are now part of an essential and global database of our ecological knowledge of marine ecosystems on an international scale. As is true at the ecosystem scale, where models representing whole ecosystems make the detection of emergent properties possible, a global approach, linking ecosystems together for an even more extensive analysis, is also fundamental for generalization applying to marine ecosystems.

Great efforts were made to assemble as much information about *Ecopath* models as possible during this Ph.D. thesis. This ended up being a very collaborative process, where many *Ecopath* users helped by providing information about their models, and sharing their interest for understanding marine ecosystem. This is particularly valuable now that these ecosystems are threatened by factors such as habitat degradation, climate change, invasive species, overexploitation, or pollution.

The use of an international ecosystem models database, which is freely available and easily accessible through the web (at <http://www.ecopath.org>), allows the comparison of similar issues encountered in different ecosystems of the world, and the exploration of diverse approaches to address them. My analysis allowed updating the original *Ecopath* web database, expanding it from originally 98 models to 393. Consequently, *Ecopath* models have become more accessible to the scientific community. This attempt to make available as many models as possible is meant to support studies of global ecosystems. Since the software along with the models is available without charge, this makes it beneficial for every scientist or manager aware of understanding of marine ecology, even in developing countries.

1.3.1 Research questions

Now that these many models are accessible, we can study a selection for analyses addressing various concepts in marine ecology. Here, I use a variety of ecosystem models (with the purpose of covering a global scale and having a better representation of the possibilities) in order to focus on three specific, but different hypotheses. First, this thesis presents an *analysis of the uncertainty of the ecosystem modeling approach*, and the importance to consider it before to address any problem with an ecosystem model (Chapter 2). As ecosystem modelling has become a very important way to study marine ecosystems processes, an essential question to address is the capacity to compare results from the model with those from observations, based on an analysis of the remaining sources of error. However, few of the currently developed *Ecopath* models have been examined in terms of their uncertainty. Thus, when addressing this problem, it is necessary to clearly define the type of uncertainty that may be encountered in ecosystem modelling, and the means by which it may handled. When doing so, we gain more confidence in ecosystem modelling as a tool to address or manage marine ecosystem matters.

In Chapter 3, an assemblage of models is used to test the hypothesis that *the quality of ecosystem model inputs plays a significant role for the relationship between complexity and stability*. My secondary hypothesis was that *there is, in ecosystems, a direct relationship between complexity and stability*. This analysis is applied to a total of 50 *Ecopath* models, all of them being 'pedigreed' for their quality in terms of their input data, in collaboration with the authors of the models. Simulations were done with *Ecosim* to test if high quality models perform better than poor ones to predict changes in biomass in the ecosystem. The construction costs of models is discussed, the actual dollar amount spent on models of different quality estimated. Finally I explore the possibility that information quality may be related to the complexity and the resilience of marine ecosystem models.

In Chapter 4, a set of *EwE* models that all share the particularity of having important marine mammals groups (and covering the major ecosystems where these animals are important) is used to test the hypothesis that *the presence of marine mammals in ecosystems and their overlap with fisheries for food resources does not have a*

significant effect on the overall productivity of the ecosystem, and the secondary hypothesis that *marine mammals extirpation can decrease this productivity because of the beneficial predation effects they can have on their prey*. Marine mammals are a very important component of marine ecosystems, and as top predators, they may compete with fishery for the same target species. Marine mammals are also exploited by whaling, mainly by Norway and Japan. The latter justify their whaling activity by stressing that whales in the world consume annually some three to five times more marine fish and invertebrates than are fished for human consumption or for reduction into fish meal and oil (Anonymous 2001; Kaschner and Pauly 2005). This situation, it is alleged, is not compatible with the world's increasing need for a stable food supply. However, the impact of top predators in marine ecosystems is not always a negative one. In many cases, there seems to be a positive predation effect from top-predators to their prey. This analysis will address that issue by using *Ecosim* to simulate a decrease in marine mammals biomass and quantifying its positive and negative trophic impacts on all other species of the foodweb. Normally, one would expect the impact of marine mammals on foodweb to be negative for their prey. However, in some cases I can see that this overall effect of marine mammals predation is a positive one; which would mean that a loss of these species may also represent a loss in usable production in the ecosystem.

Based on four *Ecopath* models that were constructed as part of this Ph.D. project, the Chapter 5 addresses the problem of collapsing fish stocks in the Northwest Atlantic. By comparing two ecosystems (Northern and Southern Gulf of St. Lawrence) and two time periods (pre- and post-collapse), I test the hypothesis that *the biomass of important predatory fish in a particular ecosystem (here the Gulf of St. Lawrence) changed over the last 20 years, and that the changes are linked to environmental and anthropogenic (overfishing) factors*. My analyses revealed that the ecosystem structure shifted dramatically from one previously dominated by piscivorous groundfish during the mid-1980s to one now dominated by small-bodied pelagic species during the mid-1990s in both the southern and northern Gulf of St. Lawrence. The species structure was different between the northern Gulf and the southern Gulf, and this may explain why these two ecosystems did not collapse to the same degree in the early 1990s.

After almost five years at the Fisheries Centre, surrounded by leaders in the marine ecology field, I realized that constructing an ecosystem model is not enough to understand a marine ecosystem. Not only do we have to deeply understand the marine ecological processes, but we also have to apply our knowledge of specific ecosystems to the global scale, draw comparisons, and trace global trends for the whole planet. Now that it becomes clearer that ecosystems are under enormous stress, it is critical that we clearly understand the biological processes of food webs, and that we figure out what is needed to keep resources as intact as possible.

Chapter summary

I developed a global database of ecosystem models based on the *Ecopath* approach. In total, 393 models were collected, which represents an addition of 295 new models to the *Ecopath with Ecosim* database that is available from the website (<http://www.ecopath.org>). A questionnaire was sent to more than 2800 users of that freely-downloadable software, and close to 350 replies were analyzed. This was completed by a literature review of other published *Ecopath* models. The majority of *Ecopath* models represent marine habitats. The most important countries in terms of models available are the USA, Mexico and Canada, but overall, more than 120 countries are represented. Most models have between 20 and 40 trophic groups, and have a pedigree between 0.400 and 0.599. The rationale of *Ecopath* modeling projects was also examined. Describing the structure of the ecosystem seems to be the major objective when constructing a model. Other uses are fisheries management, policy, and creation of marine protected areas. On the 314 models published in some way, most were in peer-reviewed journals, followed by reports, book chapters and theses. The creation of this model database allowed me to compare ecosystems on a global scale regarding various issues in marine ecology. Having a common methodology behind each ecosystem model was definitely an asset to explore the research questions presented in this thesis.

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Chapter 2

Addressing uncertainty in marine ecosystem modelling.¹

2.1 Introduction

When we want to address issues at the ecosystem level, one of the options is to create models that will represent these ecosystems and simulate different scenarios to see how they will react to diverse situations. Ecosystem modelling has become very popular in applied ecology, and perhaps even more so for marine ecosystems, which are harder to investigate directly. Even as this approach increases in popularity, only a minority of studies address the uncertainty related to the model results. For the marine environment, a very popular tool to create ecosystem models is called *Ecopath*. With this approach, many options exist to address uncertainty. However, many sources of uncertainty exist, and they are virtually infinite in ecosystems modelling. It is thus important to identify the various sources of uncertainty and to recognize how to deal with each of them. This paper will review the different options available for uncertainty analyses in marine ecosystem modelling, and propose some alternatives for a better investigation of uncertainty.

2.2 *Ecopath* ecosystem modelling and its sources of uncertainty

Ecopath is a modelling approach that creates a simple static model to describe the average interactions of the populations within an ecosystem during a certain period. The model assumes mass-balance, i.e., that we account for all flows in a foodweb. Hence, its parameters can change. Such an approach is much simpler than others that attempt to

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model multispecies interactions such as MSVPA (Sparre 1991) for which an enormous quantity of catch-at-age data and stomach contents analyses is required (Morissette 2001). The principal advantage with *Ecopath* is that the input values (mainly total mortality, consumption and diet composition) are often already available for several species or groups in the ecosystem, and that they can easily be placed in an ecological model (Christensen and Pauly 1992). *Ecopath* is thus an approach allowing the construction and the rapid evaluation of balanced ecosystem models (Christensen and Pauly 1992). The main advantage of this model is that it makes it possible to use all available data for a given food web and put it in a more global context (Christensen 1991). However, because the information at the ecosystem level is never complete, there is no unique solution for a specific region or period of time. During the last decades, *Ecopath* models were constructed for more than 314 ecosystems, and close to 80 others are presently under development (see Chapter 1 of this thesis). Models were published for ecosystems as diverse as the Peruvian upwelling system (Jarre *et al.* 1991), coral reefs in the Philippines (Aliño *et al.* 1993), the Southern Gulf of Mexico (Arreguín-Sánchez *et al.* 1993), Antarctica (Schalk *et al.* 1993), and Lake Victoria (Moreau *et al.* 1993). This type of modelling was also applied to various uses (comparison of the structure of estuaries (Monaco and Ulanowicz 1997), estimate of the trophic levels (Pauly *et al.* 1995) or the modelling of inundated rice fields in the Philippines (Lightfoot *et al.* 1993).

Most *Ecopath* models constructed so far have been based on a single set of input parameters representing the mean of the model period, typically a given year (Christensen *et al.* 2000). The way we reach a balanced solution from the input datasets consists mainly in modifying manually the parameters so as to obtain mass balance and the outcome represents one of the many possible representations of how the trophic structure of the ecosystem may have been during the period covered. Most of the time, obtaining a balanced network with the *Ecopath* approach is left to trial and error, either in the form of user intervention or Monte-Carlo simulations. However, newer models use features such as autobalance to ease the process.

In its simplest form, the master equation of *Ecopath* defines the mass-balance between consumption, production, and net system exports over a given time period for each functional group (*i*) in an ecosystem (Christensen and Pauly 1992):

$$B_i \left(\frac{P}{B} \right) EE = Y_i + \sum_j B_j \left(\frac{Q}{B} \right)_j DC_{ji} \quad \text{Eq. 2.1}$$

where B_i and B_j are biomasses (the latter pertaining to j , the consumers of i); P/B_i is the ratio of production to biomass, equivalent to total mortality under most circumstances (Allen 1971); EE_i is the ecotrophic efficiency which is the fraction of production (i.e., $P = B(P/B)$) that is consumed within, or caught from the system (by definition between 0 and 1); Y_i is equal to the fisheries catch (i.e., $Y = FB$); Q/B_j is the food consumption per unit of biomass of j ; and DC_{ji} is the contribution of (i) to the diet of (j), and the sum is over all predators (j). Biomass accumulation and migration can also be added to the right hand side of the equation. Each group can have an unknown parameter (B or EE ; P/B or Q/B) that can be estimated by the model. Most often, when the datasets are relatively complete, the EE is left unknown and is then used as a verification parameter to see which compartment of the model does not meet mass balance constraints.

The problem when we build such a model is that the estimates of biomass, production (P/B), consumption (Q/B) and diet composition (DC) do not necessarily result in an ecotrophic efficiency (EE) between 0 and 1, as required by mass-balance constraints. Having an EE higher than 1 for a trophic group means that the sum of predation and the catch for this group is exceeding its biological production.

Traditionally, to reach a balanced solution when building an *Ecopath* model, its designer generally had to modify the diet composition of the major predators of species for which we had an excess of EE . The decision process was mainly based on ecological knowledge of the modeler, but presented the risk of modifying high-quality (= reliable) estimates to balance some that were of lower-quality (Kavanagh *et al.* 2004).

When using a balanced model, it is crucially important to compare model results with observations and to analyze remaining errors. However, it is difficult to distinguish between errors which are related with the model structure and those which are due to the improper choice of parameter values (Schartau *et al.* 2001). Sources of uncertainty are virtually infinite in ecosystem modelling. However, the more we learn about species that are parts of marine ecosystems, the better we can address uncertainty in these systems.

The degree of predictability of ecosystem models is itself uncertain (Hilborn 1987). However, there are many other types of uncertainty that we need to take into account in ecosystem modelling. One of them can be called “predictable uncertainty” (Silvert 2004), which arises from the known stochastic nature of the environment (e.g., climate fluctuation that follows a historical pattern). These fluctuations in the environment, such as El Niño, can be incorporated in the model as a known fluctuation that would affect some species groups (e.g., the primary production).

A more fundamental source of uncertainty (and one much more difficult to take into account) is called “structural uncertainty” (Silvert 2004). Our lack of knowledge on marine ecosystems and fisheries is a good example of that (Gomes 1993). In Canada, for example, there is no consensus on the causes of the collapse of cod stocks. Some authors argue that it was due to intensive exploitation combined with a period of reduced productivity of cod stocks (poor condition and growth, and increased natural mortality) (Dutil *et al.* 1999; Dutil and Lambert 2000). Others believe that the collapse of cod stocks can be attributed solely to overexploitation (Hutchings and Myers 1994; Hutchings 1996). However, a large part of cod mortality remains unexplained in the Gulf of St. Lawrence’s *Ecopath* models. Savenkoff *et al.* (2004a) concluded that much of the unexplained or other mortality in the Northern Gulf of St. Lawrence ecosystem in the 1980s resulted from the under-reporting and discarding of catches. As a result, fishing mortality was substantially underestimated in the mid 1980s, just before the demise of a cod stock that historically was the second largest in the Northwest Atlantic (Morissette *et al.*, Chapter 5 of this thesis).

Sources of uncertainty in fisheries models are presented in a long list by Seijo *et al.* (1998) for the FAO, in an attempt to incorporate risk and uncertainty in bioeconomic modelling and to address some alternative ways of contending with it in a precautionary fishery management context. According to these authors, uncertainty can come from as many sources as abundance estimates, model structure, model parameters, future environment conditions, behaviour of resource users, future management objectives, and economic, political and social future conditions.

Conceptually, it is easy to agree that ecosystem models are designed to fulfill a more complex task than simpler models. However, in practice they may or may not

perform better, because we have too many functional relationships whose true functional forms are poorly known (or not known at all) and too many ecosystem components that we cannot parameterize. On a case-by-case basis, improvements have to be demonstrated, not just asserted as occurring.

Development and evaluation of new ecosystem models have to seek for optimal parameters which remain constant in time, as it is usually assumed (but not always true), in order to fully address uncertainty.

Sensitivity analyses as a tool to address uncertainty

In ecosystem modelling, there are different approaches to reach a balanced scenario. As a result, it is very important to examine how sensitive are the results (or outputs) of the model to changes in the way it was constructed and balanced. Each model constructed must carry on such sensitivity analyses in order to observe if the decisions taken when trying to get a balanced solution for an ecosystem model might conceivably have affected the results. Unfortunately, in *Ecopath* modelling, not all authors are using this approach. Indeed, my observation is that only 20% of published models explicitly present a sensitivity analysis, performed using input parameters.

Inspired by Alderson *et al.* (2004) and their study on review methods for healthcare research, we can describe the types of decisions and assumptions that might be examined in sensitivity analyses, including:

- changing the input parameters to reach the mass-balance constraints of the model;
- compare the efficiency (predictability) of the model with other studies of ecosystem models;
- reanalyzing the data using a reasonable range of possible values as new inputs;
- reanalyzing the data imputing a reasonable range of values for missing data;
- reanalyzing the data using different statistical approaches (e.g., using a random effects model instead of a fixed effect model, or *vice versa*).

Sensitivity analyses are the key to address the consequences of uncertainty, and this is particularly true for ecosystem models.

According to Silvert (2004), there is a general tendency to put too much confidence in ecosystem models, *a priori*. This is why the use of sensitivity analyses has become such an important part of the modelling approach.

The main idea when we use sensitivity analysis in an ecosystem modelling approach is to test if the results are robust or if they are very sensible to small changes in the way the models are constructed, or changes in the value of input parameters, in a way that a trivial change could radically affect the results. The approach that allows testing the performance of the models is called “sensitivity analysis”. In other words, if the sensitivity analyses do not significantly change the results, this strengthens the confidence that can be placed in the model. If the results change in a way that might lead to different conclusions, this indicates a need for greater caution in interpreting the results and drawing conclusions.

After perturbations of the input data within their range of uncertainty, the derived probability distributions are likely to be narrower than the original distributions indicating that we have gained information in the process of checking for mass balance constraints, and eliminating parameter combinations that violate thermodynamic constraints (Christensen and Walters 2004).

Sensitivity can also be a biological phenomenon. Indeed, if we perturb an ecosystem, we cannot be entirely certain of how it will respond. There are some common ecological principles however, which allow us to do general predictions on what could happen (Silvert 2004). For example, if a fish population decrease in abundance, there is a high probability that the ecological niche left by this population will be re-occupied by other species. This happened in the Gulf of St. Lawrence, where the quasi-disappearance of Atlantic cod (*Gadus morhua*) after an intense period of fishing in the 1980s left an empty ecological niche that was quickly filled by forage species such as capelin (*Mallotus villosus*), herring (*Clupea harengus*), sandlance (*Ammodytes dubius*) and Arctic cod (*Boreogadus saida*) (Morissette *et al.*, Chapter 5 of this thesis).

Sensitivity analysis in *Ecopath*

A simple sensitivity routine is included in *Ecopath*, to allow users to explore the effects of uncertainty on the model results. The method is quite simple, and consists in

plotting relative output changes against relative changes in the inputs. However, this does not allow testing of the “structural uncertainty” discussed above.

The routine varies all basic input parameters (biomass [B], production / biomass ratio [P/B], consumption / biomass ratio [Q/B], ecotrophic efficiency [EE]) in steps from -50% to +50% for each species or trophic group of the model, and then checks what effect each of these steps has for each of the input parameters on all of the “missing” basic parameters for each group in the system (Christensen *et al.* 2000). The output is then given as the proportion of the difference between the estimated and original parameter to the original parameter, and converted to a percentage (Christensen *et al.* 2000).

Unfortunately, this method only re-estimate the parameters for which no data was available, and that were left to be estimated by the model, using the mass-balance constraints. If a model uses good data on biomass, consumption and production and has no missing parameter, it is the EE that will be left to be estimated by the model. As a consequence, this becomes the only parameter to be taken into account in terms of impacts of the variation of input parameters on outputs values. The other outputs provided by *Ecopath* (diet composition, catch, mortalities, system’s emergent properties, etc.) can not be evaluated directly by this method, unless a specific routine is made to study this.

The *Ecosim* part of the software (used for temporal simulations) also includes a Monte Carlo routine to find input parameters that minimize the sum of squares with time series. This Monte Carlo simulation interface can be used with initial *Ecopath* biomass estimates chosen from normal distributions centered on the initial input estimates (Christensen and Walters 2004). Each simulation starts with a random biomass combination and re-balancing the *Ecopath* model, keeping only values that result in improved model fit. Such a search or fitting procedure is known as a “Matyas search” (Christensen and Walters 2004). The resulting balanced *Ecopath* model can then be used as the baseline for an *Ecosim* run. This approach is now beginning to be used in many analyses, such as risk evaluation (Pitcher *et al.* 2005a) to evaluate risks of extirpation, depletion, and biodiversity reduction in studied ecosystems.

In addition, Morissette and colleagues developed a complementary methodology with the CDEENA program (work in progress, described briefly in Pitcher *et al.* 2005b) to address uncertainty through temporal simulations. The idea was to construct a model for a

given period of time (in this case, the Gulf of St. Lawrence in the mid-1980s) and another one for the exact same ecosystem, but for a later period (ten years later, in the mid-1990s). The "real" 1990s model would then be compared with a 1990s model obtained after a 10-year simulation of the 1980s model, including functions such as change in fishing effort, or environmental factors (changes in water temperature, ice coverage, El Niño effect, etc.).

Moreover, it is a common misconception to believe that because we have complete databases for some ecosystem models, we can necessarily construct models that are reliable. Indeed, all the input parameters used in models can have very wide ranges of variation. Even when the data are well known, there can still be a lot of uncertainty related to the inputs, and thus, the outputs of the models.

Pedigree and Ecoranger routines

When we compare the different research fields in marine ecology, we quickly realize that charismatic species such as seals or whales are much more studied than invertebrates or parasites. However, when we analyze the ecosystem as a whole, the latter species can become very important in the global response of the system to its environment.

The interactions between the different species and the fishery in a marine ecosystem are complex, generally not well understood, and can become a major source of uncertainty. The interactions that are generally better understood are predator-prey relationships, primarily based on stomach contents analyses. On the other hand, information on production, consumption or mortality sources for each species of the system is usually less understood and thus represents a considerable part of the variability of input values in the marine ecosystems models that we construct.

The pedigree of a model is a summary of the coded statements quantifying the uncertainty related to each input value in *Ecopath* models. For each input that we use in a given model, a choice can be made to describe the kind of data used, and thus the confidence we can have in these data. The routine uses percent ranges of uncertainty based on a set of qualitative choices relative to the origin of biomass, P/B , Q/B , catch and diet input or model estimates (model estimates have a high range of uncertainty) (Table 2.1).

When these choices are made for each single input values, an overall pedigree of the model is calculated as the average of the individual pedigree values (Pauly *et al.* 2000). This overall pedigree is then very useful for comparison with other models (Christensen and Walters 2004), allowing to compare models with a different amount of trophic compartments (and thus with different amount of input values and individual pedigrees). The overall pedigree is calculated as:

$$\tau = \sum_{i=1}^n \frac{\tau_{i,p}}{n} \quad \text{Eq. 2.2}$$

where $\tau_{i,p}$ is the pedigree index value for group i and input parameter p for each of the n living groups in the ecosystem. Parameters (p) can be B , P/B , Q/B , DC or catch data (Christensen and Walters 2004).

The confidence intervals associated to each parameter attributed in the pedigree table can be defined by the constructor of the model or else left to default values (Table 2.1). Specifying the pedigree of data used to generate *Ecopath* input make users aware of the danger of constructing an *Ecopath* model mainly from input taken from other models, but also provides defaults for the Ecoranger routine of *Ecopath* (see below) (Christensen *et al.* 2000). When the pedigree table is complete, models are then implemented with this “quality footprint” that will be unique and make comparisons between models possible, based on single parameters pedigree, or overall pedigree indices.

Table 2.1. Default options for the pedigree routine, for each input parameter used in Ecopath models. Defaults (percentage CI) are means based on actual estimates of CI in various studies. Modified from Christensen *et al.* (2000).

Parameter	Pedigree index	Default CI (± %)
Biomass		
Sampling based, high precision	1.0	10
Sampling based, low precision	0.7	40
Approximate or indirect method	0.4	50-80
Guesstimate	0.0	80
From other model	0.0	80
Estimated by Ecopath	0.0	n.a.
P/B and Q/B ratios		
Same group/species, same system	1.0	10
Same group/species, similar system	0.8	20
Similar group/species, same system	0.7	30
Similar group/species, similar system	0.6	40
Empirical relationship	0.5	50
From other model	0.2	80
Guesstimate	0.1	90
Estimated by Ecopath	0.0	n.a.
Diet compositions		
Quantitative, detailed, diet composition study	1.0	30
Quantitative but limited diet composition study	0.7	40
Qualitative diet composition study	0.5	50
General knowledge for same group/species	0.2	80
From other model	0.0	80
General knowledge of related group/species	0.0	80
Catches		
Local study, high precision/complete	1.0	10
Local study, low precision/incomplete	0.7	30
National statistics	0.5	50
FAO statistics	0.2	80
From other model	0.0	>80
Guesstimates	0.0	>80

For the purpose of this analysis, two ecosystems with very different pedigree indexes are compared. In my database, the model with the lowest pedigree (0.164) corresponds to the Icelandic shelf, for the 1950s (Buchary 2001). Because it tries to reproduce an ecosystem from the past, for which less information is available, most data in this model is guessed, estimated by *Ecopath*, or taken from another model (Table 2.2). Opposed to this is a model for the northern Gulf of St. Lawrence in the 1980s (Morissette *et al.* 2003). This model is mostly based on sampling-based estimates for the exact same species than what is used in the model (Table 2.3). The colour code used in the pedigree routine allows to have a rapid idea of the quality of a model and its inherent data. Shades of blue indicate low quality information, and shades of red refer to high quality data.

Table 2.2. Pedigree of biomass (B), production (P/B), consumption (Q/B), diet and catch inputs for the fish components of the Icelandic shelf ecosystem model for the 1950s constructed by Burchary (2001) with *Ecopath*. The overall pedigree of this model was 0.164.

Species or group	Pedigree				
	B	P/B	Q/B	Diet	Catch
Adult Cod	0.0	0.0	0.2	0.2	0.5
Juvenile Cod	0.0	0.0	0.2	0.0	-
Haddock	0.0	0.0	0.2	0.2	0.5
Saithe	0.0	0.0	0.2	0.2	0.5
Redfish	0.0	0.0	0.2	0.2	0.5
Greenland Halibut	0.0	0.0	0.2	0.2	0.5
Other Flatfish	0.0	0.0	0.2	0.2	0.5
Other Dem. Fish	0.0	0.0	0.2	0.2	0.5
Herring	0.0	0.1	0.2	0.2	0.5
Capelin	0.0	0.0	0.2	0.2	0.5
Other Pelagics	0.0	0.2	0.0	0.2	0.5
Other fish	0.0	0.0	0.2	0.2	-

Table 2.3. Pedigree of biomass (B), production (P/B), consumption (Q/B), diet and catch inputs for the fish components of the northern Gulf of St. Lawrence ecosystem model constructed by Morissette *et al.* (2003) with *Ecopath*. The overall pedigree of this model was 0.651.

Species or group	Pedigree				
	B	P/B	Q/B	Diet	Catch
Large cod	1.0	0.5	0.8	1.0	0.7
Small cod	1.0	0.5	0.8	1.0	0.7
L. Greenland halibut	1.0	0.5	0.8	1.0	0.5
S. Greenland halibut	1.0	0.5	0.8	1.0	-
American plaice	1.0	0.5	0.8	0.7	0.7
Flounders	1.0	0.5	0.8	0.7	0.5
Skates	1.0	0.5	0.8	0.7	0.5
Redfish	1.0	0.5	0.8	0.7	0.7
L. demersals	0.7	0.5	0.7	0.7	0.5
S. demersals	0.7	0.5	0.7	0.0	-
Capelin	0.0	0.8	0.8	0.0	-
Sand lance	0.0	0.2	0.8	0.7	-
Arctic cod	0.0	0.2	0.8	0.7	-
L. pelagics	0.7	0.5	0.7	0.7	0.5
S. pisciv. pelagics	0.7	0.5	0.7	0.7	0.5
S. plankt. pelagics	0.7	0.2	0.7	0.0	0.7

However, even when we have a parameter for which a high pedigree score is assigned, this does not necessarily mean that the range of uncertainty associated with this parameter is small. In the Gulf of St. Lawrence, for example, the biomass estimates come from very detailed sampling survey (such as DFO groundfish survey database that was used for many species of the Gulf of St. Lawrence models, see Morissette *et al.* [2003] for more information) and still, these have quite large confidence intervals. This is also true

for diet composition studies. For example, in the Gulf of St. Lawrence, some inshore and offshore diets had to be combined, or we had to assume that the diet for the 1980s was the same as during the 1990s, or else that the diet for a key species was representative of the functional group (Morissette *et al.* 2003; Savenkoff *et al.* 2004b, c). When aware of such cases, users should change/overwrite the default values in Table 2.1.

Ecoranger is a resampling routine based on input probability distributions for B , P/B , Q/B , EE , DC , and catches, and it uses a Monte Carlo approach. The distribution ranges of each parameter can be entered explicitly for each input or Ecoranger can pick up the confidence intervals from the pedigree tables and use these as prior probability distribution for all input data. After perturbing the input data, the routine attempt to reach a balanced solution that solves the physiological and mass balance constraints (Christensen and Walters 2004). Most of the time, a balanced solution is not found, and Ecoranger proposes a “best unbalanced model” (or *BUM*) that can then be worked on manually. However, when such a situation occurs, it does not necessarily means that there is no balanced solution available for the input ranges of possible values. After running the same inputs through other perturbation methods (see inverse approach, in a section below), many models ended up having more than one possible balanced solution, that were just not found by the Ecoranger processes (L. Morissette, unpublished data for the northern Gulf of St. Lawrence model).

Because uncertainty changes with models' quality, I got very different results for the Ecoranger runs with the low-pedigree and the high-pedigree models (Table 2.4). For each model, the routine was set to reach a total of 200 successful runs, and to have a maximal number of 10,000 runs in total. The routines included a randomization process (random seed), and the selection criteria for best model was to minimize the sum of squared residuals.

For the Icelandic shelf model, because of the high ranges of uncertainty surrounding data, the model was able to reach 200 balanced solutions after 430 attempts. On the other hand, the Northern Gulf of St. Lawrence model only got to 18 balanced solutions after reaching the maximum 10,000 runs. This happened because all data with a high pedigree had very narrow ranges of possible variation. It was thus difficult for Ecoranger to find different balanced solutions. The more confident we are in the data, the

highest the pedigree is, and the most constant the model will be. This is also true for the minimum residuals (Table 2.4), which are very high for the low-pedigree model showing a highest uncertainty, and relatively low for the high-pedigree model that reflects lowest uncertainty.

Table 2.4. Ecoranger results for two models with different pedigrees.

Model	Pedigree index	Total runs	Number of balanced solutions	% of success	Minimum residuals
Low pedigree (Icelandic shelf in the 1950s; Buchary 2001)	0.164	430	200	46.51	7571
High pedigree (Northern Gulf of St. Lawrence in the 1980s; Morissette <i>et al.</i> 2003)	0.651	10,000	18	0.18	111

The Ecoranger routine also produces a summary of what went wrong in the rejected runs. For each rejected runs, the potential failure criteria are:

1. $EE > 1$
2. Production/consumption is too high
3. $EE < EE_{min}$ or $EE > EE_{max}$. EE may have been recalculated and thus can have changed
4. Output parameter is outside the range
5. Electivity outside range
6. Detritus $EE > 1$

For the Icelandic shelf and the Gulf of St. Lawrence models, the first 50 failed runs were all caused by the fact that P/Q was too high (Table 2.5). According to Christensen and Pauly (1992), the gross growth efficiency (GE, or the ratio of production to consumption) should have values between 10 and 30% for most trophic groups. Exceptions are top predators, e.g., marine mammals and seabirds, which can have lower GE (between 0.1 and 1%), and small, fast growing fish larvae, nauplii or bacteria, which can have higher GE (between 25 and 50%).

Table 2.5. Parameters causing failure for the first 50 runs of Ecoranger, with the related problematic value of each criterion.

Icelandic shelf			Northern Gulf of St. Lawrence		
Criterion	Group	Value	Criterion	Group	Value
2	Other pelagics	0.770	2	Large demersals	0.770
2	Other pelagics	1.034	2	Large demersals	1.034
2	Other fish	0.634	2	Large pelagics	0.634
2	Juvenile cod	0.638	2	Seabirds	0.638
2	Redfish	0.669	2	Large Greenland halibut	0.669
2	Northern shrimp	0.781	2	Capelin	0.781
2	Northern shrimp	0.743	2	Capelin	0.743
2	Other pelagics	0.714	2	Large demersals	0.714
2	Northern shrimp	0.913	2	Capelin	0.913
2	Other pelagics	0.635	2	Large demersals	0.635
2	Zooplankton	0.629	2	Small piscivorous pelagics	0.629
2	Juvenile cod	0.781	2	Seabirds	0.781
2	Molluscs	0.616	2	Sand lance	0.616
2	Other fish	0.658	2	Large pelagics	0.658
2	Other pelagics	1.070	2	Large demersals	1.070
2	Nephrops	0.748	2	Small demersals	0.748
2	Juvenile cod	0.779	2	Seabirds	0.779
2	Other pelagics	0.688	2	Large demersals	0.688
2	Redfish	0.607	2	Large Greenland halibut	0.607
2	Northern shrimp	0.632	2	Capelin	0.632
2	Other flatfish	0.698	2	American plaice	0.698
2	Juvenile cod	0.871	2	Seabirds	0.871
2	Other pelagics	0.721	2	Large demersals	0.721
2	Northern shrimp	0.853	2	Capelin	0.853
2	Other pelagics	1.113	2	Large demersals	1.113
2	Other pelagics	0.638	2	Large demersals	0.638
2	Juvenile cod	0.708	2	Seabirds	0.708
2	Nephrops	0.739	2	Small demersals	0.739
2	Other pelagics	0.654	2	Large demersals	0.654
2	Other flatfish	0.787	2	American plaice	0.787
2	Northern shrimp	0.667	2	Capelin	0.667
2	Northern shrimp	0.913	2	Capelin	0.913
2	Juvenile cod	1.143	2	Seabirds	1.143
2	Northern shrimp	0.611	2	Capelin	0.611
2	Other flatfish	0.686	2	American plaice	0.686
2	Juvenile cod	0.802	2	Seabirds	0.802
2	Other flatfish	0.622	2	American plaice	0.622
2	Other pelagics	0.604	2	Large demersals	0.604
2	Zooplankton	0.865	2	Small piscivorous pelagics	0.865
2	Greenland halibut	0.691	2	Small Greenland halibut	0.691
2	Zooplankton	0.647	2	Small piscivorous pelagics	0.647
2	Zooplankton	0.971	2	Small piscivorous pelagics	0.971
2	Juvenile cod	0.751	2	Seabirds	0.751
2	Zooplankton	0.651	2	Small piscivorous pelagics	0.651
2	Northern shrimp	0.607	2	Capelin	0.607
2	Juvenile cod	0.965	2	Seabirds	0.965
2	Other fish	0.700	2	Large pelagics	0.700
2	Nephrops	0.739	2	Small demersals	0.739
2	Zooplankton	0.810	2	Small piscivorous pelagics	0.810
2	Redfish	0.805	2	Large Greenland halibut	0.805

The main advantage of the Ecoranger routine is that it will change all parameters at once within the confidence interval limits defined by the constructor of the model. However, this method is not used a lot, and many users have encountered troubles using this routine (A. Bundy, Department of Fisheries and Oceans, Bedford Institute of Oceanography; and J.J. Heymans, University of British Columbia, Fisheries Centre; pers. comm.). Some authors mention that, indeed, the results of this procedure can be confusing and reverted to standard manual methods for most of their analyses (Silvert 2004).

Autobalance

An important step was done addressing uncertainty in *Ecopath* models with the *Comparative Dynamics of Exploited Ecosystems in the Northwest Atlantic (CDEENA)* program in 2003. Within this program, a total of 10 *Ecopath* models were constructed for 2 periods (the 1980s, prior to the collapse of groundfish species; and the 1990s, after that decline) and 5 different ecosystems: the Grand Banks of Newfoundland (NAFO zones 2J3KLNO), the eastern and western Scotian shelves (NAFO zones 4VsW and 4X), and the northern and southern Gulf of St. Lawrence (NAFO zones 4RS and 4T) (Figure 2.1)

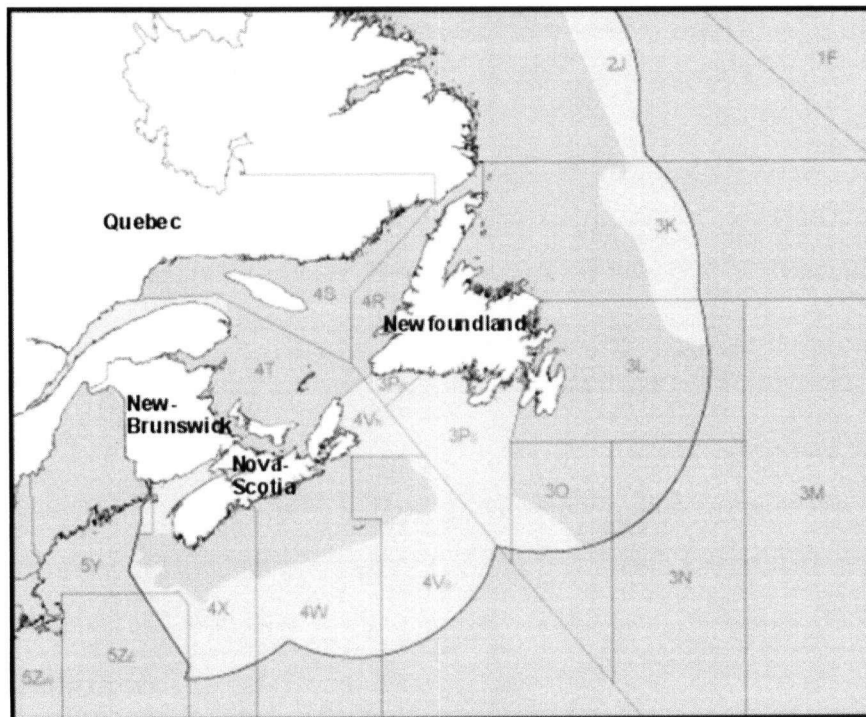


Figure 2.1. The Northwest Atlantic areas studied by the *CDEENA* program for ecosystem modelling.

The “autobalance” routine of *Ecopath* is a new parameter optimization for ecosystem models. This tool is used mainly to obtain reproducible mass-balanced models from an unbalanced state (Kavanagh *et al.* 2004), but can also be used (as it is the case here) for perturbation analyses in order to assess uncertainty associated with certain models. The *CDEENA* program represents the first case study where such an approach was used in an attempt to fully address uncertainty in *Ecopath* modelling.

Autobalance is an algorithm that allows reaching mass-balance constraints of *Ecopath* in a quantitative way. This routine should be used jointly with the traditional manual balance process which is way more informative (and can take ecological knowledge of the modeler into account).

Autobalance is a structured way (as opposed to the traditional manual approach) to use input data and get to a balanced solution for an ecosystem model, based on clear assumptions. The routine uses the uncertainty definitions associated to data provided in *Ecopath*, which are described by the pedigree (see section above on pedigree), and then apply perturbations (within these uncertainty ranges) to the data based on the degree of confidence we have in them. Perturbations on parameters with better pedigree (that we know more about) should be less important than the ones on parameters with lower pedigree. This assumes that if we know less about these parameters, there is a better chance they can have a different value than the one provided in the model.

The main objective of the autobalance process is to obtain a model for which the *EE*'s are all below one, without exceeding the confidence intervals on diet compositions or biomass. The method also allows choosing the magnitude of perturbations according to the amount of reduction needed to reach $EE < 1$ (Kavanagh *et al.* 2004). Unfortunately, only *DC* and *B* parameters are presently modified with this routine. Kavanagh *et al.* (2004) explain that they allow only *DC* and *B* to be varied, as these parameters are generally the most uncertain. However, there are models where the quality of information (i.e., the pedigree) is much better (and thus, values have narrower confidence intervals and more certain) for *B* or *DC* than it is for parameters such as *P/B*, *Q/B* or catch (L. Morissette, unpublished data). This is in fact the case for many models, such as a Caribbean coral reef (Opitz 1996), a lake of Sri Lanka (Moreau *et al.* 2001), the West

Florida shelf (Okey *et al.* 2004), or the coast of Guinea (Guénette and Diallo 2003). In these cases, when B or DC is well known, the magnitude of perturbations is reduced, and the sensitivity analysis can be less robust.

When used as an uncertainty analysis, the autobalance routine presents some limitations. Firstly, $EE < 1$ is the only hard constraint to achieve mass-balance in the autobalance process. Moreover, the approach only deals with parameters affecting species that are unbalanced. This means that not all parameters are perturbed in such an uncertainty analysis and not all species as well.

For the *CDEENA* models, 30 alternate models were created with the autobalance by perturbing the input B and DC within their pedigree confidence intervals, and then re-balanced by the automated process. Ranges of possible values used for pedigree information are fully described in Morissette *et al.* (2003), Heymans (2003), Bundy (2004), and Savenkoff *et al.* (2004b, c).

The re-balance process was not checked for ecological logic, as a complete model construction and balance would be. Thus, the 30 alternate solutions represent balanced scenarios, but may be incorrect. Since the new solution is within the confidence intervals of all parameters entered, the solution can be as logical as a manually fixed model.

Each run started with a different set of conditions, and the routine searched for the combination that will produce a balanced model. The autobalance routine was programmed to run for 10,000 runs in order to reach this target (Bundy 2004). The thirty solutions were used to define 95 % confidence intervals for the model estimates, giving an idea of the uncertainty associated with the model output.

One other weakness of this method is that only biomass and diet composition were perturbed to create a range of possible alternative scenarios for these ecosystems. The consumption and the production were not changed, but we know that these parameters can be uncertain for each species in a given ecosystem.

Finally, the uncertainty analysis consisted in comparing the two models (for the mid-1980s *versus* the mid-1990s); with confidence intervals generated from the 30 autobalance runs. We then determined whether differences between models were plausible, or artifacts created by the uncertainty of the input parameters.

Even if this method has some weaknesses, it is the first time an attempt has been made to address uncertainty in a structured way when comparing *Ecopath* models. Thus, incorporating the autobalance into an ecosystem comparison process is already a huge step forward to understand changes between models. Part of the weaknesses of the approach presented in this section were however addressed in the new method used by Morissette *et al.* (see Chapter 5 of this thesis) for the Gulf of St. Lawrence, part of the same *CDEENA* program.

A step further: combining Ecopath with other modelling approaches

There is a real advantage to using different approaches on the same data to ascertain the robustness of inferred differences between periods and among ecosystems, as done by Morissette and colleagues (Chapter 5 of this thesis) for the *CDEENA* program on ecosystem modelling. To obtain a balanced solution as well as to test the sensibility of the models, *Ecopath* was coupled with the inverse approach for the analysis of four Gulf of St. Lawrence models (one model for the northern Gulf, one model for the southern Gulf, both for the mid-1980s and the mid-1990s).

The use of inverse modelling to find balanced food-web solutions provided a substantial improvement in objectivity and quantitative rigor compared to previous ecosystem modelling approaches using only *Ecopath*, with or without its autobalance routine. This method solved the flows of the different mass-balance equation by minimizing the imbalances between inputs and outputs. This inverse approach provided a global criterion for an optimal (balanced) solution (Parker 1977; Enting 1985; Vézina and Platt 1988; Vézina *et al.* 2000; Savenkoff *et al.* 2001).

In addition to the basic steady-state constraints of ecosystem models, additional constraints had to be added to obtain a meaningful solution. Each flow was taken to be non-negative and the flows and ratios of flows (metabolic efficiencies) were assumed to fall within certain ranges to satisfy basic metabolic requirements. Gross growth efficiency (*GE*) is the ratio of production to consumption and for most groups should have values between 0.1 and 0.3 (Christensen and Pauly 1992). Exceptions were top predators, e.g., marine mammals and seabirds, which can have lower *GE*, and small, fast growing fish

larvae or nauplii or bacteria, which can have higher *GE* (Christensen and Pauly 1992). Following Winberg (1956), 80% of the consumption was assumed to be physiologically useful for carnivorous fish groups while the non-assimilated food (20% consisting of urine and feces) was directed to the detritus. For herbivores, the proportion not assimilated could be considerably higher, e.g., up to 40% in zooplankton (Christensen and Pauly 1992). Assimilation efficiency (*AE*) was also constrained to fall between 70 and 90% for all the groups except for large and small zooplankton (between 50 and 90%) (Savenkoff *et al.*, in press *a*).

Certain flows have a minimal and maximal value imposed (export for detritus, production, consumption, diet composition, etc.). The production and consumption values that were not estimated from local field studies were used as constraints. To avoid a model that was too severely constrained (constraints on production, consumption, and growth efficiency), we constrained growth efficiency and either production or consumption depending on data availability (e.g., confidence level and local sampling). Diets with reasonable estimates of uncertainty (SD greater than 0.6%) were also specified as constraints. To facilitate comparisons with other *Ecopath* models, constraints were also added on the *EE* (Savenkoff *et al.*, in press *a*).

When the system of equations was strongly underdetermined, additional constraints (inequality relations) were added to constrain the range of possible solutions and thus to obtain a meaningful solution. The mass-balance equations and the additional constraints reduced the potential range of flux values, and trophic flows were estimated using an objective least-squares criterion for an optimal (balanced) solution (sum of flows in the system is as small as possible). The solution process thus generated the simplest flow network that satisfied both the mass conservation and constraints. The best solution was the model that produced the smallest sums of squared residuals for the compartmental mass balances. The solution minimized the imbalances between inputs and outputs. The mass balance was closed by residuals (inputs-outputs) instead of ecotrophic efficiencies as in the *Ecopath* approach (Savenkoff *et al.* 2004c; Savenkoff *et al.* in press *b*). These operations were done with the Optimization Toolbox in the Mathlab® software, and the equations solution process is fully described in the work of C. Savenkoff (Savenkoff *et al.* 2004c; Savenkoff *et al.* in press *a, b*).

To assess the solution's robustness to variations in the data, random perturbations were applied to both input data and right-hand sides of the mass balance equations. A total of 31 balanced solutions corresponding to 31 random perturbations (including a response without perturbation) on each model input to a maximum of its standard deviation was used for each model. A more complete description of these balanced scenarios is given in Savenkoff *et al.* (2004a) for the northern Gulf of St. Lawrence and in Savenkoff *et al.* (in press b) for the southern Gulf of St. Lawrence models. Each of the 31 balanced inverse solutions were then transposed into *Ecopath* to obtain the fishing mortality, predatory mortality, and other mortality, as well as the basic emergent estimates and network analysis indices of the two time periods, combined with their associated uncertainties. The confidence intervals generated by the 31 balanced solutions allowed a comparison of many indices between the two ecosystems (northern and southern Gulf) and/or time periods (mid-1980s or mid-1990s) (Morissette *et al.*, Chapter 5 of this thesis).

Using conjointly inverse and *Ecopath* modelling approaches represent a useful strategy in ecosystem modelling, each tool supplying the other with optimized solutions. The inverse model is very useful to obtain a first balanced solution and to supply *Ecopath* with diet compositions and efficiencies (metabolic and ecotrophic) using an objective least-squares criterion. This approach also generates complete perturbations on all input parameters for sensibility analyses. The *Ecopath* model is then used for its strengths to estimate biomass of each groups, generate global ecosystem indices such as network analyses or emergent properties of ecological systems. An approach combining the two modelling methods thus gains robustness and represent an important step further in the comparison of marine ecosystem models through time or space.

Conclusions

Uncertainty and variability are inherent with ecosystem modelling. Therefore we need to use appropriate tools to define, represent and analyze this uncertainty. *Ecopath* is only one of the many approaches that are used worldwide for ecosystem modelling. Within this sole approach, many tools has been created and used –with more or less success– to address uncertainty. Despite the fact that there has been no comprehensive study published so far on *Ecopath* or *Ecosim* parameter sensitivity, my analysis proposes

that the combination with other modelling approaches, in order to use the strengths of each approach and thus gain more robustness, is the best way to address uncertainty and parameter sensitivity for these ecosystem models.

Chapter summary

Ecosystem modelling has become a very important way to study marine ecosystems processes, but at the same time few studies have addressed the uncertainty related to model results. This lack of information about how confident we can be in our modeling outcomes poses serious problems, as many sources of uncertainty exist. A valuable tool for model development is the use of the software package *Ecopath with Ecosim*, which enables the construction of foodwebs and their simulation over time and space according to different scenarios. An important part of the process of ecosystem modelling is to compare results from the model with those from observations, followed by an analysis of the remaining sources of error. However, few of the currently developed *Ecopath* models have gone so far as to examine the uncertainty in analyses. Thus, it is useful to address this problem, to clearly define the type of uncertainty that may be encountered in ecosystem modelling, and the means by which it may be handled. Sensitivity analyses represent one solution by which one might address uncertainty in *Ecopath with Ecosim*. This approach functions by examining the sensitive elements as revealed in model results with differing scenarios of model-building and construction. In addition, other tools can also be used to perform uncertainty analysis routines. Examples are the Pedigree, Ecoranger, Autobalance, and Monte Carlo tools, all of which are included in the *Ecopath with Ecosim* software package. The strengths and weaknesses of these different ways to address uncertainty are discussed. Finally, I propose a new approach, combining *Ecopath* with other modelling techniques in order to get an even stronger analysis of uncertainty.

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Chapter 3

Data quality and complexity in ecosystem models: does it affect resilience and model performance?

Introduction

In the past decades, biodiversity has experienced a major decline all over the planet, and increasing numbers of animal and plant species are at risk of extinction (McCann 2000). In the world's oceans, overfishing has strongly altered marine food webs, in some cases resulting in the large fish that were commercially exploited being depleted and replaced by smaller, less desirable species (Pauly *et al.* 1998). Combined with a massive degradation of the marine habitat (Chabanet *et al.* 2005), this situation threatens marine ecosystems and undermines the stable extraction of vital economic resources from the ocean (Nixon 1997). This problem is an important one, and forces us to examine in details how ecosystems work. There is, in fact, a need to understand how the ecosystems would react to decreases in biodiversity, as well as to other perturbations.

For many years, there has been a debate focusing on the question whether simple ecosystems are less stable than complex ones. To date, studies addressing the “diversity-stability debate” (McCann 2000) have yielded ambiguous results. Theoretical studies have generally supported the notion of a negative relationship between stability and complexity (May 1972; Gilpin 1975; Pimm and Lawton 1978; Hogg *et al.* 1989). Most of the time, these theories were based on mathematical models constructed using parameters drawn randomly from a statistical universe (McCann 2000). A negative complexity-stability relationship was also proposed by Kohdoh (2003), based on adaptive foraging behaviour. Conversely, in nature, studies have shown that trophic links can be connected in a way that enhances foodweb stability (Lawlor 1978, Yodzis 1981; Neutel *et al.* 2002).

It seems that empirical models assembled from real food-webs relationships, with plausible interaction strengths, are generally more stable than randomly constructed food webs (Yodzis 1981; Walters *et al.* 1997). Pauly *et al.* (2000), who presented preliminary data suggesting such a link, suggested that if the existence of such a link between model

quality and persistence could be confirmed, this would have profound implications for our understanding of ecosystem functioning and the research required for ecosystem-based management.

This issue has probably been one of the most controversial in ecology, but most studies devoted to this topic focus on terrestrial systems (Steele 2006). However, considering that the oceans occupy 71% of the surface of biosphere and probably much more in terms of volume (Groombridge and Jenkins 2000), that they are responsible for almost half of the Earth's net primary production (Schlesinger 1997), that more than half the world's population lives within 60 km of the sea, and that marine fisheries can consume up to 35% of the net primary production on shelves (Pauly and Christensen 1995), it is important to examine the relationship between complexity and stability in a marine ecosystem context as well (Naeem 2006).

This project represents the first study describing complexity/stability relationships using many marine ecosystems models based on realistic parameter values, and examining the impact of model quality on these relationships. I intend to provide insights on the relationship between diversity and stability by testing whether the quality of data used in ecosystems models, and/or the details of the models used, are related to their stability.

Thus, the main hypothesis to be tested in this study addresses an important theoretical ecology issue: is there, in ecosystems, a direct relationship between complexity and stability. My secondary hypothesis is that the quality of ecosystem model inputs also plays a significant role in predicting the relationship between complexity and stability.

To test these hypotheses, I chose to use an ecosystem modelling approach. Ecosystem modelling becomes more and more important in fisheries science, particularly for studying the properties of food webs. The *Ecopath with Ecosim* (EwE) approach allows the construction and validation of food webs (Christensen and Pauly 1992). In addition to making food web and other ecosystem analyses possible, the EwE approach allows researchers to collect and treat a variety of biological information that is available for an ecosystem and put it in a more global perspective. Since J.J. Polovina (1984) proposed the *Ecopath* approach and software in the early 1980s, many models have been created all over the world (see chapter 1), for different ecosystem and purposes. Having a plausible description of an ecosystem is very important, especially to test hypotheses at an

ecosystem scale, and for comparisons among ecosystems. Here, it is proposed to standardize the description of *EwE* models published so far and to describe the quality of input data used for their construction.

A criticism of ecosystem comparisons is that we try to “compare apples and oranges”, i.e., that ecosystems are different entities that are fundamentally incommensurable. However, it is easy to compare apples and oranges, which may differ in price, vitamin or water content, color spectrum, etc. (Pauly 2000). Similarly, it is equally possible to compare ecosystems for variables that they share (Downing 1991). In fact, ecosystem comparisons are an important, if underutilized, tool for ecologists. Indeed, many of the scientist recognized as the discoverers of major concepts in ecology, such as Charles Darwin (evolution through natural selection), Alexander von Humboldt (botanical geography and biogeography) and Ernst Haeckel (ecology, as the study of the relationship of organisms with their environment), compared and contrasted the components of ecosystems which lead to important hypotheses, and ultimately, theories (Downing 1991).

Material and methods

3.2.1 Ecopath models and their pedigree

Comparisons were carried out with 50 *Ecopath* models (Table 3.1). Each selected model was linked with a publication (thesis, peer-reviewed article, book chapter or report) where data sources were described in details.

Table 3.1. List of *Ecopath* models used for the present study.

Location	Reference
Antarctica, Weddell Sea, 1980s	Jarre-Teichmann <i>et al.</i> 1997
Australia, Darwin Harbour, 1908s	Martin 2005
Australia, South East Shelf Fishery, 1994/2043	Bulman <i>et al.</i> 2006
Burundi, Lake Taganyika, 1974-1976	Moreau <i>et al.</i> 1993a
Burundi, Lake Taganyika, 1980-1983	Moreau <i>et al.</i> 1993a
Canada, Northern Gulf of St. Lawrence 1985-1987	Morissette <i>et al.</i> 2003
Canada, Southern Gulf of St. Lawrence, 1985-1987	Savenkoff <i>et al.</i> 2004; Savenkoff <i>et al.</i> (in press)
Canada, Newfoundland, Grand Banks, 1900	Heymans and Pitcher 2002a
Canada, Newfoundland, Grand Banks, 1985-1987	Bundy <i>et al.</i> 2000
Canada, Newfoundland, Grand Banks, 1985-1987	Heymans and Pitcher 2002b
Canada, Newfoundland, Grand Banks, 1995-1997	Heymans and Pitcher 2002b
Canada, Eastern Scotian Shelf, 1980-1985	Bundy 2004
Canada, Eastern Scotian Shelf, 1995-2000	Bundy 2004
Canada, Hecate Strait, 1990s	Beattie 2001
Canada, Lake Ontario, 1983-1993	Halfon and Schito 1993
Caribbean, Puerto Rico-Virgin Islands shelf, 1990s	Opitz 1996
Denmark, Faroe Islands, 1961	Zeller and Reinert 2004
Denmark, Faroe Islands, 1997	Zeller and Freire 2001
France, Lac d'Ayda, 1988-1989t	Reyes-Marchant 1993
France, Bay of Biscay, 1970s	Ainsworth <i>et al.</i> 2001
France, Bay of Biscay, 1990s	Ainsworth <i>et al.</i> 2001
French Polynesia, Moorea Island, fringing reef, 1971-1985	Arias-González <i>et al.</i> 1997
French Polynesia, Moorea Island, barrier reef, 1971-1985	Arias- González <i>et al.</i> 1997
Galápagos, Floreana rocky reef, 1997-2000	Okey <i>et al.</i> 2004
Greenland, West coast, 1997	Pedersen and Zeller 2001
Guinea marine ecosystem, 1998	Guénette and Diallo 2004

Table 3.1 (contd.)

Iceland Shelf, 1950s	Buchary, 2001
Iceland Shelf, 1997	Mendy and Buchary 2001
Israel, Lake Kinneret, 1980-1990	Walline <i>et al.</i> 1993
Kenya, Lake Victoria, 1971-1972	Moreau <i>et al.</i> 1993b
Kenya, Lake Nakuru, 1972	Moreau <i>et al.</i> 2001a
Mauritania EEZ, 1998	Sidi and Guénette 2004
Mexico, Celestun Lagoon, 1990s	Chavez <i>et al.</i> 1993
Mexico, Tamiahua Lagoon, early 1990s	Abarca-Arenas and Pacheco 1993
Mexico, Northwest Mexico, 1990s	del Monte-Luna 2004
Morocco, Atlantic coast, mid-1980s	Stanford <i>et al.</i> 2001
New Caledonia, Western tropical Pacific, 2001	Godinot and Allain 2003
Philippines, Laguna de Bay, 1968	Delos Reyes and Martens 1993
Philippines, Laguna de Bay, 1980	Delos Reyes and Martens 1993
Philippines, San Miguel Bay, 1979-1982	Bundy 1997
Philippines, Wetland Ricefield, 1990s	Lightfoot <i>et al.</i> 1993
Portugal, Azores archipelago, 1997	Guénette and Morato 2001
South Africa, Northern Benguela, 1990s	Heymans and Baird 2000
Sri Lanka, Prakrama samudra, 1980=1990	Moreau <i>et al.</i> 2001b
Taiwan, Chiku Lagoon, 1990s	Lin <i>et al.</i> 1999
Uganda, Lake George, 1970s	Moreau <i>et al.</i> 1993c
United Kingdom, Scotland's west coast, 2000-2005	Morissette and Pitcher 2005
USA, Alaska, Prince william Sound, pre-spill period, 1980-1989	Dalsgaard and Pauly 1997
USA, Alaska's Prince William Sound, 1994-1996	Okey and Pauly 1999
USA, Atlantic Continental Shelf, 1995-1998	Okey and Pugliese 2001
USA, Mid-Atlantic Bight, 1995-2005	Okey 2001
USA, Southwestern Alaska, Bercharof Lake, 1982-1998	Mathisen and Sands 1999
USA, West Florida Shelf, 1997-1998	Okey and Mahmoudi 2002
Zimbabwe, Lake Kariba, 1975-1976	Machena <i>et al.</i> 1993

First, the pedigree was calculated for each model, describing its overall quality. The pedigree of an *Ecopath* input is a coded statement categorizing the origin and quality of a given input (Christensen *et al.* 2000; see Table 3.2 for an example of the available choices for the quality of biomass input).

Table 3.2. Default options for the pedigree of biomass used in Ecopath models. Defaults (Percentage confidence intervals [CI]) are means based on actual estimates of CI in various studies. Modified from Christensen *et al.* (2000).

Parameter	Pedigree index	Default CI (\pm %)
Sampling based, high precision	1.0	10
Sampling based, low precision	0.7	40
Approximate or indirect method	0.4	50-80
Guesstimate	0.0	80
From other model	0.0	80
Estimated by Ecopath	0.0	n.a.

After documenting and coding every input for each trophic group in a given model, an overall pedigree index for this model is obtained. The routine computes an overall index of model 'quality'; a model is of high quality when it is constructed mainly using precise estimates of various parameters, based on field data obtained from the system to be represented by the model. The pedigree index values can range from zero for a model that is not rooted in local data up to one for a model that is fully rooted in local data (Christensen *et al.* 2000). After the pedigrees were calculated for each of my 50 selected models, I contacted the authors in order to corroborate the choices taken to describe the pedigree of each input data, and therefore validate the final pedigree of their models.

3.2.2 Costs of computing trophic interaction in Ecopath models

Another measure of quality can be identified for ecosystem models: the costs of their construction. Costs can be direct, such as the time and salary it would take for a person and/or a group to construct and validate a model; but they can also be indirect. By indirect costs, I mean the data requirements, i.e., the research that was done before and that is used as input information in the model, as embodied in publication of various types. Estimating these costs is not an easy task (Pauly 1995), but objective bibliometric

indicators (e.g., the number of citations it generates) can be used to assess the value of scientific research (Nederhof and Noyons 1992).

Fisheries science has been subject to few bibliometric studies. To assess the diverse nature of the different publications used to construct a model, they were classified into categories, based on Rounsefell (1961) index of relative publication. This index was used previously by Dizon and Sadorra (1995) for quantifying scientific productivity, while accounting for different types of publications, i.e., peer-reviewed journal articles (category A in Table 3.3), reports (B and D), newsletter articles (E and F), etc. These categories proved helpful for understanding the reasons for difference in embodied modelling costs among the different types of sources used for the construction of models.

As an example, Pauly (1995) reviewed the costs of scientific productivity from various sources in fisheries science, and estimated the costs of a scientific paper to be about US\$ 1,000 per page, with higher values for international refereed journals and lower values for technical reports. Given this estimation of US\$ 1,000 per page in 1995 for fisheries sciences, one credit, in that specific case, would represent US\$ 100.

Table 3.3. Relative value of publication by types as used in this study (from Rounsefell 1961).

Categories	Type of publications included	Credit per page
Category A	Original research requiring extensive analysis or original thought published in a scientific journal, or as a textbook or reference of college level. May include articles describing original techniques and apparatus.	10
Category B	Research employing known techniques such as stream surveys, censuses, routine sampling when analysis is not extensive. Includes doctoral dissertations, revisions of textbooks or references, and taxonomic descriptions, keys, or reviews.	5
Category C	Narrative and informal reports of scientific merit not requiring analysis. Includes general books or chapters on conservation, encyclopedia articles, and technically correct information bulletins.	3
Category D	Reports designed to make raw data available, which may include short descriptions of methods and procedures but no analysis. Includes bibliographies, faunal lists, and glossaries.	0.5
Category E	Semi-popular and popular articles, short descriptions of research programs, summaries of research accomplishments.	2
Category F	Short faunal notes on species range, etc., critical book reviews, articles published only as abstracts, technical research notes in annual laboratory or commission journals but not in newspapers.	2

An important reason for classifying the different bibliographic sources used to construct ecosystem models into these six categories is to evaluate the relative value of different sources of information. Thus, I believe that using an embodied cost in terms of credits represents a way of adding up all publications and pages used to construct an ecosystem model on a comparable value criterion, whatever the publication date or the currency is.

3.2.3 Quantifying the complexity of models

The *Ecopath* methods allow the calculation of many indices that can describe the complexity of the community structure (Christensen 1995). The attributes were chosen according to a previous study by Vasconcellos *et al.* (1997), who identified ascendancy, connectance index and system omnivory index as representative of Odum's (1971) attributes of ecosystem complexity.

The ascendancy (A) of a food web is a measure developed from Ulanowicz as a measure of the network's potential for competitive advantage over other network configurations (Ulanowicz, 1986). It is computed by *Ecopath* as the product of 'total system throughput' and the mutual information inherent in the flow network (Field *et al.* 1989). When divided by the system's capacity (Ca), the relative ascendancy (A/Ca), a dimensionless ratio that excludes the influence of total system throughput and is a suitable index for comparing different ecosystems (Heymans and Baird 2000). It should increase as it matures through a series of development stages (Ulanowicz 1986).

The connectance index (C) represents the number of actual trophic links in the food web relative to the number of possible links. Consider a contingency table showing all possible trophic interactions in an ecosystem, with r rows (e.g., prey species) and c columns (e.g., predators). Connectance is calculated as:

$$C = \frac{I}{r * c} \quad \text{Eq. 3.1}$$

where I is the total number of non-zero elements in the matrix.

The connectance index does not use the strength of the flows in its calculation, but is only based on the presence or absence of trophic links. Pimm (1982) defined an omnivore as a 'species which feeds on more than one trophic level'. In *Ecopath*, an index

called system omnivory index (*SOI*) is computed based on the average omnivory index (*OI*) of all consumers weighted by the logarithm of each consumer's food uptake (Christensen and Pauly 1992). This was inspired by perceived drawbacks of the connectance index. Indeed, the connectance index is strongly dependent on how the groups of the system are defined. As this is quite arbitrary in aquatic systems, where interactions of nearly all groups are possible at some development stage, connectance would be close to one in most systems that are well described. Moreover, a prey would have the same 'score' in the connectance index whether it contributes 1, 10 or 100% of its predators' diet. Both of these drawbacks are overcome by the system omnivory index, which is computed as the variance of the trophic levels of a consumer's food groups. According to Christensen *et al.* (2000), the use of this index is recommended to characterize the extent to which a system displays web-like features. The omnivory index can be calculated as:

$$OI = \sum_{j=1}^n (TL_j - TL_{prey})^2 * DC_{ij} \quad \text{Eq. 3.2}$$

where i is the predator, j the n^{th} prey, TL_j is the trophic level of a predator, TL_{prey} is the average trophic level of n prey species of i and DC_{ij} is the diet composition, expressing the fractions of each i in the diet of i .

Finally, the Finn's cycling index (*FCI*; Finn, 1976) is the fraction of an ecosystem's throughput that is recycled. This index utilizes the Leontief matrix to assess the amount of material cycling within an ecosystem, and is calculated as:

$$FCI = \frac{T_{cyc}}{T_i} \quad \text{Eq. 3.3}$$

where $T_{cyc} = \sum_{i=1}^n z''_{ii}$ = the portion of total system throughput (TST) which represents recycled flow, and z''_{ii} = the total flow from i which returns to i (without recycling through i en route) over all pathways of all lengths. The *FCI* varies from 0 (no cycling) to 1, and is also an indicator of system's maturity (Odum 1969; Christensen 1995).

3.2.4 Dynamic simulations of ecosystem's stability with Ecosim

Pimm (1991) defined a stable ecosystem as persistent, resistant and resilient. I used *Ecosim* to simulate the stability of the ecosystems after a major perturbation of the system. The resilience refers to the 'elasticity' of the ecosystem's structure, but also to the speed and power of recuperation when an ecosystem is displaced from its equilibrium. This was here calculated as the total time of the simulation (100 years), minus the duration (in years) within which the system returned to its previous equilibrium after a perturbation, if it did. Biomass of a key species was used to calculate resilience. The persistence of an ecosystem refers to the time a variable (here a species' or group's biomass) lasts before it is changed to a new value. In my analysis, this value was calculated in years after the simulated perturbation. Finally, the term 'resistance' expresses the notion of ability to withstand perturbation, and is calculated here as a quantitative index of the ecological consequences in the ecosystem resulting from a permanent change in a variable (ranging from zero = no change, to four = severe losses of species).

Inspired by a similar study by Vasconcellos *et al.* (1997), I generated a perturbation based on a high fishing effort during a period of 10 years. The fishing pattern was a 5-fold increase in fishing mortality, F , on the most species with the largest fishery in the ecosystem. For ecosystems where no fishery was described, I created a fishing mortality of 2.5 year^{-1} on the fish species with the highest biomass in the ecosystem. This perturbation generated a situation where biomasses are severely depleted or displaced from their original condition in a relatively short period of time (Vasconcellos *et al.* 1997). After the period of 10 years with high F , this strong fishing mortality was returned to the baseline, and I let the model run for 90 years (for a total simulation of 100 years). Persistence, resilience, and resistance were calculated for each of the 50 models.

An additional variable was used to describe the type of fishery occurring in the ecosystem. Indeed, ecosystems where the 'real' fishery was increased to create a perturbation were grouped as 'fishery', while ecosystems where the fishing mortality was created on the most important fish of the ecosystem were grouped as 'pseudo-fishery'. This allowed me to test if the 'shock' I gave to the unfished models was the same as the fishery.

3.2.5 Statistical methods

Prior to perform multiple regressions, variables were examined for their linearity using the additive and variance stabilizing transformation (AVAS; Tibshirani 1988) implemented in the S-Plus 6 software. AVAS is a generalized additive method in which the predictors are non-parametrically transformed to optimize R^2 and the response is non-parametrically transformed to stabilize variances of residuals. These transformations can be used to suggest appropriate functional forms for standard linear models.

I used a multiple regression technique on the optimally transformed values to predict the resilience and persistence (response variables) from a linear combination of several other variables (our ecosystems indicators) with a least squares fitting principle. We used a forward stepwise approach to fit a model with different combinations of regressors. The process selects the best combination of predicting variables, adding regressors until no more variables are significant. Predicting variables were then identified in terms of their importance in forecasting the model's response (resilience or persistence).

Results

The 50 models analyzed covered the period from 1993 to 2005, and were mainly published as reports, but also theses, book sections and articles (Table 3.4). Many models of my analysis were published in 1993 and in 2001, when the book *Trophic models of aquatic ecosystems* (Christensen and Pauly 1993), and an extensive Fisheries Centre research report on *Fisheries impacts on the North Atlantic ecosystems: models and analyses* edited by Gu  nette *et al.* in 2001) presented modelling results for many ecosystems. Apart from these two very productive years in terms of models published, the effort to construct and publish ecosystem models changed from models published in primary literature to more detailed models published in theses or reports.

Table 3.4. Types of publications describing the *Ecopath* models sampled for the present analysis.

Year of publication	Type of publication				TOTAL
	Article	Book chapter	Report	Theses	
1993	2	9	-	3	14
1996	1	-	1	-	2
1997	1	-	3	1	5
1999	2	-	1	-	3
2000	-	-	1	-	1
2001	1	1	10	1	13
2003	-	-	7	-	7
2004	1	-	2	-	3
2005	-	-	1	1	2
TOTAL	8	10	26	6	50

Constructing an *Ecopath* model implies using data whose acquisition cost an average of 1,716 credits (Table 3.5). Models published as book chapters and journal articles usually had lower construction costs, while models published as reports and theses appeared more expensive to create. These models are also more detailed in terms of trophic groups. When published as theses or peer-reviewed articles, *Ecopath* models tend to have a higher pedigree and thus be better in terms of overall quality than when published in reports (Table 3.5).

Table 3.5. Embodied costs and quality of *Ecopath* models depending on the type of publication they represent.

Publication Type	Average embodied costs (in credits)	Average pedigree	Average number of groups
Journal article	1,373	0.473	19
Book chapter	858	0.429	12
Report	2,035	0.416	36
Thesis	2,326	0.509	29
Global average	1,716	0.440	27

Over two decades, the average number of trophic groups in *Ecopath* models increased by close to 50%, from an average 24 groups in the 1990s to an average of 33 trophic groups since 2000. As it take more pages to describe more trophic groups (while maintaining a minimum of quality), this increase in the number of trophic groups is

significantly related to increased costs to construct these models ($F = 10.95$, $df = 49$, $p = 0.002$; Figure 3.1).

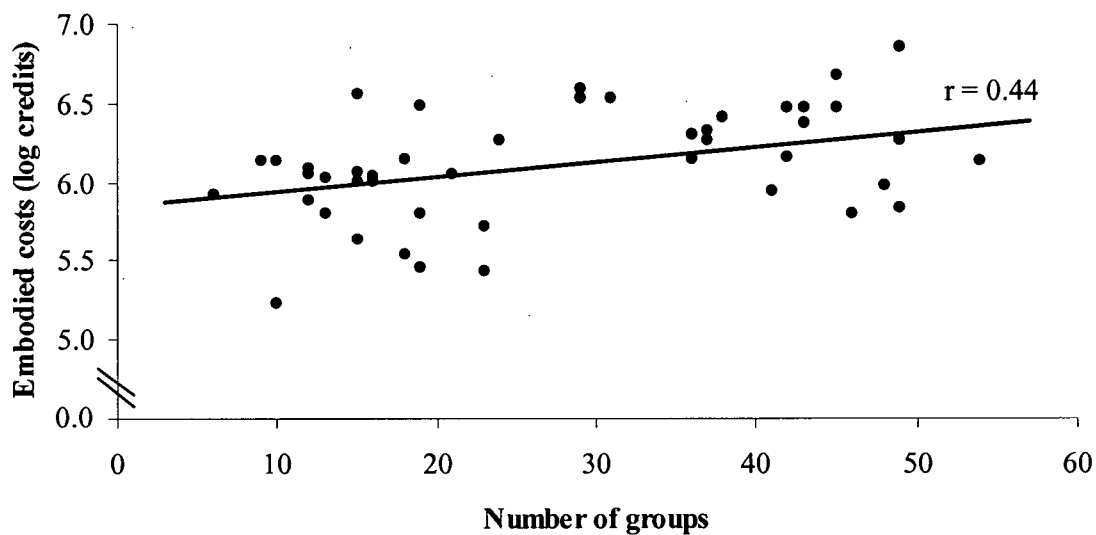


Figure 3.1. Bivariate fit of the embodied construction costs (in credits) of Ecopath models by the number of trophic groups they include.

The quality of a model also increases when construction costs are higher. This trend (significant with $F = 13.51$, $df = 49$, $p = 0.001$) is based on the log of the embodied costs, meaning that for high quality models, reaching a higher pedigree level costs more than for low quality models (Figure 3.2).

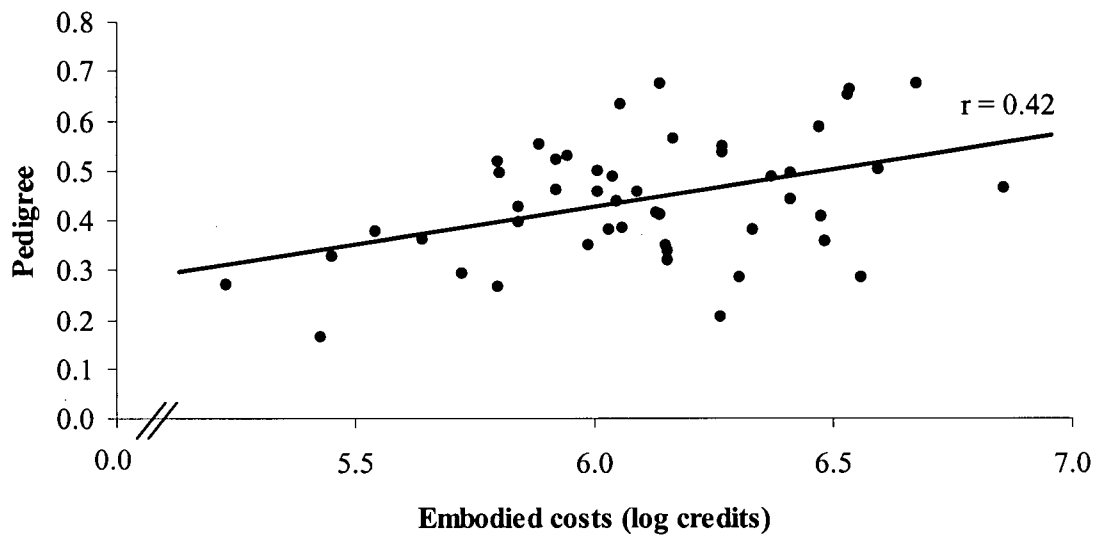


Figure 3.2. Pedigree of Ecopath models versus their embodied costs.

My results also show that the pedigree increase related to embodied costs eventually reaches a plateau, where even if more money is invested in constructing a model, the quality does not increase much (Figure 3.3).

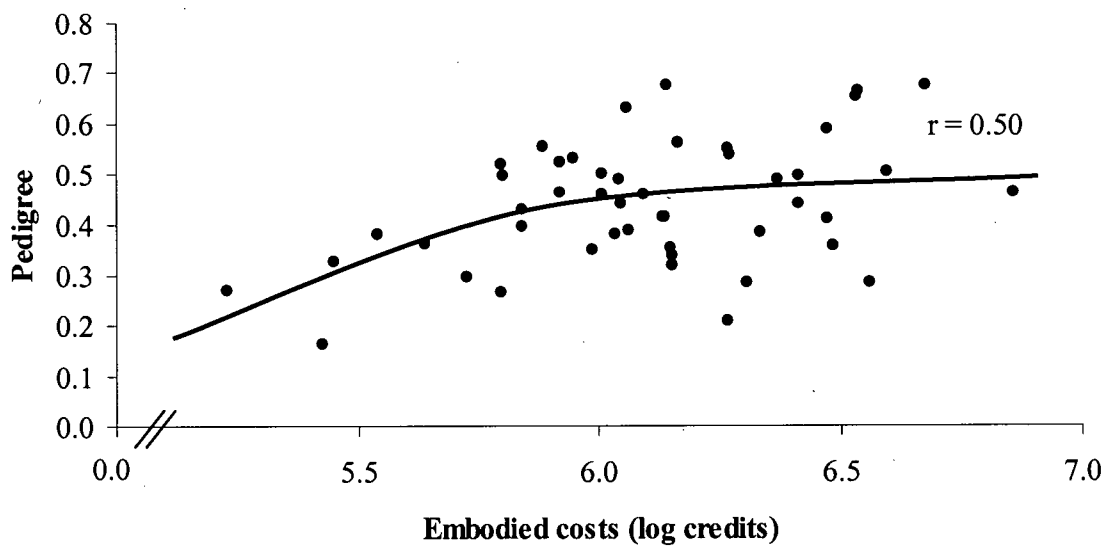


Figure 3.3. Bivariate polynomial fit of the pedigree of Ecopath models versus their embodied costs.

For both dependent variables (resilience or persistence), the plot of the AVAS transformed values against the original values (Figure 3.4) showed the same transformations required to obtain linearity in the models. Based on this, it seems that no transformation was required for connectance, while log transformations would be adequate for pedigree and SOI, and exponential transformation for ascendancy.

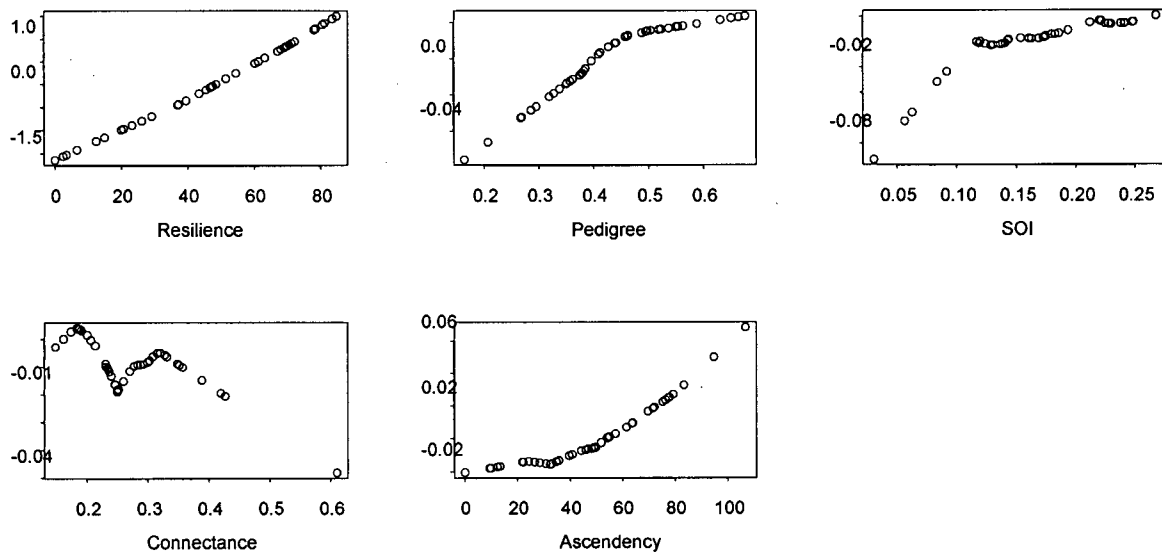


Figure 3.4. Additive and variance stabilizing (AVAS) transformations indicating how parameters (x-axis) may be transformed (y-axis indicates resilience, linear scale) to linearize the individual parameters while considering their joint effects to predict resilience. Results indicate that no transformation is required for connectance, while log transformations would be acceptable for pedigree and SOI, and exponential transformation for ascendancy. Note that the same transformations were obtained for predicting persistence.

3.3.1 Pedigree and stability (simple regression)

The following results address stability in terms of resilience, as it is the factor that produced the most significant results for the regression analyses.

When the resilience of ecosystems is tested against the pedigree for all models, there is a significant positive relationship ($F = 6.5$, $df = 46$, $p < 0.015$, $r = 0.37$), showing that resilience increase with higher pedigree (Figure 3.5).

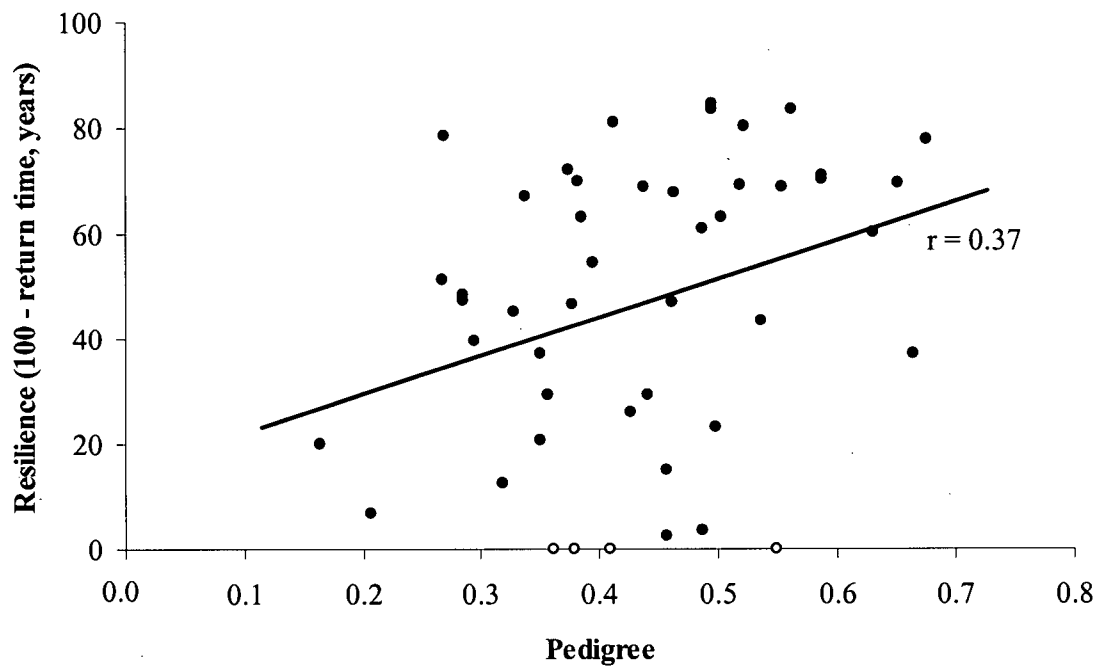


Figure 3.5. Resilience versus pedigree for 50 *Ecopath* models. Grey dots (with resilience = 0) were considered as outliers and not used in the regression analysis.

Using a leverage plot for this simple regression allow us to see with the observed versus predicted values if the relationship is significant (Figure 3.6). The points on this plot are actual data coordinates, and the horizontal line for the constrained model is the sample mean of the response. The distance from a point to the line of fit is the actual residual and the distance from the point to the mean is the residual error if the regressor is removed from the model. Because the confidence region between the curves cross the horizontal line, we can conclude that there is a significant relationship between resilience and pedigree (Figure 3.6).

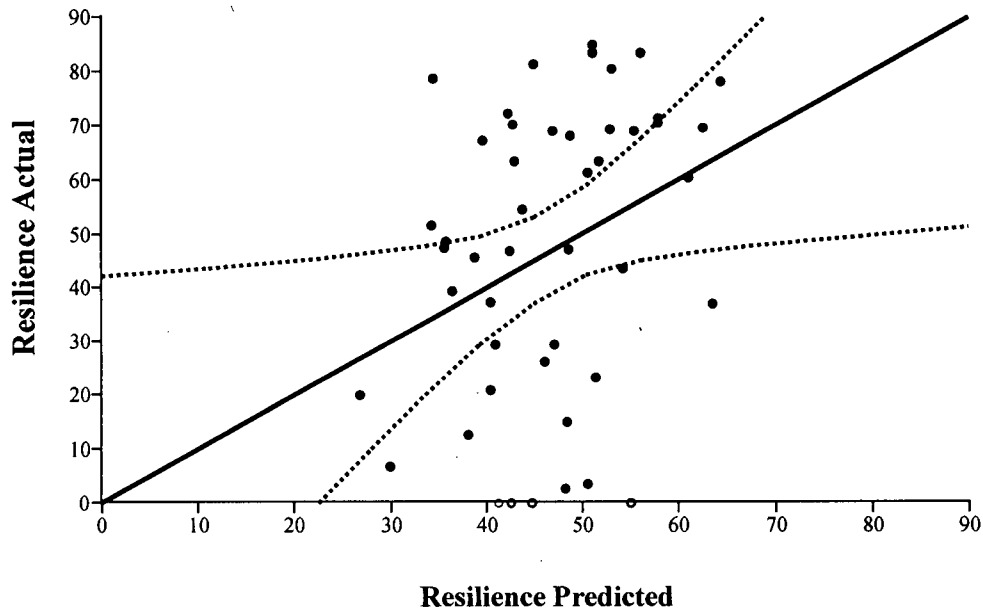


Figure 3.6. Predicted *versus* observed values for the regression of resilience and pedigree. Grey dots (with resilience = 0) were considered as outliers and not used in the regression analysis.

3.3.2 Predicting ecosystem's resilience (multiple regression)

All the optimally transformed values were standardized and then analysed together in a stepwise (backward) multiple regression, in order to select a subset of effects predicting resilience through a regression model. Different sets of predicting variables were tested and ultimately only those which increased the R^2 were included in the regression model. The significant model emerging to predict resilience ($F = 6.276$, $df = 49$, $p < 0.040$) increased in R^2 from 0.104 when it included only pedigree as a variable, to 0.189 when based on partial regression coefficients in Table 3.6.

Table 3.6. Effect of the significant regressors for predicting resilience in a multiple regression for all ecosystem models ($n = 50$).

Parameter	Partial regression coefficient	t Ratio	F ratio	<i>p</i>
Intercept	0.19	1.48	-	0.147
Pedigree (log)	0.39	2.92	8.50	0.006
Relative ascendancy	0.22	1.50	2.26	0.141
SOI (log)	0.10	0.69	0.48	0.495

When the leverage plot represents a multiple regression, the points are no longer actual data values. The horizontal line then represents a partially constrained model instead of a model fully constrained to one mean value. However, the intuitive interpretation of the plot is the same as for the simple regression. Here again, because the confidence region between the curves does not include the horizontal line, we can say that there is a significant relationship between resilience and the partial regression coefficients (Figure 3.7).

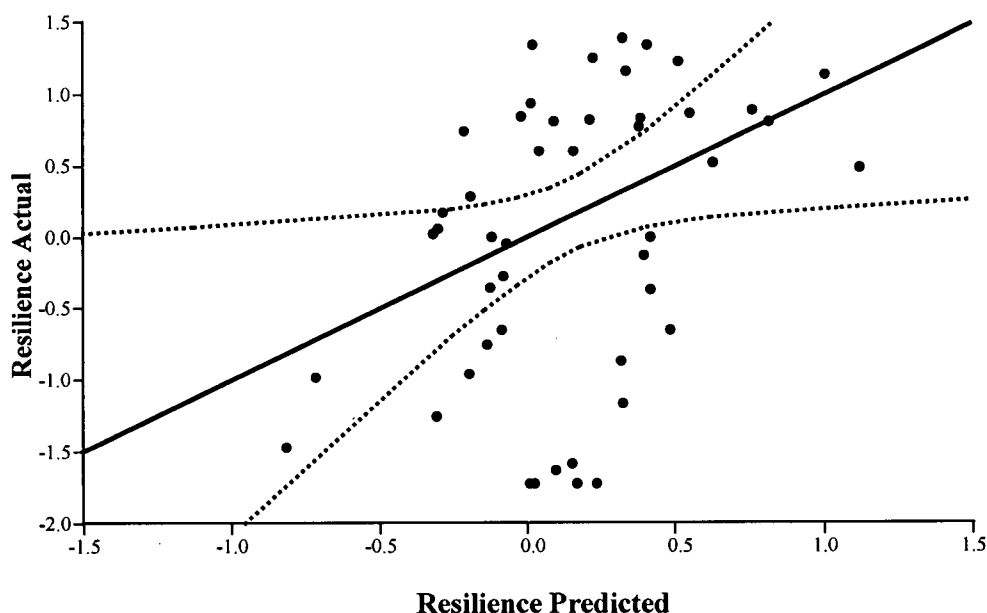


Figure 3.7. Predicted *versus* observed values for the model predicting models' resilience for the regression of resilience *versus* pedigree, ascendancy and SOI.

The variables which account for systems with a fishery versus systems with a pseudo-fishery did not show a significant difference in the ecosystem response to perturbation. This means that the 'shock' I gave to the unfished models was the same as a fishery would do.

3.3.3 Complexity versus stability

From my results, there is no direct evidence of a relationship between the stability of ecosystems (expressed here by their resilience) and their complexity (*SOI*, connectance, Finn's cycling index, or ascendancy). However, when a multiple regression is performed,

a significant model emerges predicting that stability is linked to relative ascendancy and *SOI* (Table 3.6), only when the pedigree is taken into account as regression factor. This results in a positive relationship between these three variables and the resilience of ecosystems.

Discussion

This analysis represents the first large-scale analysis of the potential relationship between diversity and stability of marine ecosystems, dealing with the possible influence of the quality of the data used to construct these ecosystem models.

3.4.1 About the modelling approach

The modelling approach presented here may have some weaknesses, but is innovative in the sense that it suggests new approaches to the analysis of the diversity-stability relationship.

With a sample size of 50 ecosystem models from all around the world, we can assume that the outcomes of this modelling effort represent global responses for marine food webs. Studies addressing theoretical issues such as the diversity-stability relationship are usually based on fewer models, and on models from a limited area of the globe.

For some particular models, running simulated perturbations (here: strong increase in fishing mortality) in *Ecosim* allowed us to discover some interesting features. For example, it seems that fishing on large predators (e.g., fishing on tuna in the Azores system) does not destabilize as much the biomass structure of other species as it would do by fishing on lower trophic levels. However, when fishing is targeting large predators, the systems do not return to their original structure, even after 100-year simulation. The loss of higher trophic levels might affect ecosystems' resistance, as opposed, for example, to the loss of keystone species (as modeled by Vasconcellos *et al.* in 1997), which seems to affect more the resilience of the ecosystem.

Most published work on the complexity-stability relationship base their analysis on connectance as an indicator of ecosystem complexity (Rozdilsky and Stone 2001; Eklöf and Ebenman 2006). Other authors examined resistance *versus* species richness (Caldeira

et al. 2005). However, such studies can include questionable assumptions about structure and dynamics (Brose *et al.* 2003; Green *et al.* 2005), and might not use the best indicator of ecosystem's complexity. My choice of analyzing relative ascendancy and SOI rather than using connectance proved to be relevant. Ascendancy was already identified by Heymans and Baird (2000) as an important indicator of system complexity. The SOI is also considered as a better descriptor of trophic interactions, as proposed by Christensen *et al.* (2000). Indeed, my database contained some models that were built for the same ecosystems but at different time periods (e.g., the Bay of Biscay, by Ainsworth *et al.* 2001). In these ecosystems, the trophic structure often remained the same, but the diet changed. The connectance index could not capture these changes, and was thus the same for both ecosystems, while *SOI* changed, as it was linked to the diet of interacting species.

3.4.2 Data quality and associated modelling outcomes

Since it is practically impossible to make controlled laboratory experiments of the dynamics of marine ecosystems, modelling has become an efficient way of addressing global food web issues. The *Ecopath* modelling approach became more and more important over time, and the size of models increased as well. With one exception, a model constructed in 1996 with 50 trophic groups (Opitz 1996), most of larger models appeared after 2000. We now see some *Ecopath* models with more than 50 trophic groups (Gu  nette and Morato 2001; Okey 2001; Heymans and Pitcher 2002b).

Obviously, there is no direct correlation between the number of groups in a model and its overall pedigree. Consequently, it is superfluous to waste time trying to construct models with a very large number of trophic groups, if in the end we have no data to describe these groups. It is instead better to focus on fewer trophic groups backed by good ecological data, from local studies, and thus have a high pedigree.

My results indicate that there is a significant relationship between the pedigree of an ecosystem model and its resilience. This means that models with better input data (high pedigree) would sustain their structure intact for a longer time before to go through important changes in terms of species biomass (persistence), and would also return faster to their previous equilibrium after the perturbation (resilience). In other words, this means

that models with high pedigree would predict a faster recovery after perturbations. In ecosystem modeling, the quality of input data has often been questioned, but was never analysed as a factor that could change the diversity-stability relationship. With this new approach, my results provide a counter example to the complexity/stability debate by showing that the quality of data used in ecosystems models, as well as the realism of the models used, are really important factors to consider while attempting to describe the relation between complexity and stability in ecosystems. Models of higher quality tend to perform better than poor ones in predicting changes in biomass after a given perturbation.

Actual ecosystems have species whose vital parameters (growth, mortality, food consumption, etc.) have co-evolved, allowing for the living part of the system to remain roughly similar for longer periods of time, notwithstanding fluctuations of the abiotic environment. Ecosystem models with high pedigree will tend to have parameter values close to the co-evolved values of the actual ecosystem. In contrast, ecosystem models assembled from random parameter sets – even if they exhibit onward stability when not disturbed, will lack such ability to withstand disturbances (environmental, or as a result of fishing), and this is likely to be worse with large (complex) model, which have more parameters.

Thus, it is easy to imagine how ecosystem models with random parameters could have misled May (1972), Pimm (1982) and other into inferring that complexity begets instability, that flew in the face of much field ecology. My findings show not only that this is erroneous, but also why.

3.4.3 Cost-effectiveness of ecosystem models

The subject of data quality is consistently addressed in many international forums and workshops, and new approaches stem from a growing consensus that management decisions are increasingly reliant on better input data. In 2003, the FAO has defined “cost-effectiveness” as a measure of the relationship between data costs and data benefits. Evaluations of the cost-effectiveness of ecosystem models in relation to improved science and better management have almost never been analysed (FAO 2003). A study by the National Research Council (2000) also states that they:

“could find no existing analyses of the costs and benefits of data collection and management for specific fisheries, particularly of the ratio of marginal costs and marginal benefits for each additional dollar spent on data collection”.

Of course, the approach presented here is only an attempt to evaluate construction costs of ecosystem models, but there is definitely a need for more in-depth analyses on the cost-effectiveness of ecosystem models in order to have a better idea on what part of a management budget should go on collecting good data and construction of reliable models.

My results have shown that ecosystem models that are to be used for management ought to be based on high quality data. Modelling is an expensive process. Unfortunately, many fisheries that would greatly benefit from high-quality ecosystem model management are in developing countries, where financial resources are scarce, and not necessarily directed to address these kinds of issues (Pauly 1995).

Nevertheless, when comparing the embodied costs of ecosystem models with their pedigree, I discovered that there is an optimal modelling effort (in terms of costs), above which quality reaches a plateau. This result could be seen as a reason, when a pedigree is high, to stop spending money on the data gathering, given the low increase of quality that would be gained. This finding could become very useful to managers in order to focus on the best way of getting a certain amount of data for an ecosystem model, and then being able to maximize its use. On the other hand, if biodiversity is an issue, adding more data on less commercially important species in an ecosystem can become very important and thus worth spending money on.

Finally, it is important to point out that as a rule, the data used for *Ecopath* models were also collected for other purposes. Thus, *Ecopath* makes use of the expensive data that are already available. I do not know of any datasets that are collected especially in the aim of constructing an *Ecopath* model. Generally, *Ecopath* data are used in collaboration with other research projects and do not involve any direct sampling.

3.4.4 On complexity-stability relationship

My results indicate that two ecosystem complexity factors –ascendancy and omnivory index– can be expected, generally, to correlate with stability. This corroborates findings that propose that complex ecosystems present more possible trophic links and energy flows between species, and if a perturbation breaks some of these links, other pathways will still be possible to maintain the food web structure and thus make it more stable. If system's complexity has a stabilizing role in the resilience of marine ecosystems, as it is proposed here, management and protection of selected trophic groups (key species of the food webs) can be very important for the overall richness of an ecosystem, and thus its stability. This is not only true for commercially important species or species with larger biomasses in the system. Indeed, non-target species may also play a crucial role in structuring the foodweb, habitats and ecosystem processes (Coleman and Williams 2002). Thus, if management choices have to be taken to protect marine species, they should be based on the entire structure of marine ecosystem, and not only on a single-species point of view.

When the complexity-stability relationship is analyzed in a context of foodweb (and not from statistical procedures), most studies are based on simplified food webs with few trophic groups (e.g., Eklöf and Ebenman 2006; Thébault and Loreau 2006). Here, my relationships are based on complex models representing more trophic groups, and for all parts of the world, making it more global and representative of a variety of marine ecosystems. The results also show that unlike other theoretical studies about the diversity-stability relationship (see Wilmers *et al.* 2002 for a review), the present study supports the notion that as community complexity (here presented as ascendancy and omnivory index) increases, stability increases too. Most of the time, this notion was supported by empirical studies conducted in controlled microcosms. This may suggest that my models were more representative of real ecosystems.

However, we should note that there is a wide range of interests in analyzing ecosystem performance, and different measures serve different interests (see Steele 2006 for a review). While conservationists want to preserve diversity by creating marine reserves, fisheries scientists and managers would prefer to preserve productivity by imposing stricter fishing quotas. However, diversity, productivity and stability provide

unrelated measures of ecosystem performance (Steele 2006). There is thus a need to address these measures separately and understand them thoroughly to preserve marine ecosystems as much as possible, whatever the interest is. Ecosystem modelling is certainly an important tool to reach that goal.

“Scientists have broken down many kinds of systems. They think they know most of the elements and forces. The next task is to reassemble them, at least in mathematical models that capture the key properties of the entire ensembles.”

Wilson 1998

Chapter summary

For many years, there has been a debate focusing on the question whether simple ecosystems are less stable than complex ones. To date, studies addressing the “diversity-stability debate” (McCann 2000) have yielded ambiguous results. Moreover, few studies devoted to this topic have been focusing on marine ecosystems, even if they cover a very important surface of the biosphere. I used fifty empirical models assembled from real food-webs relationships, with plausible interaction strengths, based on the *Ecopath* modelling approach. The relationship between complexity and stability was analyzed, along with the effect of the quality of data used in ecosystem models. Cost of constructing *Ecopath* models was discussed, based on a bibliometric analysis. My results indicate that there is a significant relationship between the pedigree of an ecosystem model and its resilience. With this new approach, I provide a counter example to the complexity/stability debate by showing that the quality of data used in ecosystems models, as well as the realism of the models used, are really important factors to consider while attempting to describe the relation between complexity and stability in ecosystems. Models of higher quality tend to perform better than poor ones in predicting changes in biomass after a given perturbation. Thus, ecosystem models that are to be used for management or prediction ought to be based on high quality data. However, modelling is an expensive process: when comparing the embodied costs of ecosystem models with their pedigree, I discovered that there is a direct relationship and an optimal modelling effort (in terms of

costs), above which quality reaches a plateau. Finally, my results also show that unlike other theoretical studies about the diversity-stability relationship, the present study supports the notion that as community complexity (here presented as ascendancy and omnivory index) increases, stability increases too.

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Chapter 4

Modelling the indirect positive feedback of marine mammal predation: outcomes for competition with fishery and ecosystem structure.

Introduction

The interaction between marine mammals and fisheries has received growing attention during the last 20 years (Yodzis 1998; Gales *et al.* 2003; Mackinson *et al.* 2003). Numerous studies and investigations of interactions between marine mammals and fisheries have been implemented around the world. Even if many studies have examined how fisheries may impact marine mammal populations (Dans *et al.* 2003; Roman and Palumbi 2003; DeMaster *et al.* 2001), the degree to which marine mammals compete for food with fisheries has been studied somewhat less broadly (Northridge 1991; Smith 1995; Bowen 1997; DeMaster *et al.* 2001; Kaschner *et al.* 2001; Kaschner and Pauly 2005). Nevertheless, this competition for fish resources between marine mammals and fisheries may be the primary source of current and future conflicts (Trites *et al.* 1997; Kaschner 2004; Dillingham *et al.* 2006). Besides the fact that many authors now document a growing concern about the widespread decline of many marine mammal populations on the planet (Bowen 1997; Trites *et al.* 1997; Springer *et al.* 2003; Estes *et al.* 2005; Kraus *et al.* 2005), there is a serious need to address the issue of their competition with fishery for the same food resources.

Understanding the ways in which marine mammals and fisheries compete, and where and when they do, is not an easy task. First of all, detailed information on the dynamics of predation rates and how these relate to either fluctuation in fish availability or fluctuations in marine mammal population size is lacking (Northridge 1991, MacKenzie *et al.* 2002). Furthermore, it is usually very difficult to observe marine mammal feeding and/or interacting with fisheries (Williams *et al.* 2004; Kaneko and Lawler 2006). Quantifying their diets with estimation models (scats, stomach contents, fatty acids, etc.)

is also problematic as diets can vary substantially over time (Lawson and Stenson 1995; Bowen and Siniff 1999; Laake *et al.* 2002; Hume *et al.* 2004). Finally, even on the fisheries side, exhaustive data on yield and precise estimates on catches, bycatch (especially the commercially less important species), or discards are known to be relatively hard to get (National Research Council 1999; Zeller and Pauly, 2005).

The use of models that are validated for ecological reliability becomes an interesting tool to address the trophic role of marine mammals in ecosystems, and their competition with fisheries. Until now, *Ecopath with Ecosim (EwE)* models have been considered inadequate to provide reliable answers in the context of competition between marine mammals and fisheries, being more used to generate hypotheses about possible impacts of fisheries on marine ecosystems (Kaschner 2004). However, even if *Ecopath* models are generally constructed in a fisheries context, and merely consider the commercially important species, in some cases marine mammal compartments are included in the models, making a better representation of all trophic interactions in the entire ecosystem (Morissette *et al.* 2006).

In order to investigate trophic interactions between marine mammals and fisheries, the present analysis has the following objectives:

1. to calculate the resource overlap between marine mammals and fisheries using ecosystem models;
2. to examine the global trophic impacts of marine mammals and fisheries on the key species of each ecosystem; and
3. to simulate the extirpation of marine mammal populations in these ecosystems and analyze the resulting changes on the structure of the foodweb.

The principal hypothesis of this chapter is that the presence of marine mammals in ecosystems and their overlap with fisheries for food resources does not have a significant effect on the overall productivity of the ecosystem, but that their removal by humans can decrease this productivity and alter the structure of the food web.

Materials and methods

4.2.1 Global ecosystem representation

The *Ecopath* approach was developed in the early 1980s by J.J. Polovina and co-workers at the NMFS Laboratory in Honolulu. It was first applied to a coral reef system, as a tool to allow quantitative analyses of biological interactions within aquatic systems (Polovina 1984). *Ecopath* was originally developed by J.J. Polovina (1984) as a tool to quantitatively analyse the biological interactions within aquatic systems. Modified and updated since then by Christensen and Pauly (1992, 1993), *Ecopath with Ecosim* is now a widespread software package widely used for the analysis of exploited aquatic ecosystems (Christensen and Walters 2004). Currently, the software counts more than 2800 registered users from approximately 120 countries (see Chapter 1 of this thesis). Because a good coverage based on the same modelling methodology is available throughout the world's oceans, I could take models constructed using this approach to quantify and analyze the impact of marine mammals' consumption in marine food webs.

The seven ecosystem models selected for this analysis were chosen in terms of their geographical distribution and the quality of their documentation. The quality of input data used in the models matters, as it has been shown that model performance is influenced by the quality of input data (see Chapter 3 of this thesis), as well as by the aggregation of trophic groups (Pinnegar *et al.* 2005). Particular effort was made to cover both northern and southern hemispheres, in an attempt to have a representative coverage of the world's oceans for the global extrapolation. Kaschner and Pauly (2005) have shown that the prominent hotspots of competition between marine mammals and fisheries include the Bering Sea where the potential negative impacts of the US groundfish fisheries on the endangered western population of Steller sea lions (*Eumetopias jubatus*) have been a great concern (Fritz *et al.* 1995, Loughlin and York 2000) and the east coast of North America where the largest annual marine mammal cull worldwide is in part being justified based on the perception that the growing harp seal (*Phoca groenlandica*) population impedes the recovery of the northwest Atlantic cod (*Gadus morhua*) stocks (see review in Yodzis 2001). In addition, their model identified areas of potential conflict in the Benguela system off southwest Africa with the potential impacts of the increasing population of South

African fur seals (*Arctocephalus pusillus*) on the hake stocks has been an issue of much debate (Wickens *et al.* 1992, Punt and Butterworth 1995). To these three ecosystems I added other hotspots identified in the Kaschner and Pauly (2005) analysis (see their Figure 7): the eastern tropical Pacific Ocean; the North Sea; the Gulf of Thailand and the Strait of Georgia (Figure 4.1).

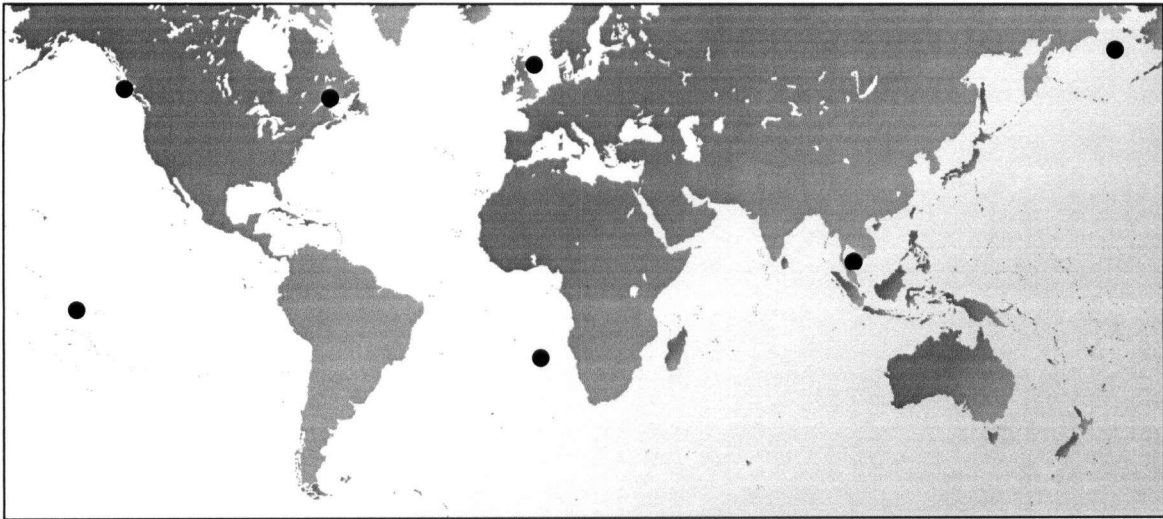


Figure 4.1. Location of the ecosystem modeled with *Ecopath* and used for this analysis.

For each of the ecosystem selected, an *Ecopath with Ecosim* model was obtained from the scientists who created it, and verified for its ecological reliability. By this, I mean models reliable enough to re-create time series of biomass changes that are similar to official data. The general information on each ecosystem model used for my analysis is described in Table 4.1.

The eastern Bering Sea model (National Research Council, 2003) was constructed to examine interactions between Alaska groundfish fisheries and Steller sea lions and the role of these fisheries on the evolving status of the sea lion population. A total of 26 functional groups (representing hundreds of species that make up the Bering Sea ecosystem) are included in this model. Data on marine mammals mainly came from local studies and are quite precise. Six groups of marine mammals are represented in that model, covering whale and seal species (Table 4.1).

In the northwest Atlantic, *Ecopath* models were developed for the Northern and the Southern Gulf of St. Lawrence ecosystems, for the periods before (mid-1980s) and

after (mid-1990s) the collapse of demersal fish stocks in the two areas. The objective was to determine if significant changes in ecosystem structure had occurred between the two time periods that might contribute to the failure of the cod stocks to recover in the 1990s (see Chapter 5 of this thesis). The northern Gulf of St. Lawrence model was here used to represent a typical Northwest Atlantic ecosystem. This model contains five marine mammals groups, covering whale and seal species (Table 4.1).

An *EwE* model of the southern Benguela was fitted to available time-series data to explore how changes in target fish populations could be attributed to feeding interaction terms and population control patterns, the impact of fishing, and environmental forcing (Shannon *et al.* 2004). Two marine mammal groups are present in the ecosystem: cetaceans and seals (Table 4.1).

An *EwE* model was constructed by Olson and Watters (2003) to represent the tropical region of the eastern Pacific Ocean, aiming to get insights into the relationships among the various species in the system. The model was also used to explore ecological implications of alternative methods of harvesting tunas. Even if the model was primarily built around the latter species, four groups of marine mammals were nevertheless represented: baleen whales; toothed whales; spotted dolphin (*Stenella attenuata*) and mesopelagic dolphins (Table 4.1).

Many ecosystems of northern Europe have been modeled over the past years (Harvey *et al.* 2003; Booth and Zeller 2005; Morissette and Pitcher 2005; Skaret and Pitcher, in press). I chose to use the model of the North Sea ecosystem (Christensen *et al.*, 2002) as it shows a better representation of marine mammals in the foodweb, and is also recent. This model was built to represent the period from 1963 to 1999, as part of a comparative analysis with MSVPA. Two marine mammals groups are present in the model, representing cetacean and seal species (Table 4.1).

In the Gulf of Thailand, an *Ecopath* model was developed by Thai scientists and Dr. Villy Christensen at an FAO workshop for the implementation of a Code of Conduct for Responsible Fisheries (FISHCODE). This model was used to address the impact on the Gulf of Thailand ecosystem and on biodiversity of a continuation of the very high levels of mostly indiscriminate fishing effort, especially bottom trawling (FAO 2001). Marine

mammals are present in the model, but they were aggregated in only one trophic group (Table 4.1).

Finally, the Strait of Georgia *Ecopath* model was developed to simulate various management policies and analyze their consequences (Martell *et al.* 2002). The model builds on another one created for the 'Back to the Future' project (Pauly *et al.* 1998b). It has four marine mammal groups out of a total of 27 trophic groups. The marine mammal species represented are transient killer whales (*Orcinus orca*), dolphins & resident killer whales, seals, and sea lions (Table 4.1).

Table 4.1. *Ecopath* models used for analyses of marine mammals consumption.

Ecosystems	No. of trophic groups	Marine mammals groups	Average pedigree of marine mammals' diets	Reference
Eastern Bering Sea	26	1) Baleen whales 2) Toothed whales 3) Sperm whales 4) Beaked whales 5) Walrus and bearded seals 6) Other seals 7) Steller sea lions	0.7	National Research Council, 2003
Northwest Atlantic (Gulf of St. Lawrence)	32	1) Cetaceans 2) Harp seals 3) Hooded seals 4) Grey seals 5) Harbour seals	0.6	Morissette <i>et al.</i> 2003
Benguela system	32	1) Seals 2) Cetaceans	0.7	Shannon <i>et al.</i> 2004
Eastern tropical Pacific Ocean	39	1) Baleen whales 2) Toothed whales 3) Spotted dolphins 4) Meso. Dolphins	0.8	Olson and Watters 2003
North Sea	32	1) Seals	0.7	Christensen <i>et al.</i> 2002
Gulf of Thailand	40	1) Marine mammals	0.5	FAO/FISHCODE 2001
Strait of Georgia	27	1) Transient orcas 2) Dolphins & Resident orcas 3) Seals 4) Sea lions	0.6	Martell <i>et al.</i> 2002

Since most models represent the major hotspots of conflict between fishery and marine mammals, and because they cover very well both northern and the southern

hemispheres (Figure 4.1), I argue that it is reasonable to extrapolate these results to the whole world.

4.2.2 Modelling approach

Our modelling approach used the *Ecopath with Ecosim* software package (Christensen and Pauly, 1992). In *Ecopath*, several system's indices are computed to describe the food web, its complexity, and the way trophic groups interact with one another.

Ecopath models used here will first serve as comparison points for the global resource overlap analysis done by Kaschner and Pauly (2005). Based on different modelling techniques and offering an in-depth analysis of the entire foodweb in some of the 'hotspots' that were identified, this approach gives a closer look at the trophic interactions (especially consumption by marine mammals and catch by fisheries) in the zones where there is potential competition for marine resources.

The software also allows making dynamic simulations based on *Ecosim*, a dynamic modelling application for exploring past and future impacts of fishing and environmental disturbances (Christensen and Walters 2004). *Ecosim* converts the trophic flows of *Ecopath* into dynamic, time-dependent predictions (full details of the *EwE* modelling approach and equations are available from <http://www.ecopath.org>). Each model has different complexity levels (in terms of number of trophic groups). However, all are rather complex, with at least more than 25 compartments (see Chapter 3 of that thesis for comparative information). Obviously, all models that were selected include one or more marine mammal groups.

4.2.3 Static ecosystem indices (*Ecopath* outputs)

For each model, a comparison of the *Ecopath* outputs for food consumption by marine mammals *versus* the catch by fisheries was performed. The estimated annual catch (i.e., "food consumption") of fisheries and marine mammals calculated by each ecosystem modeled is presented, as well as the estimated composition of the catch and the diet,

respectively, of fisheries and marine mammals. Finally, the primary production required (PPR) to sustain fisheries is compared with the PPR to sustain marine mammals groups.

The mean trophic level of marine mammals' consumption (TL_Q) and of fisheries catch (TL_C) were derived from *Ecopath* outputs. The TL_C is a dimensionless index computed by *Ecopath* to measure ecosystem health (Christensen *et al.* 2005), and is an indicator of the ecosystem health and the state of the fisheries (Pauly and Watson 2005). The TL_C is based on Lindeman's (1942) concept of trophic levels, but can be fractional (e.g., 1.3, 2.7, etc.) as suggested by Odum and Heald (1975). A routine assigns definitional trophic levels (TL) of one to producers and detritus. For the remaining species of the ecosystem, TL is calculated as:

$$TL = 1 + \left(\sum_i p_j * TL_j \right) \quad \text{Eq. 4.1}$$

where p_j is the proportion (in weight) of each prey group in the diet of its predator. TL_j is the trophic level of each prey group j .

The mean trophic level of the catch is calculated from:

$$TL_C = \sum_i \left(TL_i \left(\frac{Y_i}{\sum Y} \right) \right) \quad \text{Eq. 4.2}$$

where Y_i is the total landings of species i (in tons), $\sum Y$ is the sum of landings for all species, and TL_i is the trophic level for species i .

Similarly, I developed an equation to calculate the trophic level of consumption (TL_Q) by marine mammals using an equation derived from the TL_C , and modified to represent the consumption by marine mammals and make it comparable with the fisheries catch:

$$TL_Q = \sum_i \left(TL_i * \left(\frac{\sum_{j=1}^n Q_{ij}}{\sum_{j=1}^n Q_j} \right) \right) \quad \text{Eq. 4.3}$$

where Q_{ij} is the consumption of prey i (in tons) by marine mammal j , Q_j is the total consumption of all species by marine mammal j , and TL_i is the trophic level for species i . Eq. 4.3 represents the average trophic level on which marine mammals feed, i.e., the average TL of each species, multiplied by their proportion in the consumption matrix (tonnes per km^{-2} per year that marine mammals consume).

Patterns of marine mammal consumption *versus* fisheries catches were based on categories that were first described in Pauly *et al.* (1998c). Table 4.2 describes the prey categories used to apportion dietary information for marine mammals.

Table 4.2. Eight prey categories used to apportion dietary information for marine mammals (adapted from Pauly *et al.* 1998c).

Group	Description
BI	Benthic invertebrates. Mainly molluscs (notably bivalves and gastropods, but also including octopus, echinoderms and crustaceans.
LZ	Large zooplankton. Mainly small crustaceans, especially euphausiids (krill) such as <i>Euphausia superba</i> in Antarctic waters.
SS	Small squids. Families with mantle lengths of up to 50 cm, such as Gonatidae, (see Roper <i>et al.</i> , 1984).
LS	Large squids. Families with mantle lengths above 50 cm, such as Onychoteuthidae.
SP	Small pelagic fishes. Consisting of clupeoids, small scombroids and allied groups.
MP	Mesopelagic fishes. Predominantly fish of the family Myctophidae and other groups of the Deep Scattering Layer.
MF	Miscellaneous fishes. A diverse group consisting mainly of demersal round fish such as gadoids and perciforms, but also including anadromous fishes such as salmon.
HV	High vertebrates. Marine mammals, seabirds, plus the occasional turtle.
NM	Non-marine mammal food. Includes all species not taken by marine mammals, e.g., fish larger than 150 cm.

For the purposes of my analysis, the miscellaneous fish group is particularly broad and imprecise, as it was originally used for more global analyses. For the present study, when addressing the overlap between marine mammals consumption and fisheries catch for this group, the particular species components will be discussed in more details for each ecosystem.

Using *Ecopath* estimates of fisheries catches and marine mammals consumption, the assessment of overlap between marine mammal and fisheries for each ecosystem was performed using a modified version of the resource overlap index of Kaschner (2004). This index originally included a weighting factor to provide a measure of the importance of each cell (from a global model of all oceans) for either fisheries or marine mammals, based on the overall quantity of catch or food taken by either consumer in this cell. The resource overlap index presented here ($\alpha_{f,m}$) uses a different weighting factor representing the relative importance of fisheries *versus* marine mammals as consumers within a given ecosystem:

$$\alpha_{f,m} = \left(\frac{2 \sum_k p_{m,k} p_{f,k}}{\sum_k p_{m,k}^2 + p_{f,k}^2} \right) * (pQ_m * pC_f) \quad \text{Eq. 4.4}$$

where $\alpha_{f,m}$ is the quantitative overlap between a fishery f and a marine mammal group m in each ecosystem, and the first term expresses the qualitative similarity in diet/catch composition between the marine mammal group m and fisheries f sharing the resource or food type k , with $p_{m,k}$ and $p_{f,k}$ representing the proportions of each food type in the diet of marine mammals or the catch by fisheries. This term is multiplied by the product of the proportion of total food consumption by marine mammals in the ecosystem Q and the total fisheries catches C in the ecosystem. Two versions of this index were calculated for the purpose of my study: firstly, the overlap index by food type, using the same categories than Kaschner (2004), will allow global comparisons. Secondly, the index calculated by trophic group will give a closer look at the overlap at the species level, giving the fact that species falling into each food categories may change from one ecosystem to another, and that fisheries and marine mammals may target different species from the same food type.

The mixed trophic impact (TI) analysis of *Ecopath* was used to compare the ‘with/without’ impact of predation by marine mammals on the whole ecosystem. This analysis allows the estimation of the relative impact of a change in the biomass of one group on other components of the ecosystem, under the assumption that the diet composition remains constant (Ulanowicz and Puccia 1990). Beneficial predation was calculated as the percentage of the overall trophic impact by marine mammals that is positive for any prey group of this predator.

4.2.4 Dynamic simulations (*Ecosim*)

The *Ecosim* model behaviour is based on a ‘foraging arena’ theory (Walters and Martell, 2004), which assumes that predator and prey behaviours cause partitioning of prey populations, which are either available or unavailable to predators. There is continuous change between these two stages for any given potential prey, whether it is hiding from predation in some refuge, or it is out to feed. This availability of prey to predators is called ‘vulnerability’ in *Ecosim*. Mackinson *et al.* (2003) demonstrated the

importance of setting the vulnerabilities to fit model predictions to time-series data, as *Ecosim* predictions are very sensitive to this parameter. Using default values for ν has strong implications for assumptions about species abundance relative to their carrying capacity (V. Christensen, Fisheries Centre, UBC, personal communication). Basically, it assumes that each group can at most increase the predation mortality they impose on their prey with a factor of 2.0 (the default ν value). A lower value implies a donor driven density-dependant interaction. On the other hand, a higher value involves a predator driven density-independent interaction, in which predation mortality is proportional to the product of prey and predator abundance (i.e., Lotka-Volterra). This implies a high flux rate for prey species in and out of vulnerable biomass pools (Ainsworth 2006).

Instead of using default vulnerability settings across the predation matrix, some authors chose to use values scaled to trophic level (e.g., Pitcher and Cochrane 2002), representing the hypothesis that higher trophic level groups are less risk-averse than lower one. Another way to adjust ν 's is to fit them to time series, using an automated procedure in *Ecosim*. Here, I used a set of models that were already adjusted for vulnerabilities and fitted to historical data following Walters *et al.* (2005). Vulnerabilities were adjusted based on the specific ecology of each species or trophic groups (if their behaviour, niche, or diet make them more or less vulnerable to predators), rather than assumed to scale to trophic levels. Using credible models that can reproduce observed historical response to disturbances such as fishing allow us to gain confidence when analyzing the possible impact of removing marine mammals in the ecosystem.

The first thing that was analyzed based on *Ecosim* runs was the overall behaviour of trophic groups driven by original time series of fishing effort. Increases or decreases in abundance were noted for the major impacted groups.

Some Japanese studies asserts that fisheries would globally benefit from a major marine mammals cull (Anonymous, 2001). In order to quantify the potential impact of marine mammal predation on the ecosystem, and to examine if there really is strong competition with the fisheries, *Ecosim* simulations were done over 22 to 89 years time periods, depending on the model's available time series. A first simulation was done with the original ecosystem structure (and original catch of fish and marine mammals), another was performed with a very high catch of marine mammals species, with the purpose of

driving down their biomass close to zero. Both scenarios were analyzed to see which groups and/or fisheries would suffer or benefit (in terms of increase or decrease in biomass) from the extirpation of marine mammals in the ecosystem.

A hunting pattern was chosen which generated an important increase in the mortality on the marine mammal mortality, in order to drive their populations close to extinction. Vasconcellos *et al.* (1997) showed that for fish species, a 5-fold increase leads to serious depletion in a group. Also, such an extreme scenario is routinely applied to many fish populations and often associated with stock collapse (Patterson, 1992). This has never been done for marine mammals, but my tests have shown that the same kind of increase in anthropogenic mortality is needed to simulate a crash in marine mammal biomass. However, because some marine mammal species are not targeted at all by any fishery, I could not only multiply fishing mortality (F) by five. Thus, an F of 1.0 (representing an average five-fold increase for marine mammal species that were already hunted) was applied to each marine mammal groups in the models. Since each model was fitted to different time series, covering different periods, I did not perform a 100 years simulation as it was done by Vasconcellos *et al.* (1997). Here, the higher values of F were kept constant for the first 20% of the time series, and then returned to the baseline, with the model running for the remaining 80% of the time.

Results

4.3.1 Total annual food consumption of marine mammals and fisheries catches

The global pattern of marine mammal consumption *versus* fisheries catches is similar to what was found by Kaschner (2004), indicating that a high overlap occurs between marine mammals and fisheries in the predicted 'hotspots' of potential conflict. When all the models' results are combined (Figure 4.2), I find that the major source of competition between marine mammals and fisheries in the principal 'hotspots' is for 'miscellaneous fish', with attributes such as: demersal; benthic; benthopelagic; bathydemersal; reef-associated habitat & common length <150 cm; or pelagic habitat & common length >60 cm and <150 cm (see Pauly *et al.* [1998c] for detailed food types categories) and 'small pelagic' (FishBase attributes: pelagic habitat & common length <60

cm; see Pauly *et al.* [1998c] for detailed food types categories). Marine mammals consumption is diversified and represents a great array of marine organisms, while the catches are much more concentrated on 'miscellaneous fish', which account for about 75% of all the fish biomass taken. While marine mammals can consume different prey groups (mainly large zooplankton, cephalopods, small pelagic fish and macrobenthos), fisheries in the seven studied ecosystems combined are mainly focused on small crustaceans such as shrimp, pelagic fish (redeye, *Etrumeus whiteheadi*; redfish, *Sebastes* spp.; anchovy, *Eugraulis capensis*; sprat, *Sprattus sprattus*) and demersal species such as hake species, lingcod (*Ophiodon elongates*), and sandeel (*Ammodytes tobianus*).

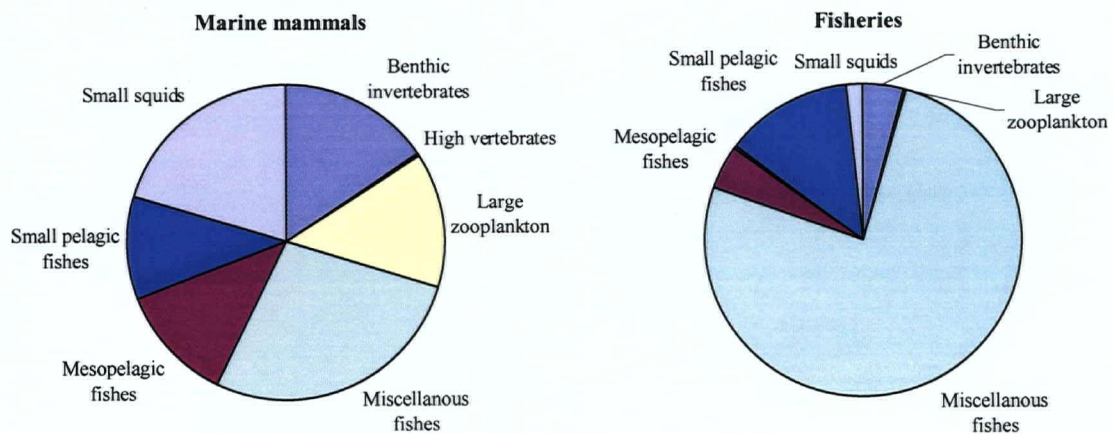


Figure 4.2. Estimated mean annual catch and food consumption by food types expressed as proportions of total amounts taken ($t \cdot km^{-2}$) for all ecosystems combined. Note the greater proportion of miscellaneous fish taken by the fisheries.

While a global comparison is useful, it is also important to compare marine mammals and fisheries on an ecosystem-by-ecosystem basis. In the Eastern Bering Sea system (Table 4.3), all fisheries catches fell into three types: miscellaneous fishes; mesopelagic fishes and higher vertebrates. In contrast, these food types accounted for less than a third of marine mammal consumption, which was more diverse and principally composed of benthic invertebrates, large zooplankton and miscellaneous fish.

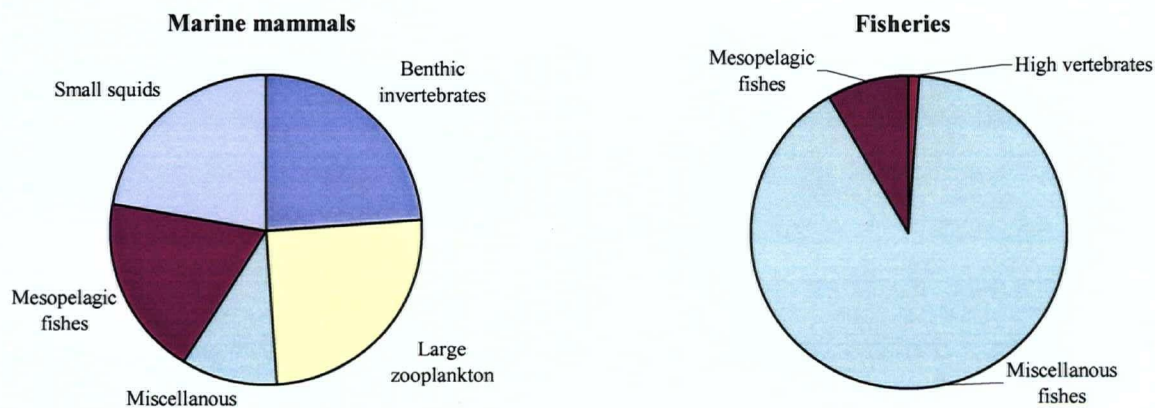


Figure 4.3. Estimated mean annual catch and food consumption by food types expressed as proportions of total amounts taken ($t \cdot km^{-2}$) in the Eastern Bering Sea ecosystem.

In the Northern Gulf of St. Lawrence (Figure 4.4), miscellaneous fish are the main target, accounting for 32% and 74% for marine mammal consumption and fisheries, respectively. However, the remaining marine mammal consumption is shared between three important groups (small pelagics, benthic invertebrates, and large zooplankton), while the fishery mainly catch miscellaneous fish (cod, redfish, and large Greenland halibut), benthic invertebrates (shrimp, crab, and molluscs) and small pelagics (herring). Marine mammal catch (mainly seal hunt) also occurs in the Gulf of St. Lawrence, accounting for about 1% of the total catch (high vertebrates).

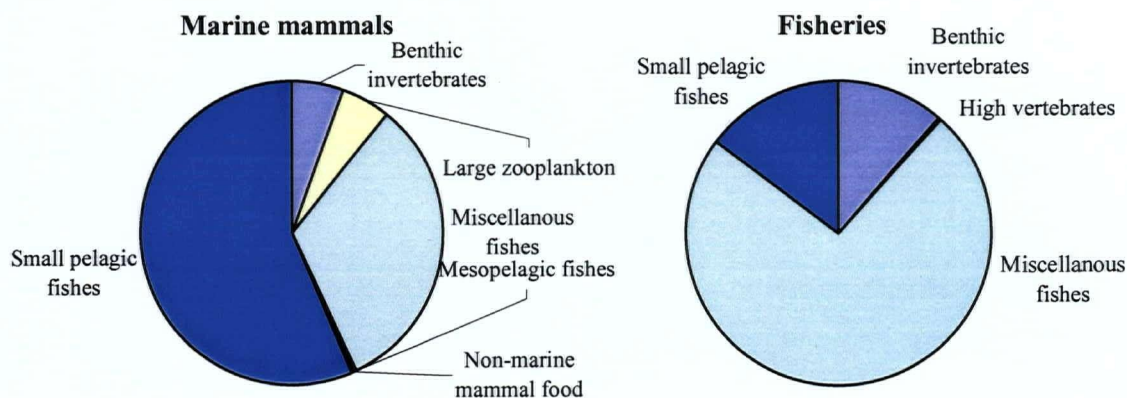


Figure 4.4. Estimated mean annual catch and food consumption by food types expressed as proportions of total amounts taken ($t \cdot km^{-2}$) in the northern Gulf of St. Lawrence ecosystem.

In the Benguela system (Figure 4.5), more than 95% of all fisheries fell into three types: miscellaneous; mesopelagic and small pelagic fishes. Similarly, these food types were also the most important for marine mammals of this ecosystem, whose diets also included an important part of small squids.

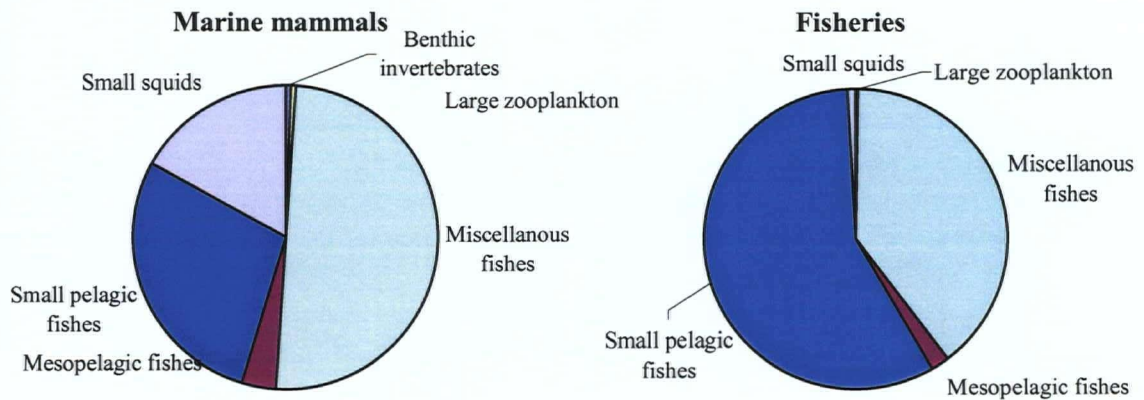


Figure 4.5. Estimated mean annual catch and food consumption by food types expressed as proportions of total amounts taken ($t \cdot km^{-2}$) in the Benguela ecosystem.

The Eastern tropical Pacific model (Figure 4.6) shows that most resources taken by fisheries are composed of only two food types: miscellaneous fish and non-mammal food. On the other hand, marine mammals feed on a variety of food types in this ecosystem, mainly small squids, mesopelagic, and small pelagic fish.

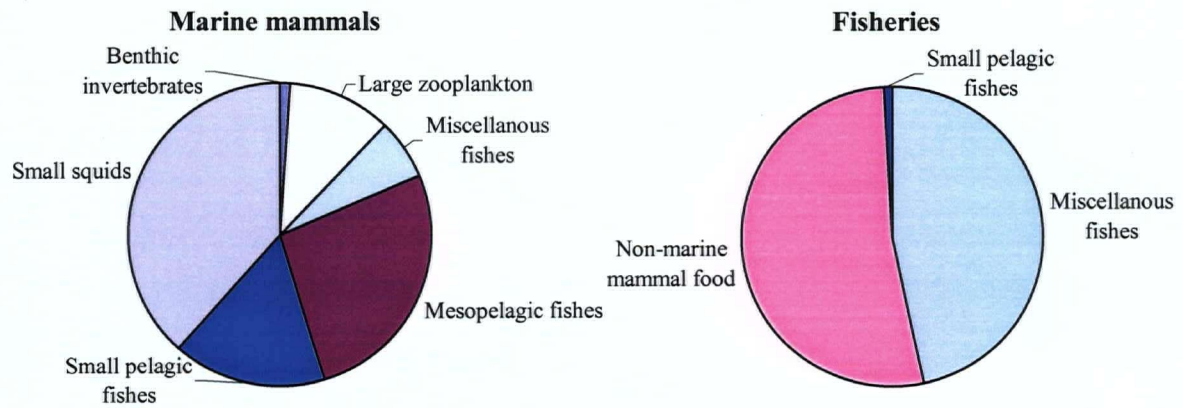


Figure 4.6. Estimated mean annual catch and food consumption by food types expressed as proportions of total amounts taken ($t \cdot km^{-2}$) in the Eastern Tropical Pacific ecosystem.

The North Sea model (Figure 4.7) shows that about 75% of resources taken by marine mammals or by fisheries is composed of miscellaneous fish. However, the difference between marine mammals and fisheries is in the kind of miscellaneous fish they exploit. The main fishes eaten by marine mammals are dab and cod, while fisheries mostly target Norway pout (*Trisopterus esmarkii*), sprat and sandeel. In this model, both marine mammals and fisheries catch fell in three categories: miscellaneous fish and small pelagic for both, as well as benthic invertebrates for marine mammals and mesopelagic fish for fisheries.

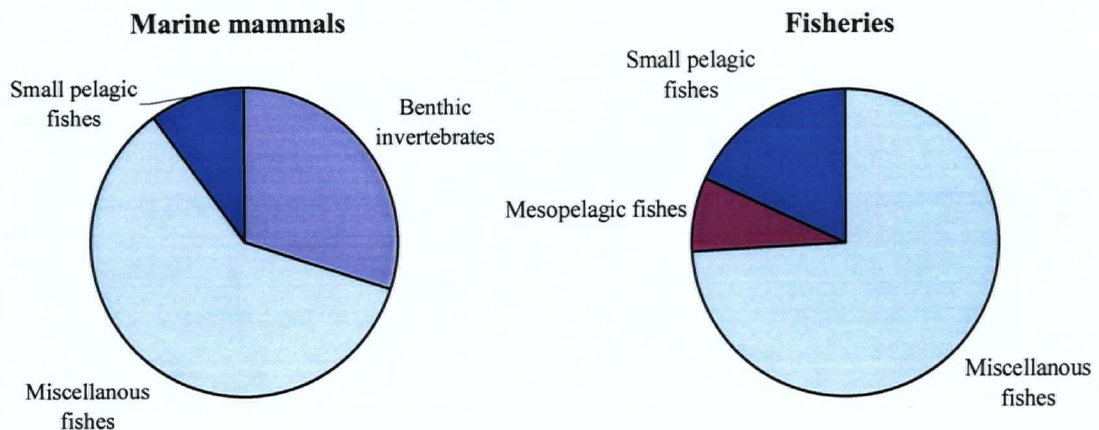


Figure 4.7. Estimated mean annual catch and food consumption by food types expressed as proportions of total amounts taken ($t \cdot km^{-2}$) in the North Sea ecosystem.

In the Gulf of Thailand (Figure 4.8), marine mammals feed on a great variety of groups, while fisheries mainly catch benthic invertebrates and miscellaneous fish. These two food types represent more than 75% of the catch by fisheries and about a third of consumption by marine mammals. 'Trash fish' (bycatch catches that are used in the production of fishmeal) is one of the most important miscellaneous fish to be taken by fisheries and marine mammals, but then the two competing groups differ as marine mammals consume more small pelagic and benthos, and fisheries catch more shellfish and shrimp.

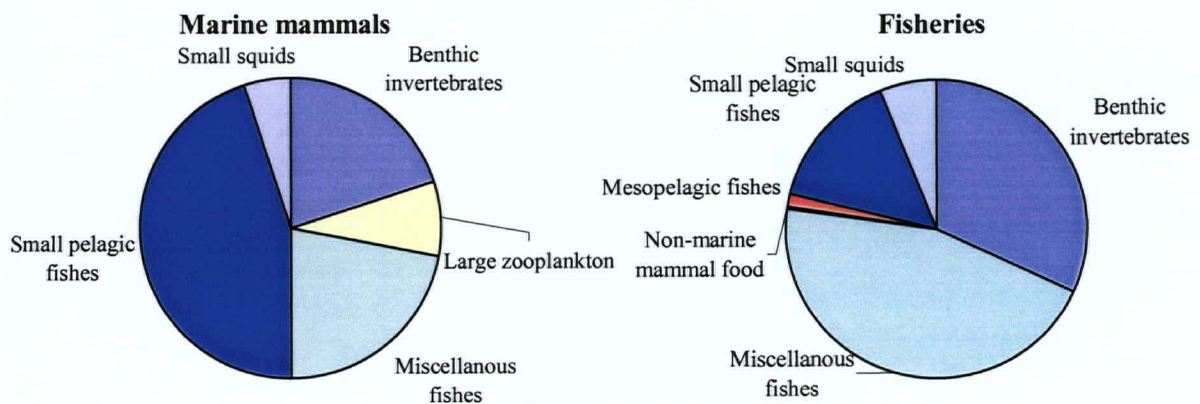


Figure 4.8. Estimated mean annual catch and food consumption by food types expressed as proportions of total amounts taken ($t \cdot km^{-2}$) in the Gulf of Thailand ecosystem.

In the Strait of Georgia ecosystem, almost all fish caught by the fisheries fell into one food group: miscellaneous fish (Figure 4.9). The same food type represents about 70% of the consumption by marine mammal, which is completed by mesopelagic and small pelagic fishes. Here again, fish taken by marine mammals are different than the one targeted by fisheries, even if they are all in the miscellaneous fish group: marine mammal consume more hake (*Merluccius capensis*) and demersal fish, while fisheries mostly catch herring (*Clupea harengus*), chinook salmon (*Oncorhynchus tshawytscha*) and lingcod.

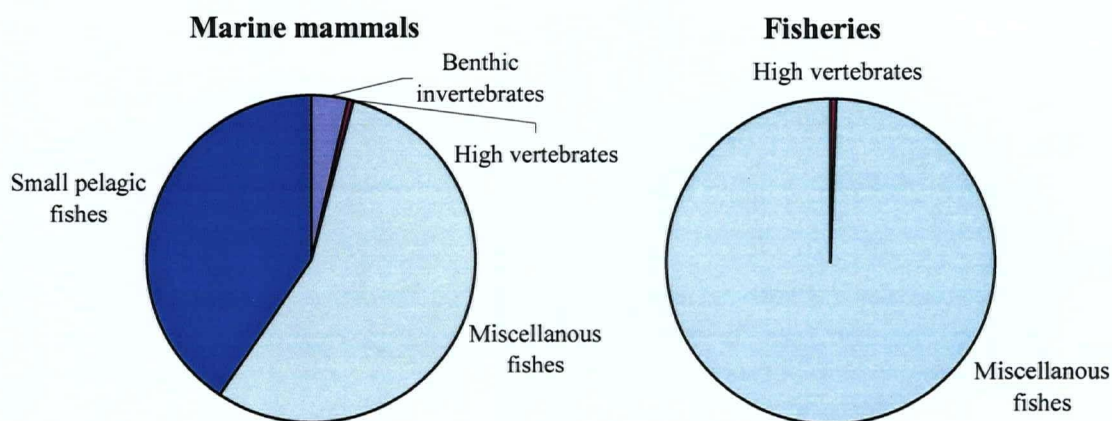


Figure 4.9. Estimated mean annual catch and food consumption by food types expressed as proportions of total amounts taken ($t \cdot km^{-2}$) in the Strait of Georgia ecosystem.

Thus, overall, I find that the degree of overlap depends largely on the resolution of the marine mammals prey and fisheries catches. Instances of direct overlap at the species level are observed in the Eastern Bering Sea (mainly for small flatfish, large flatfish, adult pollock [*Pollachius virens*], and other demersal fish), Gulf of St. Lawrence (planktivorous small pelagics, piscivorous small pelagics, shrimps and large crustaceans), Benguela (anchovy, redeye, and sardine [*Sardinops sagax*]), Eastern Tropical Pacific (small yellowfin tuna [*Thunnus albacares*], skipjack [*Katsuwonus pelamis*], and *Auxis* sp.), Gulf of Thailand (“trashfish”, *Rastrelliger* spp., cephalopods, small demersals, and small pelagics), and Strait of Georgia (resident coho salmon [*Oncorhynchus kisutch*], resident chinook salmon, and lingcod). However, even at the species level, few overlap occurs between marine mammals prey and fisheries catches in the North Sea.

4.3.2 Mean trophic level of marine mammals' consumption and fisheries catches

In most ecosystems, marine mammals feed on lower trophic level species (Table 4.3). Except for the northern Gulf of St. Lawrence and the Strait of Georgia, TL_Q has lower values than TL_C . The largest discrepancy between these two values is observed in the Eastern Tropical Pacific, where TL_C is about 25% larger than the TL_Q (4.70 versus 3.76).

Table 4.3. Mean trophic level of marine mammals' consumption and fisheries catches.

Ecosystem model	TL_Q (Marine mammals)	TL_C (Fisheries catch)
Eastern Bering Sea	2.83	3.42
Gulf of St. Lawrence	3.24	3.71
Benguela	3.65	3.73
Eastern Tropical Pacific	3.76	4.70
North Sea	3.25	3.44
Gulf of Thailand	2.08	2.46
Strait of Georgia	3.36	3.25
Mean	2.88	3.42

4.3.3 Primary production required to sustain marine mammals' consumption and fisheries catch

The primary production required (PPR) to sustain marine mammal consumption is always lower than PPR to sustain the fisheries (Table 4.4). Globally, PPR for fisheries is 50% higher than PPR for marine mammals. In terms of percentage, the PPR for fisheries is twice as high as PPR for marine mammals' consumption (20% *versus* 10%). Marine mammals of the Benguela system have the lowest PPR (they require only 2.2% of total primary production of the system), compared to marine mammals in the Eastern Bering Sea, where the PPR is 31.8% of total primary production. For fisheries, the lowest value is seen in the Benguela system (3.2%), while the highest PPR for fisheries catch is in the Eastern Bering sea (53.9%), closely followed by the North Sea (50.1%).

Table 4.4. Primary production required to sustain marine mammals' consumption and fisheries catches. Numbers in parentheses are PPR in percentage of total primary production in the system.

Ecosystem models	PPR Marine mammals' Q (t·km⁻²·year⁻¹)	PPR Marine mammals' Q (% of total PP)	PPR Fisheries catch (t·km⁻²·year⁻¹)	PPR Fisheries catch (% of total PP)
Eastern Bering Sea	949.48	31.8	1607.97	53.9
Gulf of St. Lawrence	296.61	9.8	559.11	18.4
Benguela	510.68	2.2	751.98	3.2
Eastern Tropical Pacific	121.62	14.1	54.19	6.3
North Sea	212.69	3.0	3512.05	50.1
Gulf of Thailand	191.20	1.8	245.63	2.3
Strait of Georgia	1339.65	6.0	1488.29	6.7
Mean	517.42	9.7	784.53	20.1

4.3.4 Resource overlap between marine mammals and fisheries

When marine mammals are considered as a whole group, their resource overlap with the fisheries varies a lot within the seven studied ecosystems (Table 4.5). The calculated resource overlap index, α , indeed varied from low (0.005 in the Eastern Tropical Pacific Ocean) to high (0.890 in the North Sea) values. Ecosystems with higher resources overlap seem to be the ones with lower diversity of food groups caught/eaten by fisheries/marine mammals. Models with a very high proportion of miscellaneous fish tend to have a higher resource overlap than systems where other food types are more important. When analysed per trophic group instead than per food type, the overlap is always lower. Highest overlap value is seen in the Benguela system, while lowest overlap happens in the Eastern Tropical Pacific. Interestingly, the North Sea ecosystem, which had the highest overlap per food type, has the third lowest value when overlap is calculated by trophic group. The number of trophic links in the ecosystem also has an effect on the resource overlap between marine mammal and fisheries. Indeed, food webs with lower connectance (less trophic links) tend to have higher overlap values (Table 4.5).

Table 4.5. Estimated resource overlap index between marine mammals and fisheries and connectance of the related ecosystem models.

Ecosystem model	$\alpha_{j,l}$	$\alpha_{j,l}$	Connectance
	per food type	per trophic group	
Eastern Bering Sea	0.031	0.006	0.274
Gulf of St. Lawrence	0.161	0.034	0.298
Benguela	0.714	0.120	0.231
Eastern Tropical Pacific	0.005	0.0003	0.218
North Sea	0.890	0.020	0.219
Gulf of Thailand	0.468	0.100	0.139
Strait of Georgia	0.163	0.024	0.250
GLOBAL (average)	0.149	0.043	-

4.3.5 Marine mammals and their impact on the trophic structure

The effect of a change in marine mammals' biomass can be analyzed in two ways in *EwE*. First, from the *Ecopath* model, the mixed trophic impact shows that an increase in marine mammals' biomass would impact negatively or positively the biomass of other

groups in the foodweb. Second, *Ecosim* analyses allow simulating the effect of the removal of marine mammals populations on the rest of the foodweb over time.

4.3.5.1 Eastern Bering Sea

The mixed trophic impact of marine mammals and fishery in the Eastern Bering Sea model shows that both marine mammals and fishery have an overall negative impact on the entire ecosystem (MM = -2.98; fishery = -3.04). The groups that are mostly impacted by marine mammal consumption are deepwater fish, large flatfish and other demersal fish. Conversely, small flatfish, deep pelagics and flatfish trawl seem to benefit from the presence of marine mammals in the ecosystem (Figure 4.10).

The same *TI* analysis for the fishery shows that the main negatively impacted groups of the Eastern Bering Sea ecosystem are most marine mammals, as well as flatfish (large and small). Deepwater fish, juvenile pollock and beaked whales (*Mesoplodon stejnegeri*) seem to benefit from the fishery (Figure 4.10).

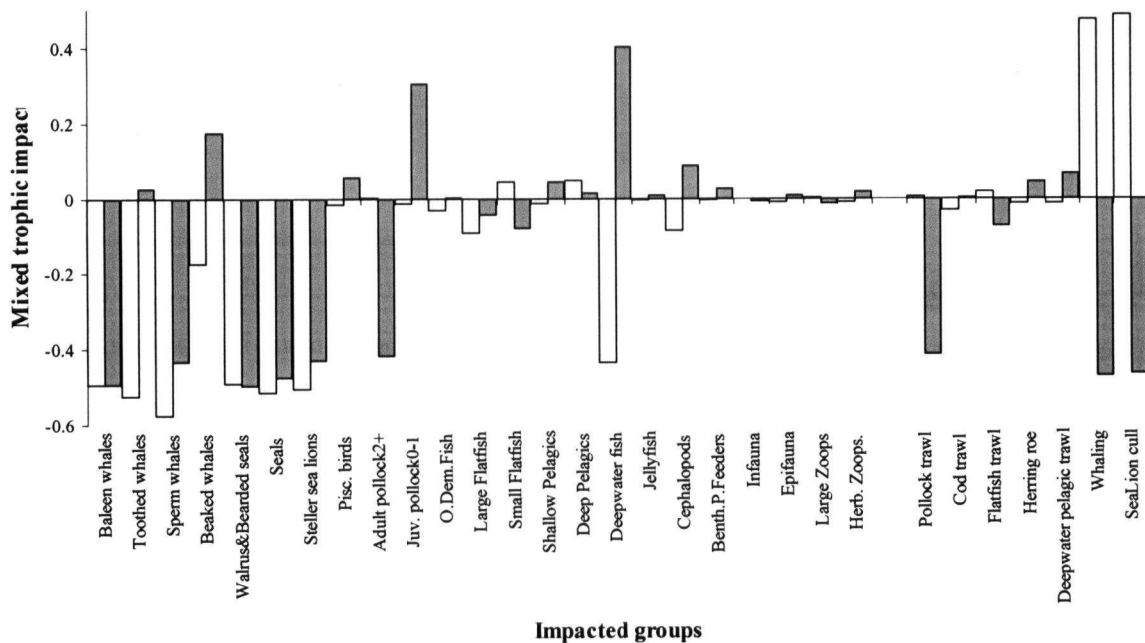


Figure 4.10. Mixed trophic impact of marine mammals (white) and fisheries (grey) on fish and fleet groups of the Eastern Bering Sea.

In *Ecosim*, the Eastern Bering Sea model was first analyzed with time series of fishing mortality (F) to see which groups' biomass decline or increase over time. The model covers four sources of fishing mortality (pollock trawl, cod trawl, flatfish trawl, herring roe, deepwater pelagics, and whaling & sea lion cull), which were combined to see the overall effect on the whole ecosystem. Time series cover a period of 51 years, from 1950 to 2000. At the end of the simulation with the "true" fishing effort, some groups stabilized at higher biomass (deep pelagics, benthic pelagic feeders, small flatfish, large zooplankton, phytoplankton and cephalopods). Other groups stabilized after a decrease of biomass (deep-water fish, juvenile and adult pollock, shallow pelagics, sperm whales [*Physeter macrocephalus*], baleen whales, Steller sea lions, and epifauna). However, the biomasses of jellyfish and large flatfish exploded, while other demersal fish and piscivorous birds suffered from a substantial decline, or near extinction, respectively (Figure 4.11).

After simulating marine mammal extirpation in the Bering Sea ecosystem (Figure 4.12), there was an increase in biomass (compared to the simulation without marine mammal extirpation) in the other demersal fish, deep pelagics, deepwater fish, jellyfish and cephalopods. All other groups showed a decrease in biomass if marine mammals were removed from the ecosystem (Figure 4.12). Over a period of 51 years, there is an overall decrease of 6% of total biomass if marine mammals are eradicated ($B_{\text{tot}} = 316 \text{ t}\cdot\text{km}^{-2}$ with marine mammals, and $298 \text{ t}\cdot\text{km}^{-2}$ without them; Table 4.6). This represents of course the complete extirpation of marine mammals biomass itself, but also seabirds, and other fish species such as small flatfish, as well as critical biomass decrease for shallow pelagics (-99%), or epifauna (-97%).

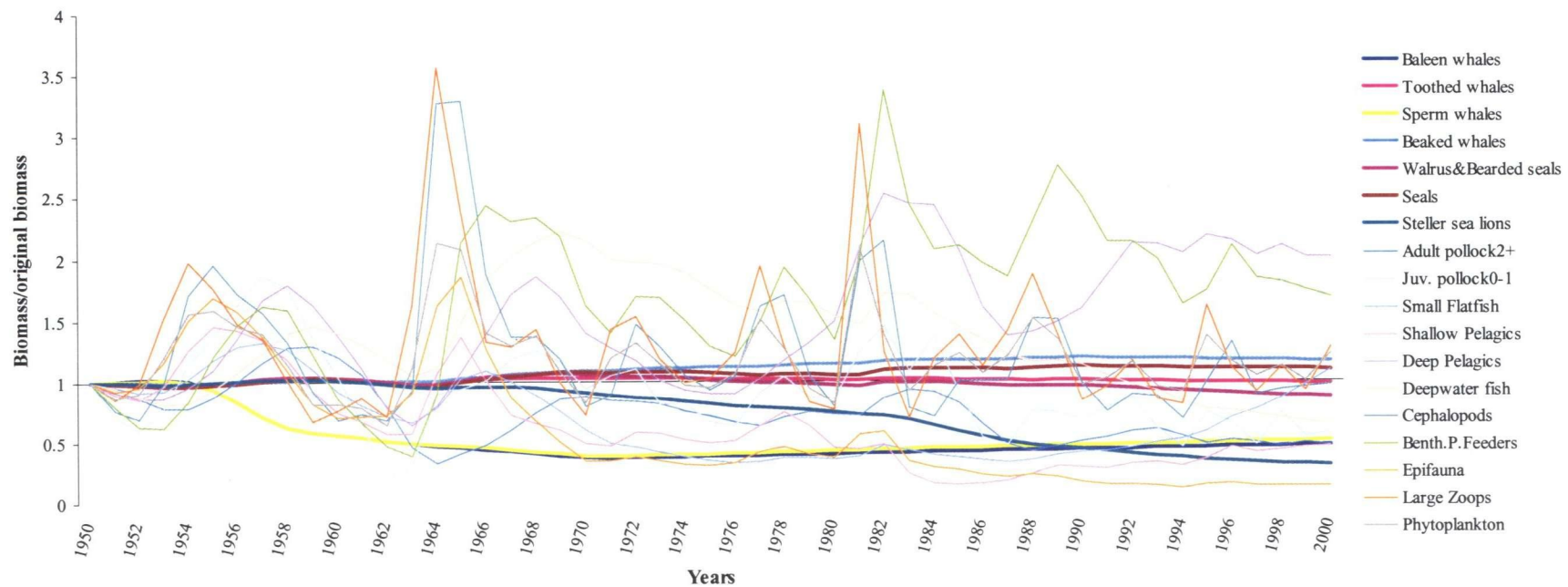


Figure 4.11. Ecosim results for the Eastern Bering Sea model with original fishing effort.

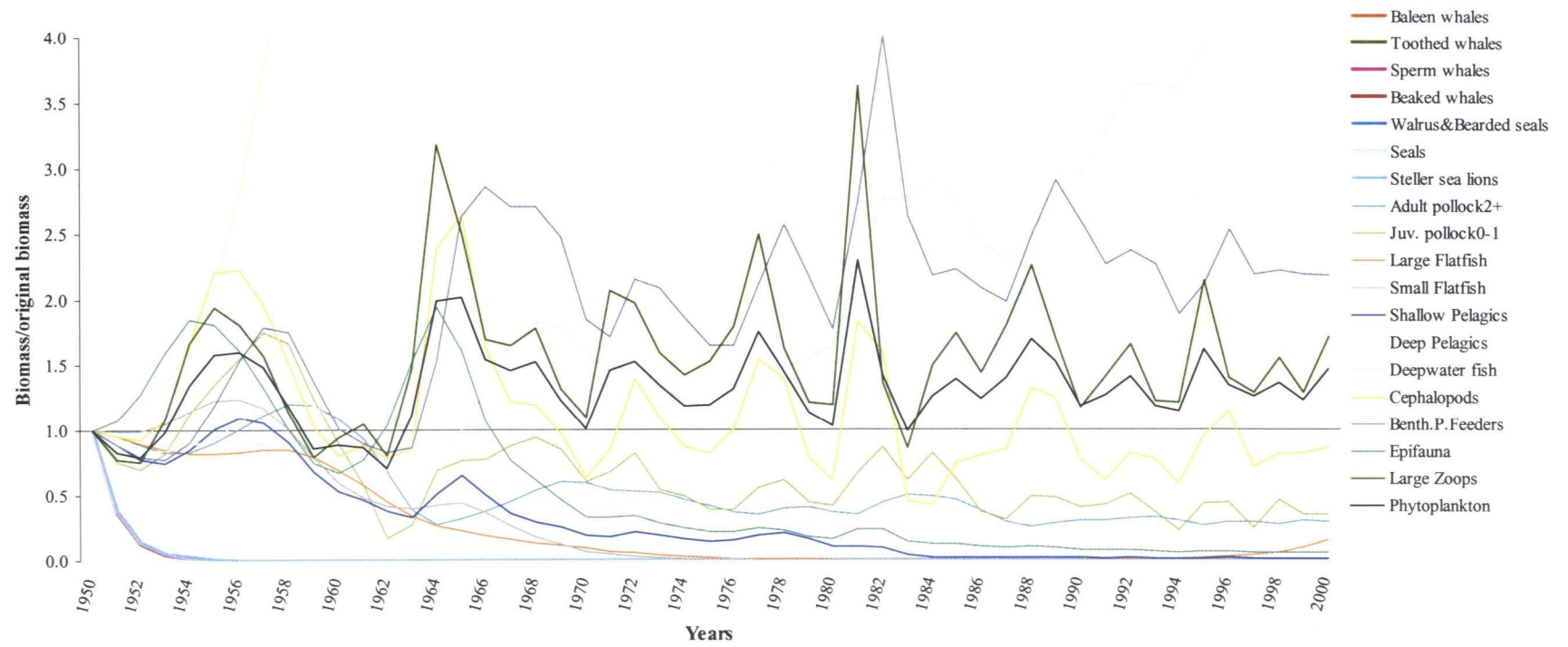


Figure 4.12. *Ecosim* results for the Eastern Bering Sea model with extirpation of marine mammals.

The main species targeted by the Eastern Bering Sea fisheries, all fleets combined, are adult pollock and shallow pelagics. When marine mammals are absent of the system, *Ecosim* predicts that there are less fish to catch for both fisheries than if marine mammals were present in the system (a decrease of 16% for adult pollock, and of 99% for shallow pelagics) (Figure 4.13). Out of eight fisheries (excluding whaling and sea lion cull), five suffer from a decrease in the biomass of their target species if there is no marine mammals in the ecosystem (Table 4.6).

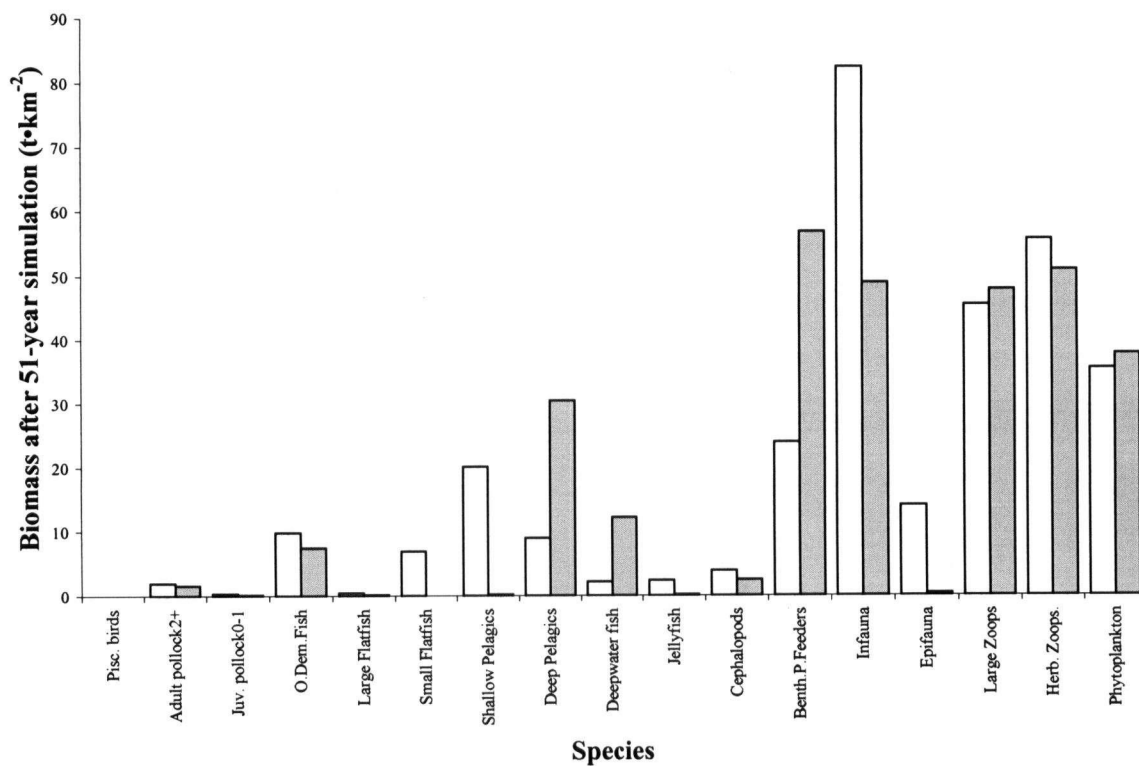


Figure 4.13. Biomass change after a 51-year simulation in the Eastern Bering Sea ecosystem, with (white) and without (grey) marine mammals.

Table 4.6. Biomass ($\text{t}\cdot\text{km}^{-2}\cdot\text{year}^{-1}$) change from the start (S) to the end (E) of the 51-year *Ecosim* simulation in the Eastern Bering Sea ecosystem, with and without marine mammals (MM). Groups in bold represent the commercially important species.

Group name	With MM			Without MM			B change after MM extirpation (%)
	Biomass (Start)	Biomass (End)	Biomass (E/S)	Biomass (Start)	Biomass (End)	Biomass (E/S)	
Baleen whales	0.694	0.432	0.620	0.547	0.000	0.000	-100.0
Toothed whales	0.009	0.009	1.020	0.007	0.000	0.000	-100.0
Sperm whales	0.438	0.259	0.590	0.345	0.000	0.000	-100.0
Beaked whales	0.001	0.001	1.170	0.001	0.000	0.000	-100.0
Walrus & Bearded seals	0.054	0.075	1.400	0.043	0.000	0.000	-100.0
Seals	0.106	0.112	1.050	0.084	0.000	0.010	-100.0
Steller sea lions	0.029	0.028	0.950	0.023	0.000	0.000	-100.0
Piscivorous birds	0.006	0.005	0.850	0.006	0.000	0.000	-100.0
Adult pollock 2+	5.063	1.985	0.390	5.494	1.658	0.300	-16.5
Juvenile pollock 0-1	0.901	0.349	0.390	0.903	0.185	0.200	-47.0
O. Demersal Fish	8.918	9.851	1.100	8.956	7.503	0.840	-23.8
Large Flatfish	1.155	0.473	0.410	1.158	0.146	0.130	-69.1
Small Flatfish	8.519	6.954	0.820	8.519	0.000	0.000	-100.0
Shallow Pelagics	20.818	20.142	0.970	20.914	0.216	0.010	-98.9
Deep Pelagics	7.814	8.992	1.150	7.811	30.506	3.910	239.3
Deepwater fish	1.010	2.175	2.150	1.016	12.198	12.010	460.8
Jellyfish	0.047	2.428	51.280	0.047	0.171	3.610	-93.0
Cephalopods	3.406	3.945	1.160	3.485	2.478	0.710	-37.2
Benth.Pel. feeders	28.758	23.957	0.830	28.772	56.987	1.980	137.9
Infafauna	75.058	82.789	1.100	75.056	49.053	0.650	-40.7
Epifauna	7.995	14.074	1.760	8.003	0.418	0.050	-97.0
Large Zooplankton	38.937	45.625	1.170	38.914	47.986	1.230	5.2
Herb. Zooplankton	48.909	55.863	1.140	48.944	51.094	1.040	-8.5
Phytoplankton	27.493	35.565	1.290	27.486	37.892	1.380	6.5
Discards	0.000	0.000	1.000	0.000	0.000	1.000	0.0
Detritus	0.000	0.000	1.040	0.000	0.000	1.340	0.0
Total	286.137	316.088	1.100	286.535	298.494	1.040	-5.6

4.3.5.2 Northern Gulf of St. Lawrence

In the Northern Gulf of St. Lawrence, the mixed trophic impact of marine mammals and fishery shows that fisheries have an overall negative impact (-4.93) that is much higher than that of marine mammals (-2.93). The groups that are the most negatively impacted by marine mammal consumption are large demersals, large pelagics and Greenland halibut (*Reinhardtius hippoglossoides*; large and small). In contrast, skates, small demersals, shrimp and most benthic invertebrates seem to benefit from marine mammals in the ecosystem (Figure 4.14).

All marine mammals and seabirds, large cod, shrimp, small demersals and most benthic invertebrates are negatively impacted by fisheries in the Gulf of St. Lawrence. Small Greenland halibut, large demersals, and small cod seem to benefit from fisheries (Figure 4.14).

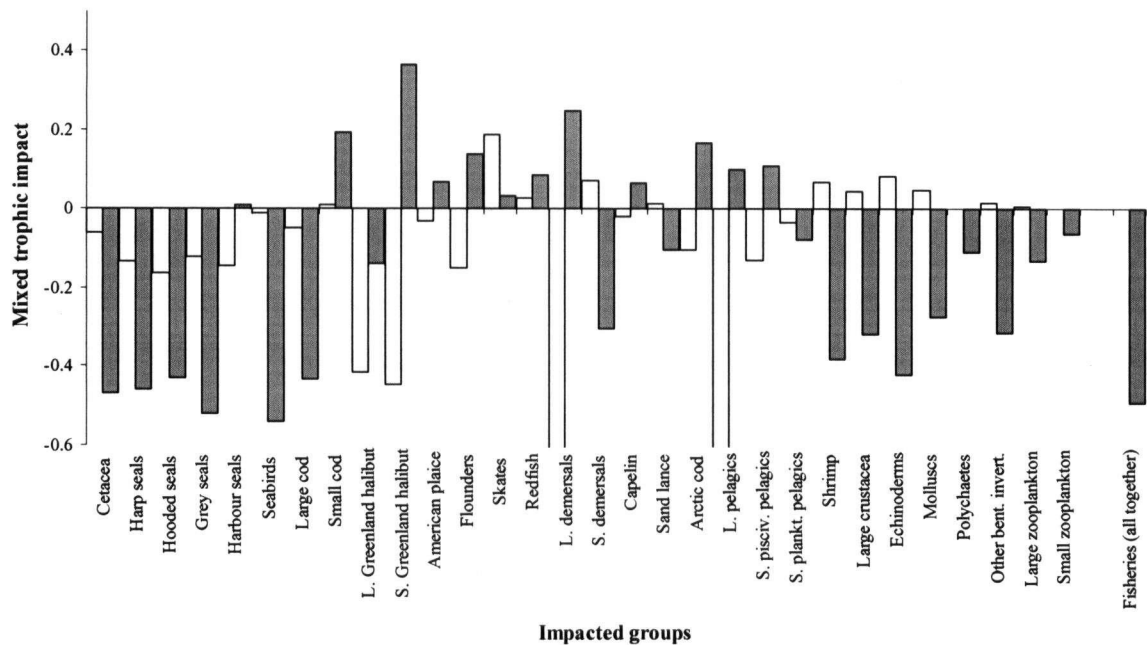


Figure 4.14. Mixed trophic impact of marine mammals (white) and fisheries (grey) on fish and fleet groups of the Gulf of St. Lawrence.

When analyzed with time series of fishing mortality in *Ecosim*, the Gulf of St. Lawrence model was analyzed to see which groups' biomass decline or increase over time. The model covers one source of combined fishing mortality that represents all fishing fleets operating in the system. Time series cover a period of 42 years, from 1960 to 2002, but only the last 22 years are documented in terms of fish biomass (the first 20 years are time series of marine mammal biomasses and catches). At the end of the simulation with original fishing effort, some groups show a relatively constant increase in biomass (Greenland halibut, harbour seals, grey seals, and hooded seals), while most groups stabilized after a slight increase of biomass. No groups show severe depletion (Figure 4.15).

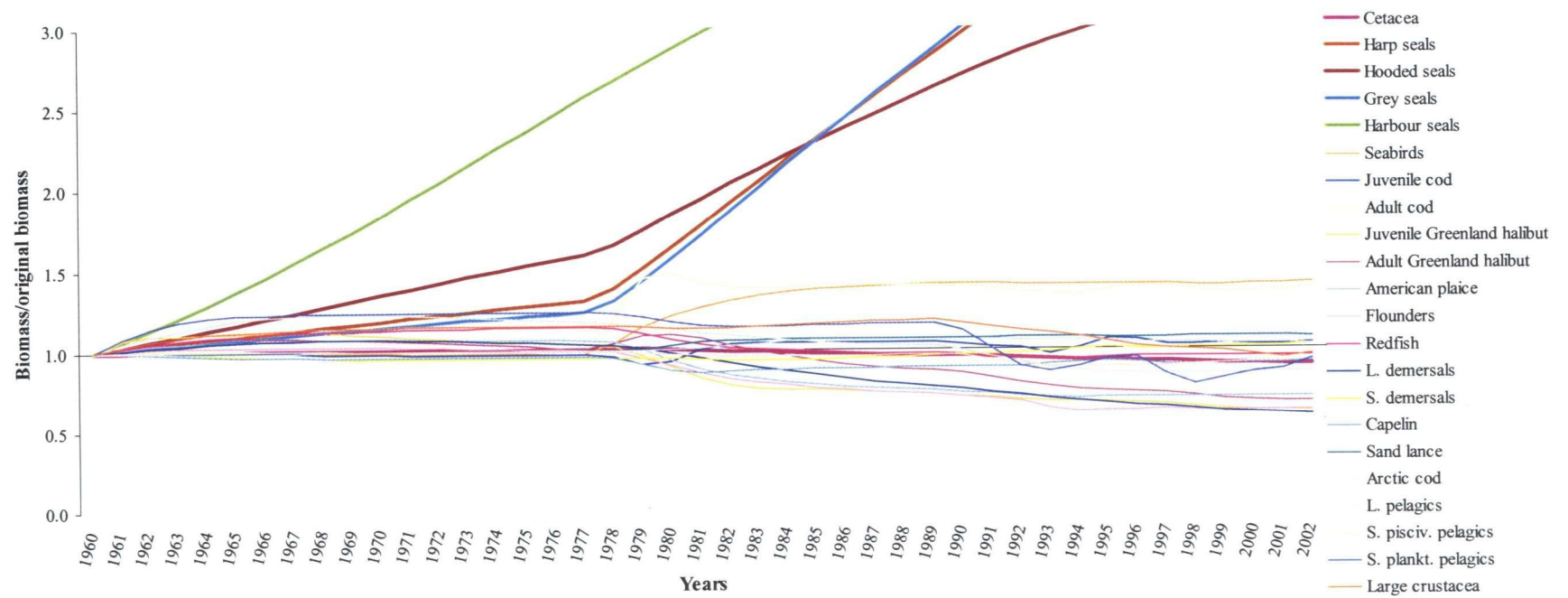


Figure 4.15. *Ecosim* results for the Gulf of St. Lawrence model with original fishing effort.

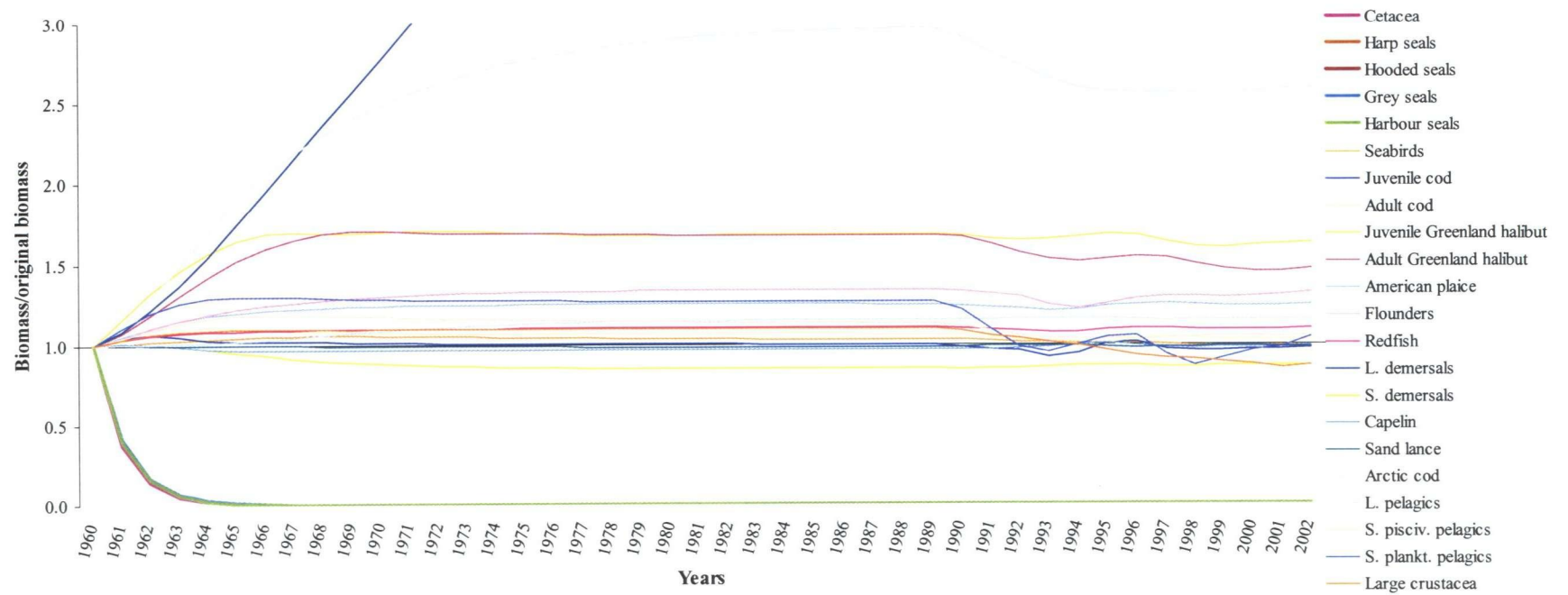


Figure 4.16. *Ecosim* results for the Gulf of St. Lawrence model after the extirpation of marine mammals.

When all seal and cetacean species are removed from the ecosystem, its structure changes (Figure 4.16). There is an explosion in the biomass of Greenland halibut (adult and juveniles), and an increase in large pelagic and demersal groups. The remaining groups of that simulated system without marine mammals stabilized around a similar equilibrium, and there is no significant change in total biomass ($439 \text{ t}\cdot\text{km}^{-2}$) over the 43-year simulation (Table 4.7).

Most groups which originally had lower biomasses in the Gulf of St. Lawrence system appeared to increase their biomass after the extirpation of marine mammals. However, for groups that were important in the system (e.g., adult cod, capelin, and small planktivorous pelagics), the increase was limited (Table 4.7).

The most important fishery in the Gulf of St. Lawrence in terms of landings in the 1980s was cod, redfish, small planktivorous pelagics (herring) and shrimp. In a scenario without marine mammals, most of these target species show no significant change, or decrease slightly as in the case of shrimp (Figure 4.17).

Table 4.7. Biomass ($\text{t}\cdot\text{km}^{-2}\cdot\text{year}^{-1}$) change from the start (S) to the end (E) of the 43-year *Ecosim* simulation in the Gulf of St. Lawrence ecosystem, with and without marine mammals (MM). Groups in bold represent the commercially important species.

Group name	With MM			Without MM			B change after MM extirpation (%)
	Biomass (Start)	Biomass (End)	Biomass (E/S)	Biomass (Start)	Biomass (End)	Biomass (E/S)	
Cetacea	0.104	0.107	1.030	0.082	0.000	0.000	-100.0
Harp seals	0.048	0.051	1.060	0.025	0.002	0.070	-96.1
Hooded seals	0.003	0.004	1.100	0.003	0.000	0.000	-100.0
Grey seals	0.007	0.008	1.060	0.006	0.000	0.000	-100.0
Harbour seals	0.002	0.002	1.150	0.001	0.000	0.000	-100.0
Seabirds	0.002	0.002	1.010	0.002	0.003	1.050	50.0
Juvenile cod	0.805	0.911	1.130	0.805	0.904	1.120	-0.8
Adult cod	1.813	1.986	1.100	1.813	2.027	1.120	2.1
Juv. Greenland halibut	0.144	0.209	1.450	0.144	0.385	2.680	84.2
Ad. Greenland halibut	0.280	0.350	1.250	0.280	0.615	2.190	75.7
American plaice	0.773	0.790	1.020	0.773	0.806	1.040	2.0
Flounders	0.498	0.527	1.060	0.498	0.577	1.160	9.5
Skates	0.190	0.204	1.080	0.190	0.214	1.130	4.9
Redfish	7.840	8.045	1.030	7.840	8.046	1.030	0.0
L. demersals	0.746	0.790	1.060	0.746	0.930	1.250	17.7
S. demersals	1.508	1.503	1.000	1.509	1.480	0.980	-1.5
Capelin	11.765	11.741	1.000	11.768	11.782	1.000	0.3
Sand lance	2.230	2.229	1.000	2.230	2.238	1.000	0.4
Arctic cod	0.036	0.036	1.000	0.036	0.036	1.020	0.0
L. pelagics	0.051	0.054	1.060	0.051	0.075	1.480	38.9
S. pisciv. pelagics	2.213	2.217	1.000	2.214	2.319	1.050	4.6
S. plankt. pelagics	1.651	1.688	1.020	1.651	1.696	1.030	0.5
Shrimp	0.919	0.910	0.990	0.919	0.899	0.980	-1.2
Large crustacea	0.951	0.970	1.020	0.951	0.968	1.020	-0.2
Echinoderms	104.490	104.507	1.000	104.490	104.503	1.000	0.0
Molluscs	57.757	57.770	1.000	57.757	57.769	1.000	0.0
Polychaetes	13.380	13.379	1.000	13.380	13.375	1.000	0.0
O. benthic invertebrates	6.750	6.750	1.000	6.750	6.749	1.000	0.0
Large zooplankton	12.850	12.849	1.000	12.850	12.847	1.000	0.0
Small zooplankton	61.069	61.072	1.000	61.069	61.072	1.000	0.0
Phytoplankton	14.850	14.850	1.000	14.850	14.850	1.000	0.0
Detritus	132.609	132.636	1.000	132.608	132.638	1.000	0.0
Total	438.334	439.146	1.000	438.291	439.805	1.000	0.2

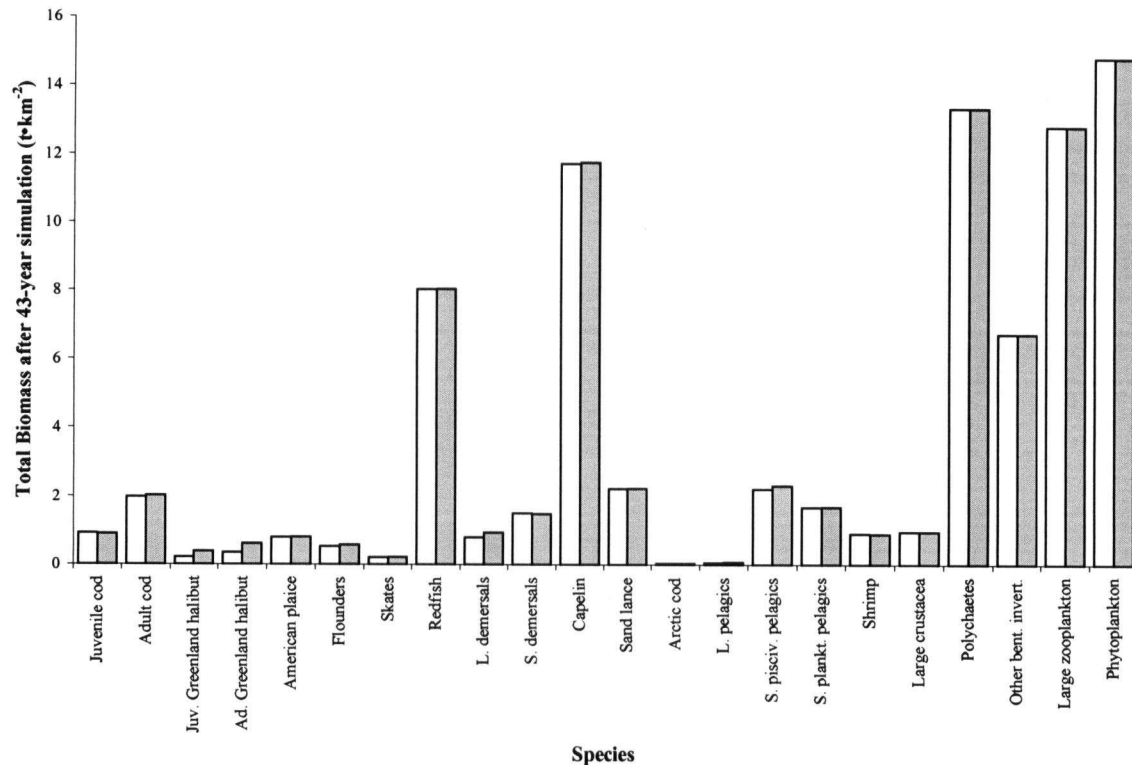


Figure 4.17. Biomass change after a 43-year simulation in the Gulf of St. Lawrence ecosystem, with (white) and without (grey) marine mammals (echinoderms, polychaetes and small zooplankton (not shown) have very high and nearly identical biomasses with and with out marine mammals in the system, i.e., 105, 58, and 51 t·km⁻², respectively).

4.3.5.3 Benguela system

The mixed trophic impact of marine mammals and fishery in the Benguela model shows that both marine mammals and fishery have an overall negative impact on the entire ecosystem (-0.011 and -0.105, respectively). However, fisheries' negative impact on the groups' biomass in the Benguela ecosystem is larger by an order of magnitude. Fish groups that are the most negatively impacted by marine mammal consumption are cape hake (*Merluccius capensis*), horse mackerel (*Trachurus capensis*) and cephalopods. Conversely, apex chondrichthyans, mesopelagics and redeye seem to benefit from marine mammals presence in the ecosystem. The fleet "other fisheries" would also benefit from an increase in marine mammal biomass in terms of mixed trophic impacts (Figure 4.18).

The same analysis of mixed trophic impacts for the fishery shows that the main negatively impacted groups in the Benguela ecosystem are snoek (*Thyrsites atun*), sardine,

other large pelagics, shallow-water cape hake, and deep-water cape hake (*Merluccius paradoxus*) (Figure 4.18).

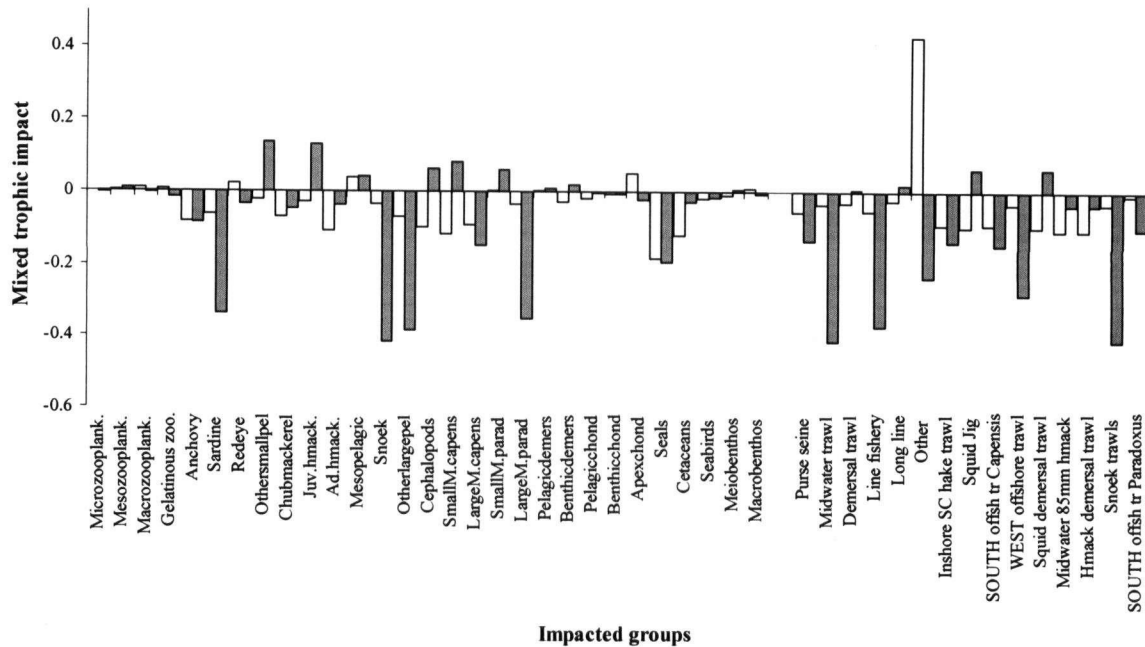


Figure 4.18. Mixed trophic impact of marine mammals (white) and fisheries (grey) on fish and fleet groups of the Benguela system.

With *Ecosim*, the Benguela model was first analyzed with fishing mortality to check which groups decline or increase. The total 15 fishing fleets (purse seine, midwater trawl, demersal trawl, line fishery, long line, inshore shallow Cape hake *capensis* trawl, squid jig, South offshore Cape hake *capensis* trawl, West offshore trawl, squid demersal trawl, midwater horse mackerel trawl, demersal horse mackerel trawl, snoek trawls, South offshore Cape hake *paradoxus* trawl, and other) were combined to analyze their overall effect on the entire ecosystem. Time series cover a period of 25 years, from 1978 to 2002. At the end of the simulation with the original fishing effort, some groups stabilized at higher biomass (seals, benthic chondrichthyans, pelagic chondrichthyans, benthic demersals, large shallow-water Cape hake, macrobenthos, large deep-water Cape hake, cephalopods and apex chondrichthyans). Other groups slightly decreased in biomass (Chub mackerel [*Scomber japonicus*], pelagic demersals, juvenile horse mackerel, small Cape hake *M. paradoxus*, mesopelagics, macrozooplankton, and mesozooplankton).

Sardine, anchovy, other large pelagics, snoek, seabirds and cetaceans showed an important explosion in biomass (Figure 4.19).

When marine mammals are removed from the ecosystem, the dynamics change (Figure 4.20). The removal of the cetaceans and seals groups seems to generate an explosion of sardine, as well as anchovy, snoek, other pelagics and seabirds. On the other end, mesopelagics, redeye and mesozooplankton groups decrease more than in the basic simulation. The remaining groups seem to stabilize around equilibrium after the 25-year simulation. There is no significant decrease in total biomass (258 *versus* 256 t·km⁻²), even if marine mammals are severely depleted. Other groups that showed important decrease in biomass are mesopelagics (-64%), other small pelagics (-27%), redeye (-20%), and pelagic demersals (-19%). An important increase in biomass is observed for snoek (47%), other large pelagics (28%), seabirds (27%), and large *M. capensis* (20%). No group except from marine mammals seems to be totally depleted (Table 4.8).

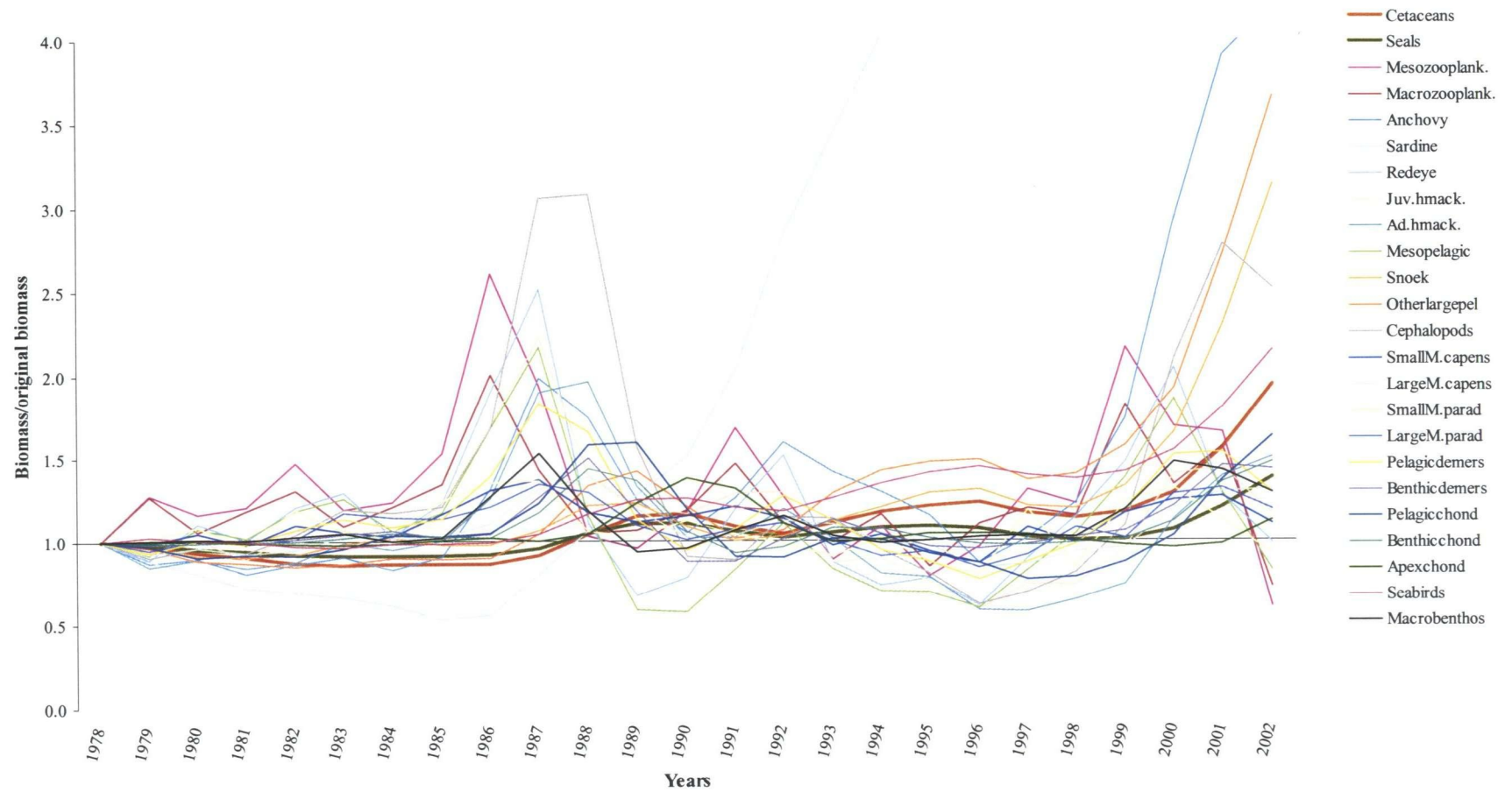


Figure 4.19. *Ecosim* results for the Benguela model with original fishing effort.

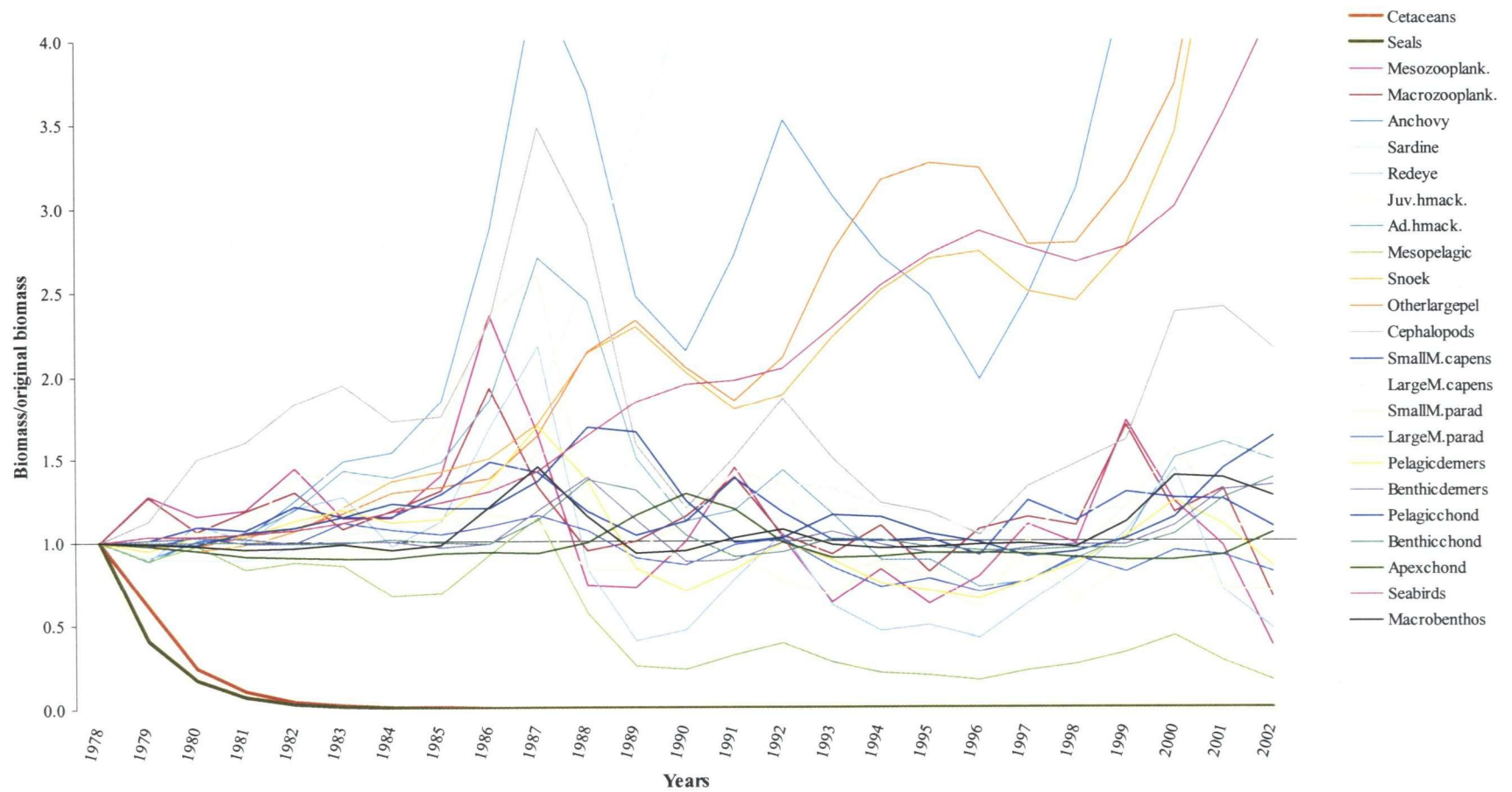


Figure 4.20. *Ecosim* results for the Benguela model after the extirpation of marine mammals.

Table 4.8. Biomass ($\text{t}\cdot\text{km}^{-2}\cdot\text{year}^{-1}$) change from the start (S) to the end (E) of the 25-year *Ecosim* simulation in the Benguela ecosystem, with and without marine mammals (MM). Groups in bold represent the commercially important species.

Group name	Ecosim with MM			Ecosim without MM			B change after MM extirpation (%)
	Biomass (Start)	Biomass (End)	Biomass (E/S)	Biomass (Start)	Biomass (End)	Biomass (E/S)	
Phytoplankton	61.330	84.115	1.370	61.330	83.973	1.370	-0.2
Benthic producers	6.606	6.111	0.920	6.606	6.119	0.930	0.1
Microzooplankton	1.296	1.830	1.410	1.296	1.891	1.460	3.3
Mesozooplankton	5.682	6.158	1.080	5.682	5.297	0.930	-14.0
Macrozooplankton	9.533	11.063	1.160	9.531	10.393	1.090	-6.1
Gelatinous zooplank.	4.504	5.444	1.210	4.504	4.687	1.040	-13.9
Anchovy	4.380	14.973	3.420	4.380	22.752	5.190	52.0
Sardine	0.788	8.021	10.170	0.788	7.964	10.100	-0.7
Redeye	5.429	4.904	0.900	5.436	3.922	0.720	-20.0
Other small pelagics	0.357	0.376	1.050	0.358	0.275	0.770	-26.9
Chub mackerel	0.280	0.285	1.020	0.281	0.253	0.900	-11.2
Juvenile h. mackerel	0.193	0.234	1.210	0.193	0.217	1.130	-7.3
Adult horse mackerel	1.611	1.688	1.050	1.618	1.645	1.020	-2.5
Mesopelagic	7.820	7.283	0.930	7.821	2.648	0.340	-63.6
Snoek	0.148	0.383	2.580	0.149	0.564	3.800	47.3
Other large pelagics	0.131	0.379	2.890	0.131	0.485	3.700	28.0
Cephalopods	1.344	1.640	1.220	1.354	1.652	1.220	0.7
Small <i>M.capensis</i>	0.420	0.448	1.070	0.422	0.463	1.100	3.3
Large <i>M.capensis</i>	0.822	1.083	1.320	0.823	1.301	1.580	20.1
Small <i>M.paradoxus</i>	1.231	1.230	1.000	1.233	1.070	0.870	-13.0
Large <i>M.paradoxus</i>	0.840	1.033	1.230	0.841	0.959	1.140	-7.2
Pelagic demersals	2.924	2.941	1.010	2.925	2.386	0.820	-18.9
Benthic demersals	3.494	4.579	1.310	3.496	4.497	1.290	-1.8
Pelagic chondrichth.	0.582	0.749	1.290	0.582	0.728	1.250	-2.8
Benthic chondrichth.	0.873	1.166	1.340	0.873	1.156	1.320	-0.9
Apex chondrichth.	0.045	0.047	1.050	0.045	0.044	0.990	-6.4
Seals	0.133	0.168	1.270	0.084	0.005	0.060	-97.0
Cetaceans	0.074	0.128	1.740	0.047	0.006	0.130	-95.3
Seabirds	0.015	0.030	1.980	0.015	0.038	2.510	26.7
Meiobenthos	12.310	15.056	1.220	12.310	15.055	1.220	0.0
Macrobenthos	58.475	74.005	1.270	58.473	73.549	1.260	-0.6
Total	193.672	257.549	1.330	193.627	255.995	1.320	-0.6

The main targeted species in the Benguela ecosystem are anchovy, sardine, redeye (all caught by purse seine) and large deep-water Cape hake (caught by west offshore trawl). When marine mammals are removed from the ecosystem, most of these commercially important fish end up with less biomass than in the initial ecosystem, except for anchovy (Figure 4.21). Out of 15 different fisheries in the Benguela ecosystem, eight

underwent an important loss in the biomass of their target species after 25-year without marine mammals. Moreover, four of these were in the top-five fisheries with the most important catch at the beginning of the simulation.

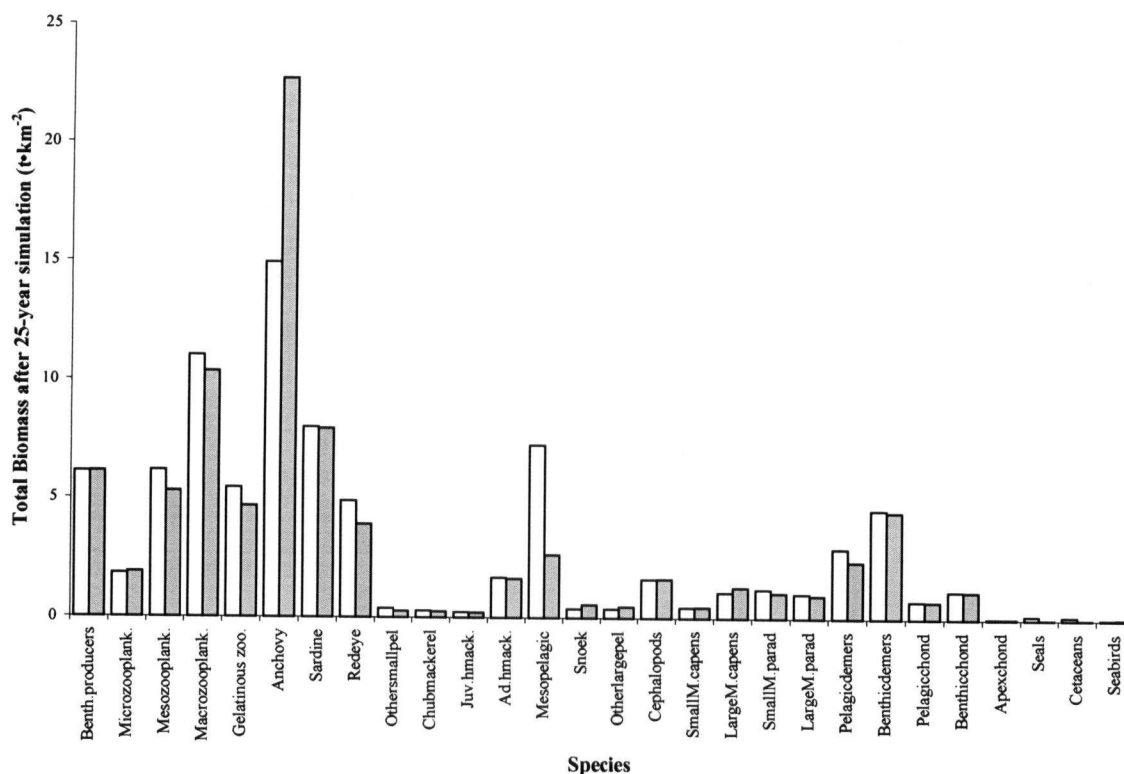


Figure 4.21. Biomass change after a 25-year simulation in the Benguela ecosystem, with (white) and without (grey) marine mammals (phytoplankton and macrobenthos [not shown] have very high and nearly identical biomasses with and with out marine mammals in the system, i.e., 84 and 74 t·km⁻², respectively).

4.3.5.4 Eastern tropical Pacific Ocean

In the Eastern tropical Ocean, the mixed trophic impact of marine mammals and fisheries shows that fishery (-1.869) and marine mammals (-2.334) have an overall negative impact on the entire ecosystem. Nevertheless, the negative impact of marine mammals on other groups of the foodweb is larger than the impact of fisheries. Fish groups that are the most negatively impacted by marine mammal consumption are small bigeye (*Priacanthus arenatus*), small wahoo (*Acanthocybium solandri*), albacore (*Thunnus alalunga*) and skipjack. On the other hand, large bigeye, large dorado

(*Coryphaena hippurus*), large wahoo, large sharks, rays and flying fish (*Cypselurus naresii*) all benefit from the presence of marine mammals in the ecosystem, while they are negatively affected by fisheries. Some fisheries also benefit from the presence of marine mammals in the system: the horse mackerel fisheries (midwater and demersal fleets) and snoek trawls (Figure 4.22).

The mixed trophic impact analysis also shows that groups that are the most positively impacted by the combined effect of all fisheries in the Eastern tropical Pacific Ocean are mainly the juveniles of important commercial fish (wahoo, dorado, swordfish [*Siphias gladius*], sailfish [*Istiophorus platypterus*], marlins, bigeye). When all the fisheries are put together, their combined effect on the individual fishing fleets is mostly negative (Figure 4.22).

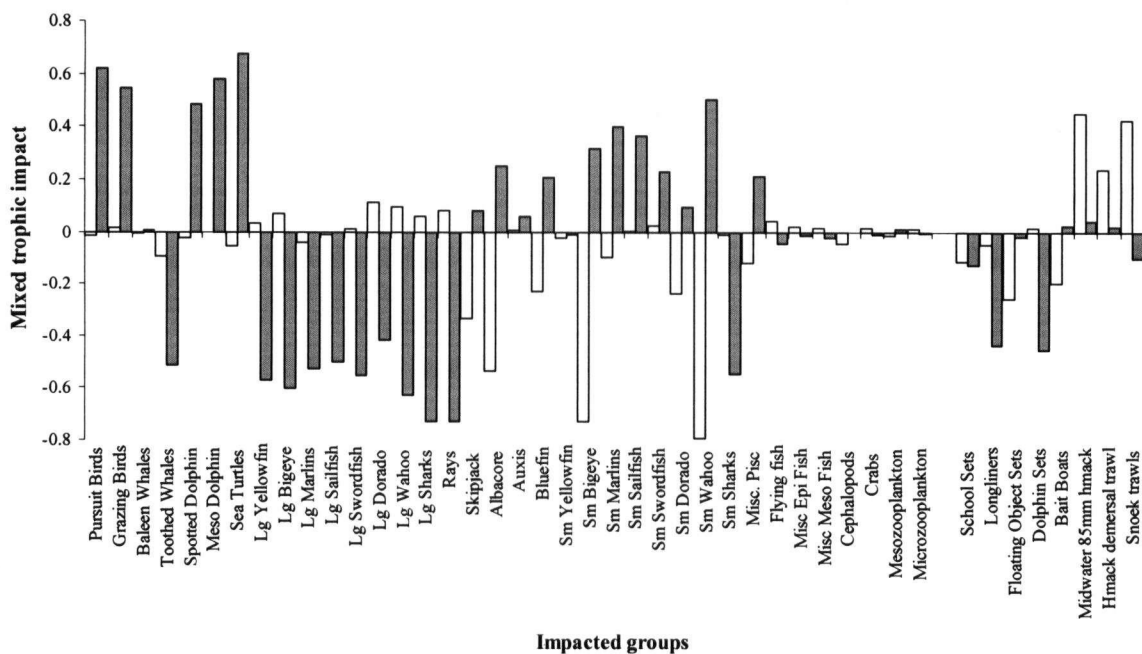


Figure 4.22. Mixed trophic impact of marine mammals (white) and fisheries (grey) on fish and fleet groups of the Eastern tropical Pacific system.

The Eastern tropical Pacific model was first analyzed in *Ecosim* with the current fishing mortality to see which groups decline or increase over time. A total of five fishing fleets (school sets, longliners, floating, dolphin sets, and bait boats) were combined to see their overall effect on the entire ecosystem. Time series cover a period of 89 years, from

1910 to 1998. At the end of the simulation with the original fishing effort, some groups showed large variation and increased a lot (large swordfish, large and small marlins), and other stabilized at higher biomass (rays, small swordfish, albacore, small sailfish, and small wahoo). Most remaining groups stabilized after a slight change in biomass, but large yellowfin tuna and large phytoplankton strongly declined (Figure 4.23).

When marine mammals are removed from the ecosystem, its dynamics is altered (Figure 4.24). The absence of marine mammals species seems to generate large oscillations in the biomass of commercially important fish (mainly large bigeye, but also yellowfin tuna, marlins, swordfish, small sharks, and small bigeye).

Over a period of 89 years, there is no significant change in total biomass, even if marine mammals are totally removed from the ecosystem. Marine mammals predation seems to have been replaced by increase in the biomass and hence predation of large fish such as wahoo (strongest increase in biomass; 248%), yellowfin tuna, bigeye, sharks, skipjack, albacore, bluefin tuna (*Thunnus orientalis*), and dorado (Table 4.9).

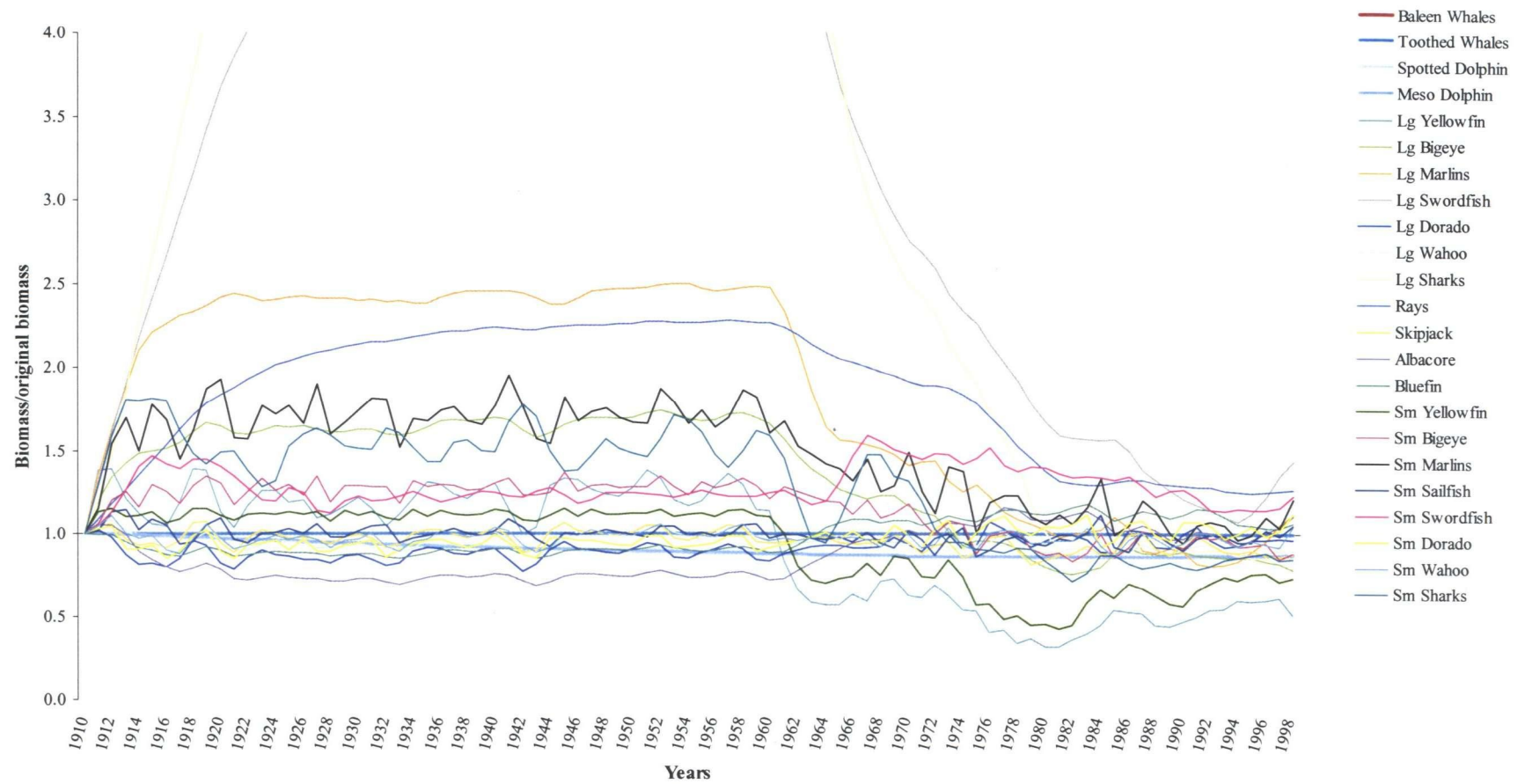


Figure 4.23. *Ecosim* results for the Eastern tropical Pacific model with original fishing effort.

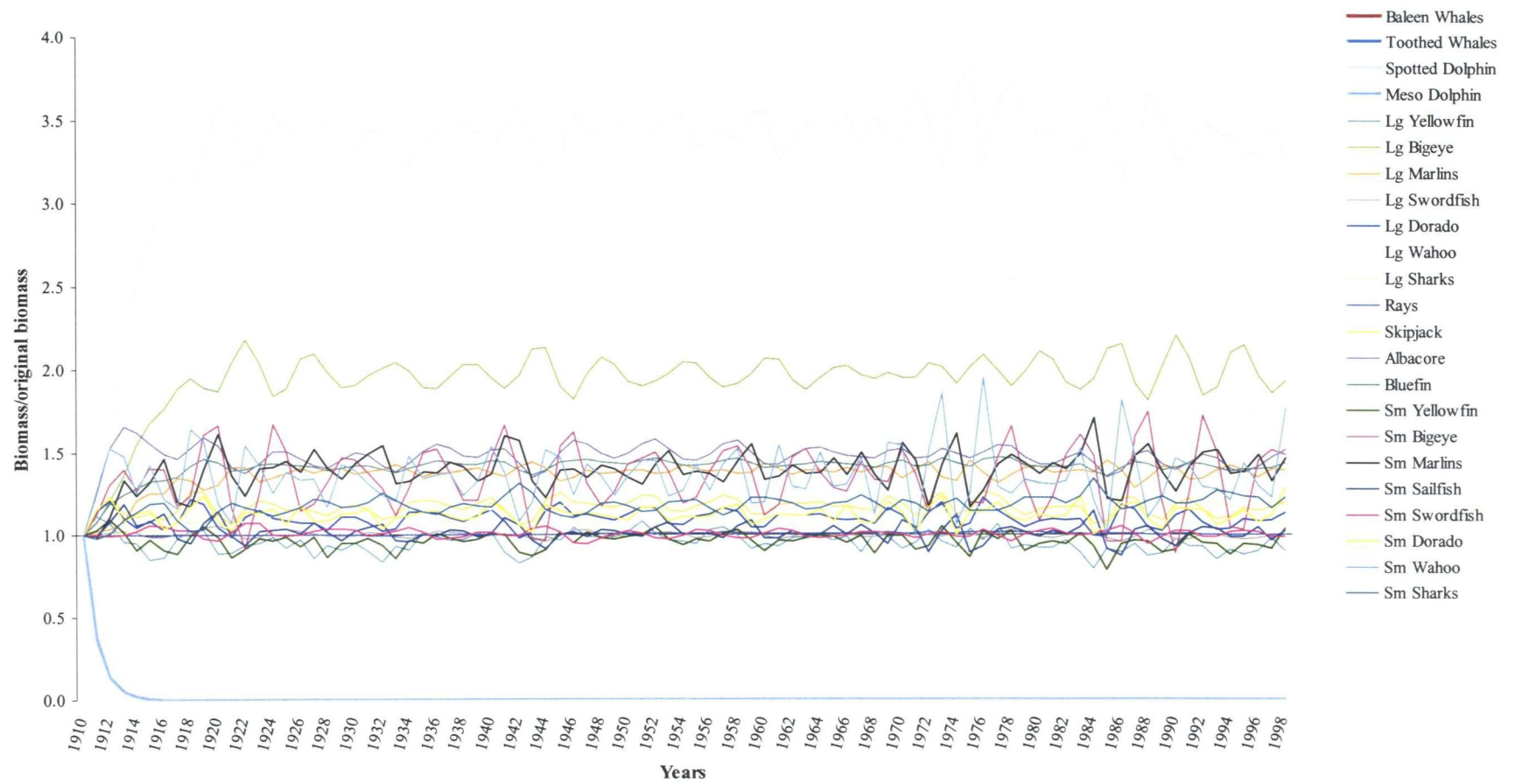


Figure 4.24. *Ecosim* results for the Eastern tropical Pacific model after the extirpation of marine mammals.

Table 4.9. Biomass ($\text{t}\cdot\text{km}^{-2}\cdot\text{year}^{-1}$) change from the start (S) to the end (E) of the 89-year *Ecosim* simulation in the Eastern Tropical Pacific ecosystem, with and without marine mammals (MM). Groups in bold represent the commercially important species.

Group name	With MM			Without MM			B change after MM extirpation (%)
	Biomass (Start)	Biomass (End)	Biomass (E/S)	Biomass (Start)	Biomass (End)	Biomass (E/S)	
Pursuit Birds	0.001	0.001	0.840	0.001	0.001	0.840	0.2
Grazing Birds	0.000	0.000	0.880	0.000	0.000	0.860	-2.9
Baleen Whales	0.009	0.009	1.000	0.007	0.000	0.000	-100.0
Toothed Whales	0.031	0.031	1.000	0.024	0.000	0.000	-100.0
Spotted Dolphin	0.004	0.003	0.870	0.003	0.000	0.000	-100.0
Meso Dolphin	0.017	0.015	0.870	0.013	0.000	0.000	-100.0
Sea Turtles	0.000	0.000	0.840	0.000	0.000	0.810	-3.6
Large Yellowfin	0.008	0.005	0.660	0.008	0.005	0.660	-0.4
Large Bigeye	0.010	0.008	0.860	0.010	0.016	1.650	93.0
Large Marlins	0.001	0.001	1.250	0.001	0.001	1.760	40.6
Large Sailfish	0.000	0.000	1.060	0.000	0.000	1.090	2.2
Large Swordfish	0.000	0.000	1.540	0.000	0.000	1.540	-0.3
Large Dorado	0.000	0.000	1.010	0.000	0.000	1.150	14.5
Large Wahoo	0.001	0.001	0.920	0.001	0.004	3.190	247.5
Large Sharks	0.000	0.000	0.900	0.000	0.000	1.100	22.3
Rays	0.000	0.000	1.300	0.000	0.000	1.310	0.7
Skipjack	0.027	0.025	0.900	0.027	0.030	1.100	23.3
Albacore	0.003	0.003	1.110	0.003	0.005	1.730	57.3
Auxis sp.	0.144	0.149	1.040	0.144	0.141	0.980	-5.0
Bluefin	0.001	0.001	1.050	0.001	0.002	1.490	41.7
Small Yellowfin	0.009	0.007	0.760	0.009	0.007	0.760	0.1
Small Bigeye	0.010	0.009	0.840	0.010	0.015	1.450	73.2
Small Marlins	0.000	0.000	1.070	0.000	0.000	1.530	43.3
Small Sailfish	0.000	0.000	0.960	0.000	0.000	0.990	3.1
Small Swordfish	0.000	0.000	1.210	0.000	0.000	1.220	0.9
Small Dorado	0.002	0.002	1.050	0.002	0.003	1.270	23.0
Small Wahoo	0.003	0.003	0.950	0.003	0.005	1.600	70.6
Small Sharks	0.000	0.000	0.900	0.000	0.000	1.090	21.7
Misc. Piscivores	0.017	0.018	1.080	0.017	0.019	1.110	3.7
Flying fish	0.162	0.162	1.000	0.162	0.158	0.980	-2.0
Misc. Epi. Fish	2.283	2.266	0.990	2.284	2.253	0.990	-0.6
Misc. Meso. Fish	2.013	2.020	1.000	2.015	2.003	0.990	-0.9
Cephalopods	1.105	1.170	1.060	1.109	1.229	1.110	5.1
Crabs	0.122	0.119	0.980	0.122	0.117	0.960	-1.8
Mesozooplankton	0.735	0.663	0.900	0.735	0.670	0.910	1.0
Microzooplankton	0.818	0.840	1.030	0.818	0.839	1.030	-0.2
Lg Phytoplankton	0.485	0.335	0.690	0.485	0.333	0.690	-0.6
Sm Producers	3.013	2.986	0.990	3.013	2.990	0.990	0.1
Detritus	2.022	1.977	0.980	2.022	1.979	0.980	0.1
Total	13.056	12.831	0.980	13.051	12.827	0.980	0.0

Figure 4.25 shows that the most important fish in terms of biomass (*Auxis* sp., flying fish, and miscellaneous epipelagic fish) would decline if marine mammals were removed from the ecosystem. However, commercially important species (especially bigeye, wahoo and skipjack), which tend to have lower biomasses, would benefit from the extirpation of marine mammals in the Eastern tropical Pacific system. After 89 years of simulation, the total biomass of the system is not changed, even if marine mammals are extirpated. Their original biomasses appear to be replaced by other trophic groups in the system.

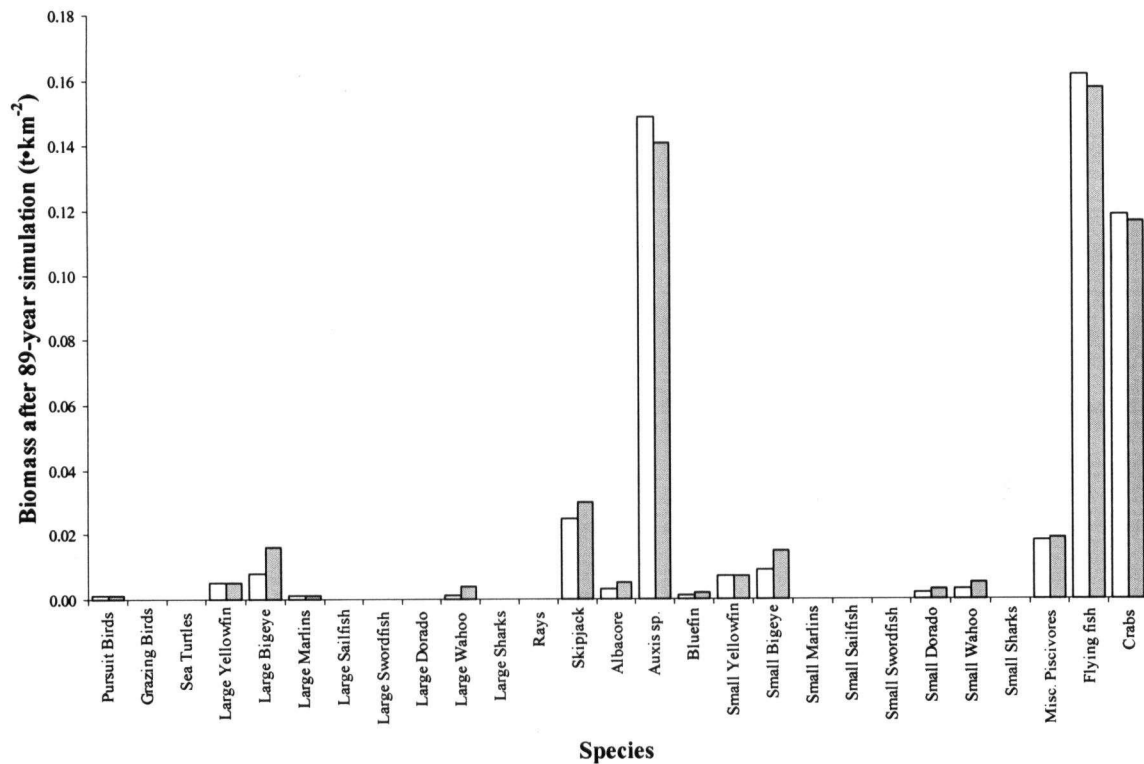


Figure 4.25. Biomass change after a 89-year simulation in the Eastern tropical Pacific ecosystem, with and without marine mammals. Note that the miscellaneous epipelagic fish, miscellaneous mesopelagic fish, cephalopods, mesozooplankton, microzooplankton, large phytoplankton, small producers and detritus groups were excluded from the graph due to their large biomass. No significant difference was observed with or without marine mammals for these groups (see Table 4.9).

4.3.5.5 Gulf of Thailand

The mixed trophic impact analysis for shows that most groups in the Gulf of Thailand model are negatively impacted by fisheries. This is especially true for Scianidae, sharks, cephalopods, large piscivores, *Saurida* spp., and Lutjianidae. When all the

fisheries are analyzed as a whole, their combined effect on each and every fishing fleet is mostly negative on the different fleets in the ecosystem (Figure 4.26). In the Gulf of Thailand, the mixed trophic impact of the fisheries is overall negative (-7.735), and much higher than that of marine mammals (-1.899). Marine mammals have their larger negative impact on small pelagics, Carangidae and *Rastrelliger* spp., and on the purse seine fishery as well (Figure 4.26).

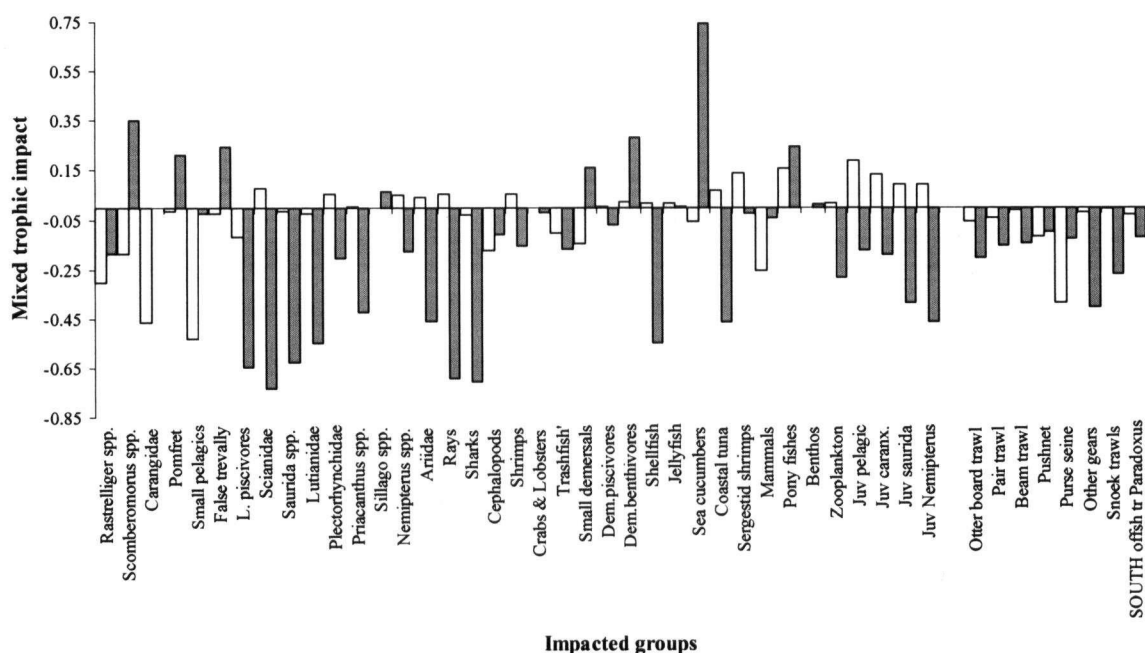


Figure 4.26. Mixed trophic impact of marine mammals (white) and fisheries (grey) on fish and fleet groups of the Gulf of Thailand system.

The Gulf of Thailand model was first analyzed, using *Ecosim*, with the time series of fishing mortality to see which groups decline or increase over time. The model covers six sources of fishing mortality: pair trawls; beam trawls; pushnets; purse seines; otter board trawls and other gears. All fisheries were combined to see their general effect on the entire ecosystem. Time series cover a period of 24 years, from 1973 to 1996. At the end of the simulation with the original fishing effort, some groups stabilized at higher biomass, such as false trevally (*Lactarius lactarius*), demersal piscivores, *Sillago* spp. and small demersals. Most of the remaining groups stabilized after a slight decrease of biomass. Nevertheless, Plectorhynchidae, shellfish, coastal tuna, pelagic species (large and small),

Scomberomus and *Priacanthus* spp. collapsed, while demersal benthivores' exploded after approximately 15 years of simulation (Figure 4.27).

When all marine mammals of the Gulf of Thailand are extirpated, ecosystem structure changes (Figure 4.28). Their extirpation still leads to an explosion in demersal benthivore species, but also to large variation in the biomass of small demersals, small pelagics and *Rastrelliger* spp. The remaining groups seem to stabilize around equilibrium after the 24-year simulation. Over that period, there is no significant decrease in total biomass (91 versus 92 t·km⁻²), even if marine mammals are severely depleted (Table 4.10).

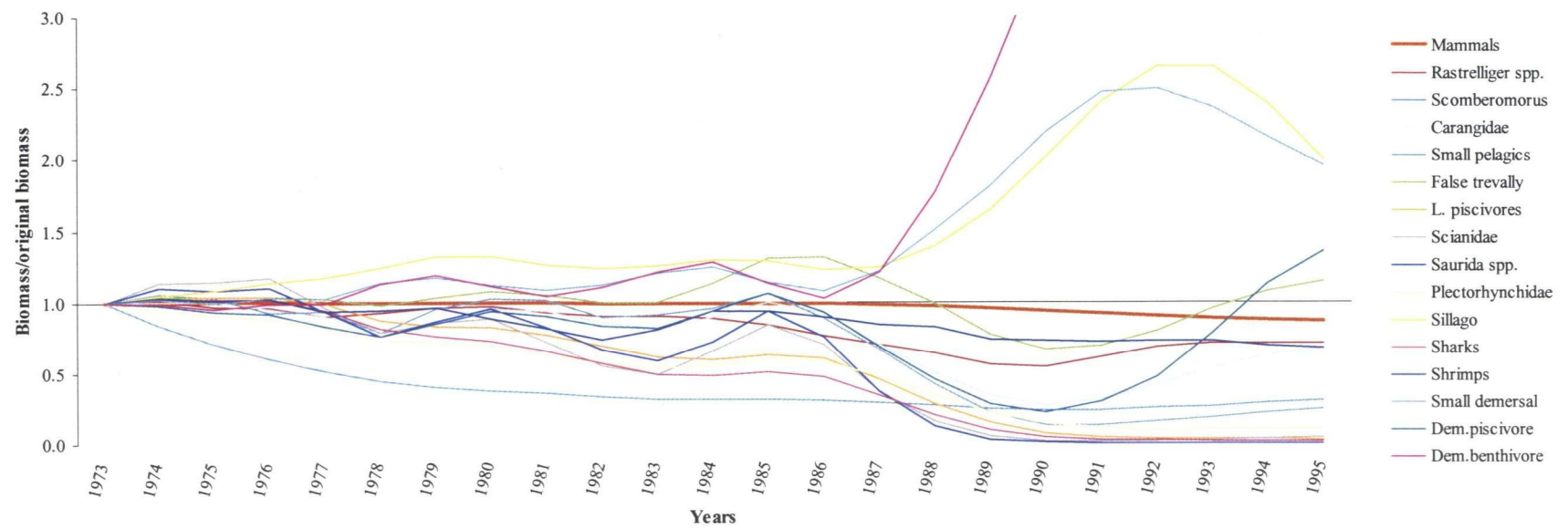


Figure 4.27. *Ecosim* results for the Gulf of Thailand model with original fishing effort.

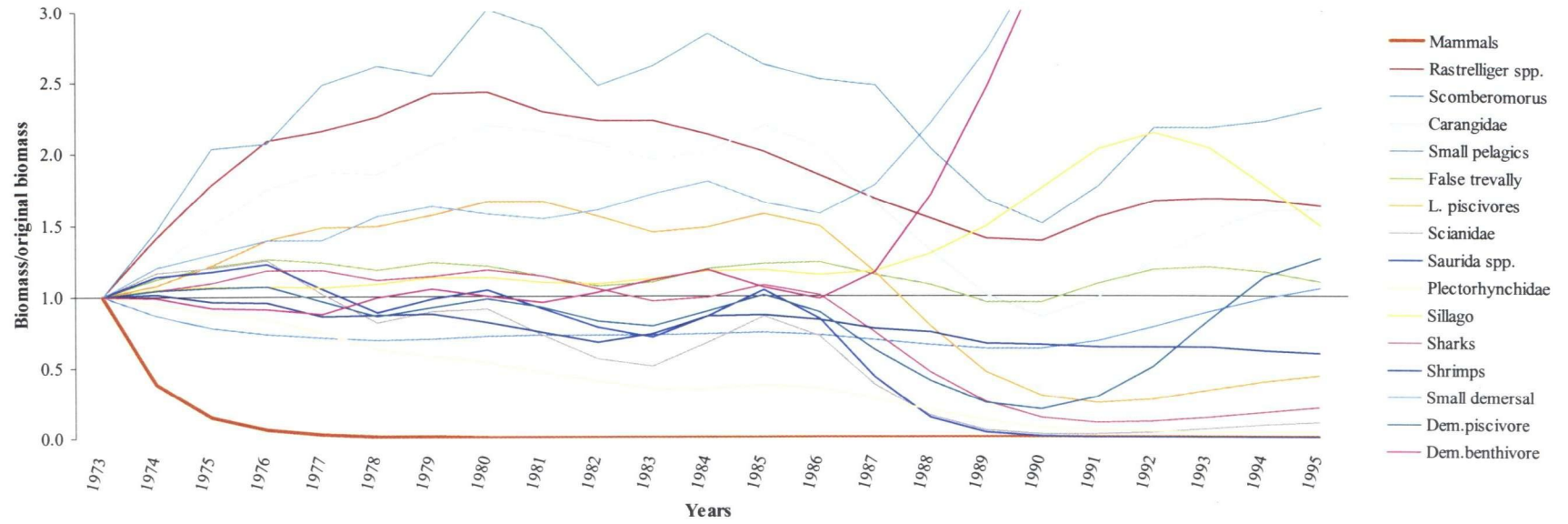


Figure 4.28. *Ecosim* results for the Gulf of Thailand model after the extirpation of marine mammals.

Many groups that had small biomass in the Gulf of Thailand ecosystem increased considerably: large piscivores (750%); small pelagics (724%); coastal tuna (700%); *Scomberomorus* spp. (225%) and Sciaenidae (200%). However, except for small pelagics, these groups have small biomasses (all less than $0.5 \text{ t}\cdot\text{km}^{-2}$), and remain minor in the ecosystem. In addition to marine mammals, Plectorhynchidae show a total depletion in an ecosystem without marine mammals (Table 4.10).

Table 4.10. Biomass ($t \cdot km^{-2} \cdot year^{-1}$) change from the start (S) to the end (E) of the 24-year *Ecosim* simulation in the Gulf of Thailand ecosystem, with and without marine mammals (MM). Groups in bold represent the commercially important species.

Group name	Ecosim with MM			Ecosim without MM			B change after MM extirpation (%)
	Biomass (Start)	Biomass (End)	Biomass (E/S)	Biomass (Start)	Biomass (End)	Biomass (E/S)	
<i>Rastrelliger</i> spp.	0.190	0.134	0.710	0.195	0.308	1.580	129.9
<i>Scomberomorus</i> spp.	0.015	0.004	0.290	0.015	0.013	0.870	225.0
Carangidae	0.082	0.054	0.660	0.082	0.120	1.460	122.2
Pomfrets	0.007	0.006	0.790	0.007	0.006	0.830	0.0
Small pelagics	0.455	0.107	0.240	0.466	0.882	1.890	724.3
False trevally	0.003	0.004	1.130	0.003	0.004	1.080	0.0
Large piscivores	0.053	0.002	0.030	0.054	0.017	0.320	750.0
Sciaenidae	0.031	0.001	0.040	0.031	0.003	0.090	200.0
<i>Saurida</i> spp.	0.054	0.000	0.000	0.054	0.000	0.000	-
Lutianidae	0.016	0.000	0.010	0.016	0.003	0.210	-
Plectorhynchidae	0.008	0.001	0.100	0.008	0.000	0.040	-100.0
<i>Priacanthus</i> spp.	0.071	0.032	0.450	0.071	0.037	0.520	15.6
<i>Sillago</i> spp.	0.033	0.071	2.160	0.033	0.055	1.660	-22.5
<i>Nemipterus</i> spp.	0.093	0.000	0.000	0.093	0.000	0.000	-
Ariidae	0.018	0.011	0.600	0.018	0.010	0.580	-9.1
Rays	0.048	0.004	0.080	0.048	0.004	0.070	0.0
Sharks	0.020	0.000	0.020	0.020	0.003	0.150	-
Cephalopods	0.400	0.309	0.770	0.403	0.505	1.250	63.4
Shrimps	0.181	0.123	0.680	0.181	0.110	0.610	-10.6
Crabs & lobsters	3.518	3.434	0.980	3.518	3.441	0.980	0.2
'Trash fish'	0.524	0.336	0.640	0.531	0.429	0.810	27.7
Small demersals	0.181	0.367	2.030	0.183	0.556	3.030	51.5
Demersal piscivores	0.058	0.072	1.250	0.058	0.070	1.210	-2.8
Dem. Benthivores	0.090	0.338	3.760	0.090	0.316	3.520	-6.5
Shellfish	0.170	0.025	0.150	0.170	0.025	0.150	0.0
Jellyfish	2.000	2.038	1.020	2.000	1.999	1.000	-1.9
Sea cucumbers	1.000	0.997	1.000	1.000	1.001	1.000	0.4
Seaweeds	1.000	1.000	1.000	1.000	1.000	1.000	0.0
Coastal tuna	0.021	0.003	0.140	0.021	0.024	1.150	700.0
Sergestid shrimps	0.058	0.049	0.850	0.058	0.034	0.590	-30.6
Mammals	0.100	0.087	0.870	0.078	0.007	0.090	-92.0
Pony fishes	0.054	0.085	1.570	0.054	0.071	1.310	-16.5
Benthos	33.001	33.074	1.000	33.008	33.193	1.010	0.4
Zooplankton	17.300	17.461	1.010	17.299	17.296	1.000	-0.9
Juvenile pelagic	0.076	0.026	0.340	0.076	0.090	1.190	246.2
Juvenile <i>Caranx</i>	0.027	0.020	0.740	0.027	0.035	1.300	75.0
Juvenile <i>Saurida</i>	0.019	0.000	0.000	0.019	0.000	0.000	-
Juvenile <i>Nemipterus</i>	0.023	0.000	0.000	0.023	0.000	0.000	-
Phytoplankton	30.000	29.906	1.000	30.000	30.014	1.000	0.4
Detritus	9999.924	9984.550	1.000	9999.787	10002.780	1.000	0.2
Total	10090.920	10074.730	1.000	10090.790	10094.460	1.000	0.2

The most important groups in the Gulf of Thailand in terms of landings are ‘trash fish’, shellfish, shrimps, *Rastrelliger* spp., cephalopods, small pelagics, and crabs & lobsters. In a scenario without marine mammals in the ecosystem, most of these target species increase, except for shrimp, which is commercially very important (V. Christensen, Fisheries Centre, UBC, personal communication) (Figure 4.29).

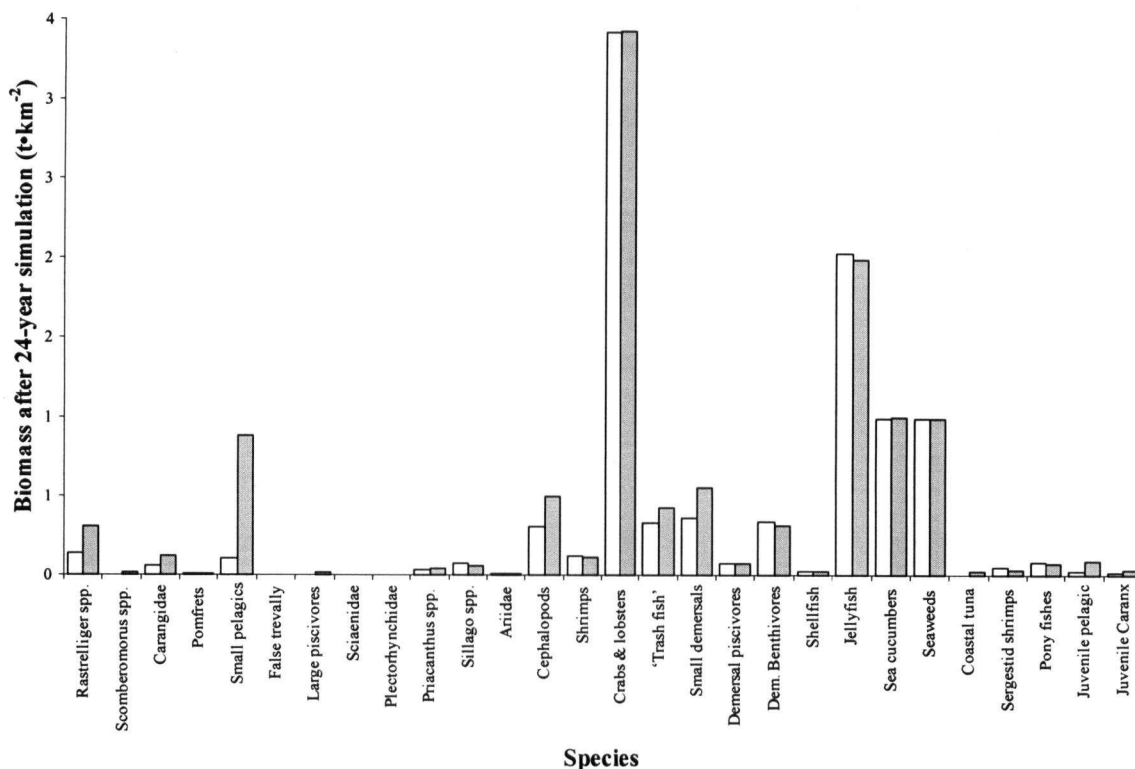


Figure 4.29. Biomass change after a 24-year simulation in the Gulf of Thailand ecosystem, with (white) and without (grey) marine mammals.

4.3.5.6 North Sea

Seals' and fisheries' mixed trophic impacts in the North Sea model shows that both marine mammals and fishery have an overall negative impact on the entire ecosystem. However, the negative impact of fisheries (-7.79) is three times larger than the impact of seals (-2.22). Many of the groups that are seriously impacted by fisheries present a positive impact by seals; this is the case, for instance, for gurnards (*Lepidotrigla* spp.), horse mackerel (*Trachurus trachurus*), sole (*Solea solea*), juvenile saithe (*Pollachius*

virens), rays and herring. Some groups are positively impacted by fisheries, such as dab (*Limanda limanda*), sandeel, juvenile haddock (*Melanogrammus aeglefinus*), juvenile cod and birds. All of the groups (except for dab) are also positively impacted by seals. Negative impacts from seals are mainly observed for cod, saithe, plaice and dab (Figure 4.30).

Here again, the overall impact of all fisheries grouped together is damaging for each single fishing fleets. Finally, seals have a slight positive impact on seiners (Figure 4.30).

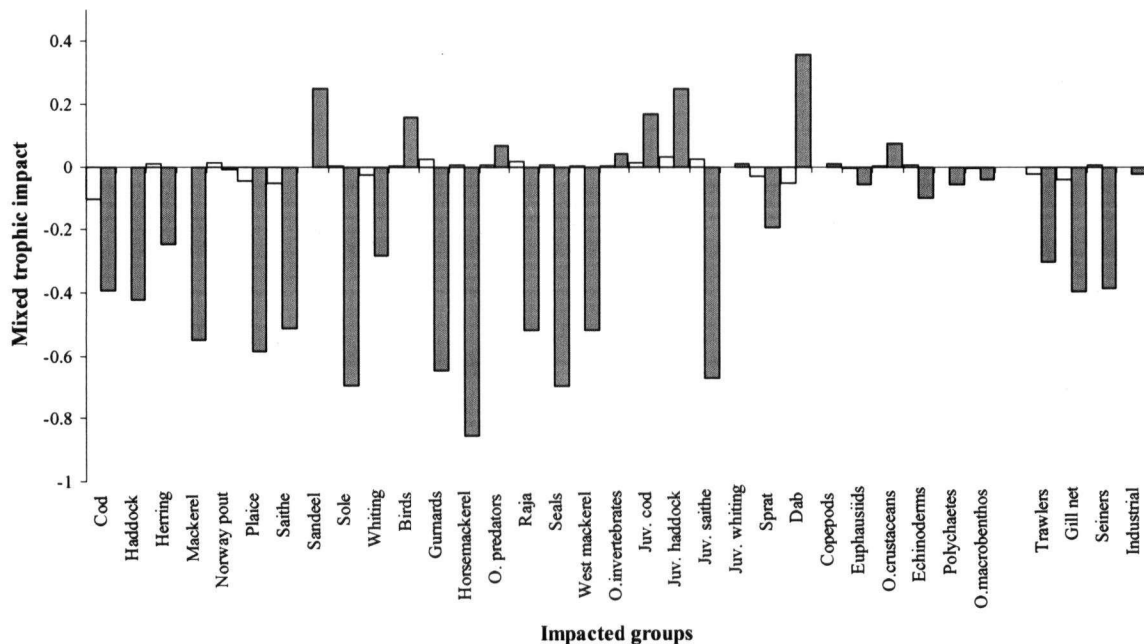


Figure 4.30. Mixed trophic impact of marine mammals (white) and fisheries (grey) on fish and fleet groups of the North Sea system.

In *Ecosim*, the North Sea model was first analyzed with time series of fishing mortality to see which group decline or increase over time. The model includes four sources of fishing mortality (trawlers, gill nets, seiners and industrial fisheries), which were combined to quantify overall effects on the ecosystem. Time series cover a period of 22 years, from 1974 to 1995. At the end of the simulation with the original fishing effort, horse mackerel are strongly increasing, while other groups seems to stabilize at slightly higher biomass (juvenile cod, sole, birds, herring, haddock, juvenile saithe, Norway pout,

whiting [*Merlangius merlangus*], and gurnards). Other groups stabilized after a decrease of biomass (juvenile haddock, cod, plaice [*Pleuronectes platessa*]), and mackerel (*Scomber scombrus*) biomass is in constant decrease, reaching near extirpation at the end of the simulated period (Figure 4.31).

Finally, the simulated seal extirpation in the North Sea ecosystem (Figure 4.32), the dynamics of the rest of the groups remains approximately the same. No fish species shows a clear increase in biomass linked to the removal of seals. Over a period of 22 years, the biomass remains approximately the same ($B_{\text{tot}} = 290 \text{ t}\cdot\text{km}^{-2}$ with marine mammals, and $293 \text{ t}\cdot\text{km}^{-2}$ without; Table 4.11, Figure 4.32), but seals are completely extirpated from the ecosystem. Their biomass may have been replaced by cod and saithe, which show an increase in biomass following the decline of seals (Table 4.11).

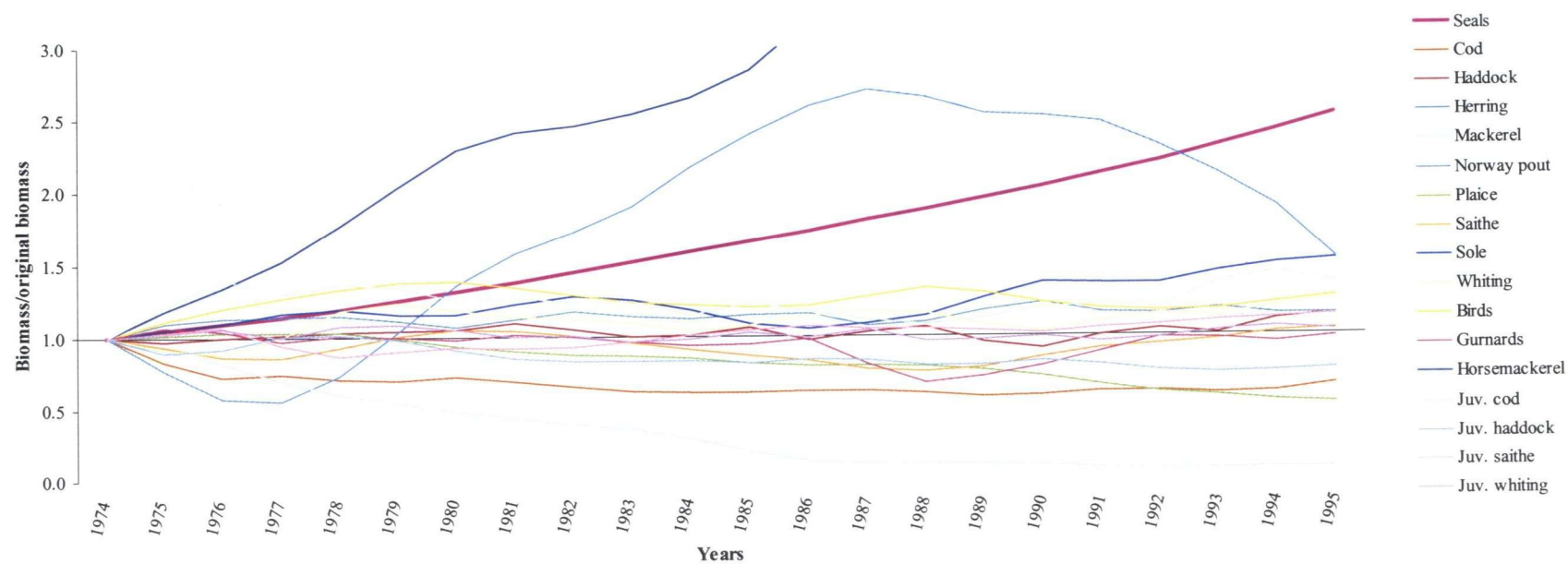


Figure 4.31. *Ecosim* results for the North Sea model with original fishing effort.

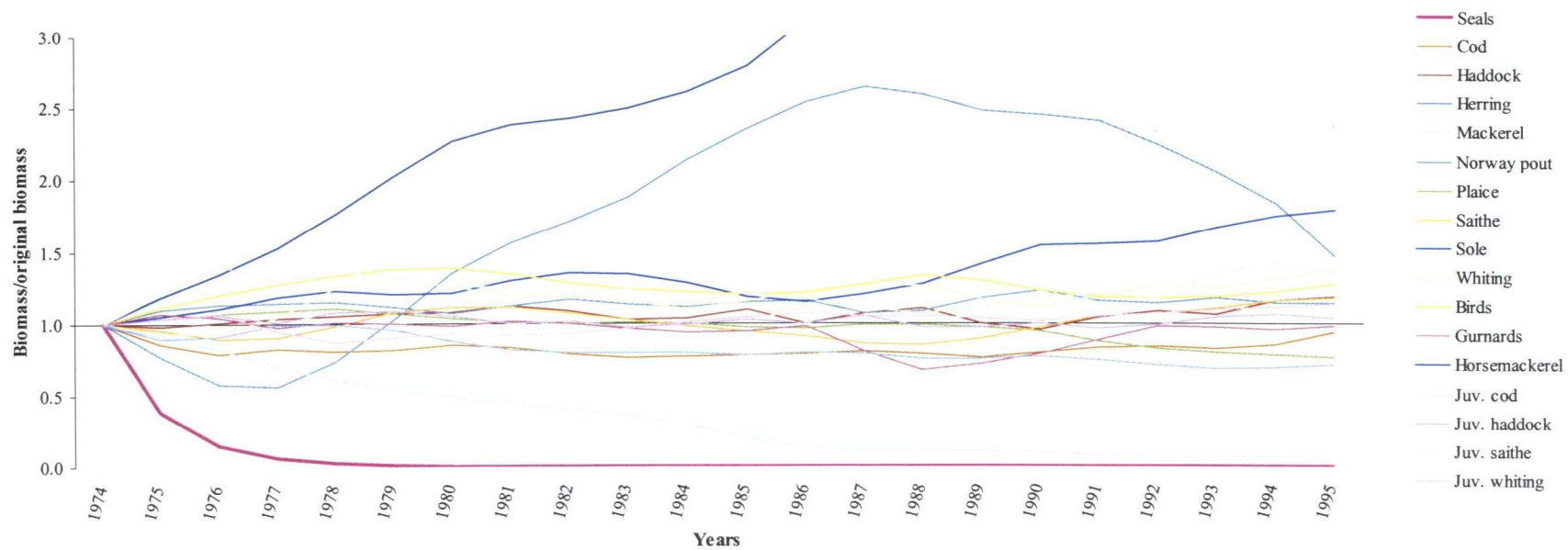


Figure 4.32. *Ecosim* results for the North Sea model after the extirpation of seals.

Table 4.11. Biomass ($\text{t}\cdot\text{km}^{-2}\cdot\text{year}^{-1}$) change from the start (S) to the end (E) of the 22-year *Ecosim* simulation in the North Sea ecosystem, with and without marine mammals (MM). Groups in bold represent the commercially important species.

Group name	Ecosim with MM			Ecosim without MM			B change after MM extirpation
	Biomass (Start)	Biomass (End)	Biomass (E/S)	Biomass (Start)	Biomass (End)	Biomass (E/S)	
Cod	0.426	0.248	0.580	0.428	0.357	0.840	44.2
Haddock	0.512	0.597	1.170	0.513	0.627	1.220	4.9
Herring	0.738	1.178	1.600	0.738	1.135	1.540	-3.6
Mackerel	1.906	0.132	0.070	1.906	0.133	0.070	0.3
Norway pout	3.243	3.679	1.130	3.243	3.671	1.130	-0.2
Plaice	0.713	0.375	0.530	0.713	0.541	0.760	44.2
Saithe	1.299	1.318	1.010	1.300	1.499	1.150	13.8
Sandeel	9.829	9.413	0.960	9.829	9.515	0.970	1.1
Sole	0.094	0.145	1.540	0.094	0.170	1.810	17.3
Whiting	0.492	0.578	1.180	0.493	0.639	1.300	10.5
Birds	0.003	0.004	1.300	0.003	0.004	1.300	0.0
Gurnards	0.530	0.538	1.020	0.530	0.540	1.020	0.3
Horse mackerel	0.291	1.343	4.620	0.291	1.314	4.520	-2.2
Other predators	0.543	0.559	1.030	0.543	0.551	1.020	-1.3
Skates & rays	0.090	0.092	1.030	0.090	0.096	1.070	4.0
Seals	0.002	0.005	2.520	0.002	0.000	0.030	-100.0
West mackerel	0.677	0.761	1.120	0.677	0.764	1.130	0.4
Other invertebrates	24.387	23.545	0.970	24.388	23.471	0.960	-0.3
Juvenile cod	0.084	0.129	1.540	0.084	0.128	1.520	-1.0
Juvenile haddock	1.708	1.249	0.730	1.708	1.159	0.680	-7.1
Juvenile saithe	0.040	0.046	1.130	0.040	0.046	1.130	0.0
Juvenile whiting	1.114	1.163	1.040	1.115	1.172	1.050	0.8
Sprat	0.513	0.501	0.980	0.514	0.525	1.020	4.8
Dab	4.401	4.728	1.070	4.404	5.110	1.160	8.1
Copepods	25.400	25.158	0.990	25.400	25.150	0.990	0.0
Euphausiids	20.329	21.583	1.060	20.329	21.624	1.060	0.2
Other crustaceans	13.241	12.807	0.970	13.241	12.795	0.970	-0.1
Echinoderms	24.000	24.128	1.010	24.000	23.779	0.990	-1.4
Polychaetes	32.000	32.906	1.030	32.000	32.802	1.030	-0.3
Other macrobenthos	49.002	51.030	1.040	49.004	51.363	1.050	0.7
Phytoplankton	46.999	47.358	1.010	46.999	47.366	1.010	0.0
Detritus	24.997	24.798	0.990	24.997	24.817	0.990	0.1
Total	0.426	0.248	0.580	0.428	0.357	0.840	44.2

The main species targeted by the North Sea fisheries are adult Norway pout, sandeel, sprat, saithe, herring, whiting, and haddock. When marine mammals are absent from the system, *Ecosim* predicts that these fisheries are catching about the same amount of fish than if marine mammals were present in the system (the largest changes are increases of 11% and 14% for whiting and saithe, respectively; Table 4.11). Out of four fisheries, one (seiners, catching herring and mackerel) is definitely decreasing in terms of

catch if there are no marine mammals in the ecosystem. In general, all trophic groups stay at approximately the same level of biomass, with or without marine mammals in the ecosystem (Figure 4.33).

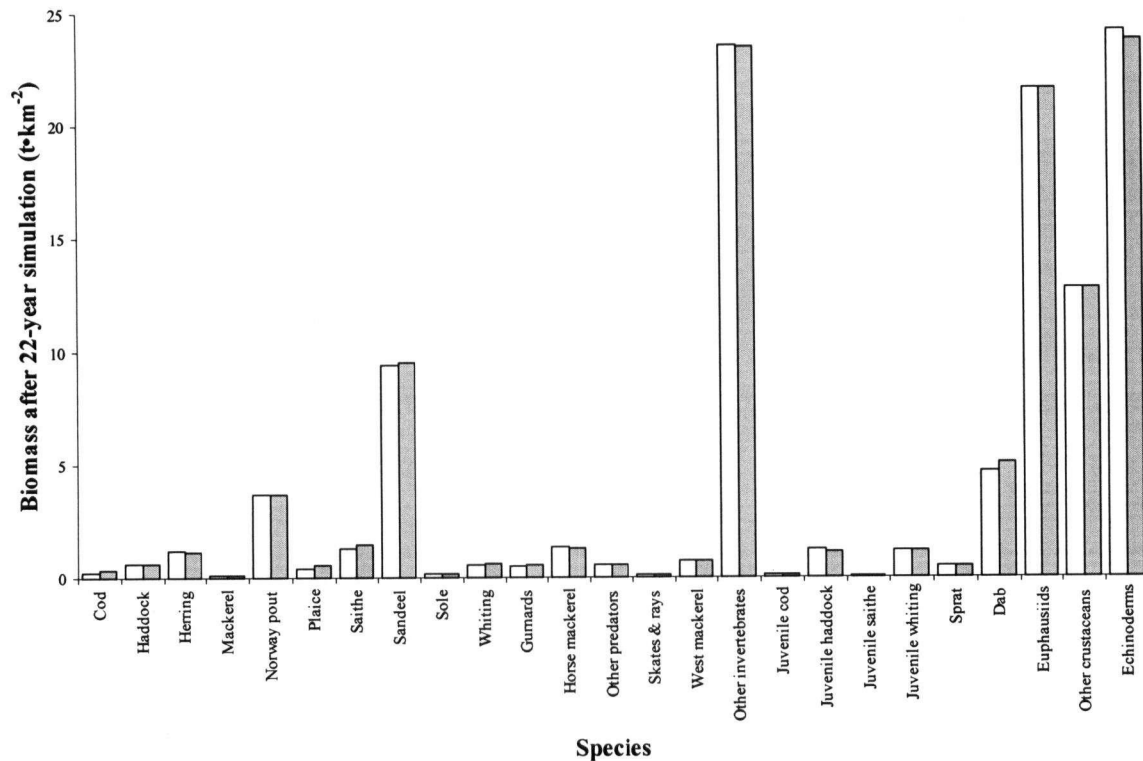


Figure 4.33. Biomass change after a 22-year simulation in the North Sea ecosystem, with (white) and without (grey) seals (polychaetes, other macrobenthos and phytoplankton [not shown] have very high and nearly identical biomasses with and with out marine mammals in the system, i.e., 32, 51, and 47 t·km⁻², respectively).

4.3.5.7 Strait of Georgia

The mixed trophic impact analysis for the Strait of Georgia shows that while the overall trophic impact of marine mammals is near neutral (-0.83), there is a strong negative impact by fisheries on the foodweb (-7.79). This negative impact of fisheries affects almost all fish species in the ecosystem (Figure 4.34), except for dogfish (*Squalus acanthias*), juvenile herring and juvenile coho salmon, which seem to benefit from the presence of fisheries. The strongest positive impact of the fisheries is seen on benthic invertebrates, jellyfish and plankton.

When marine mammals have a negative impact on fish in the Strait of Georgia ecosystem, this is always smaller than fisheries' impact on the same groups. Interestingly, the overall effect of marine mammal on fishing is positive for trawlers, gill nets, seiners and industrial fleets. Total marine mammals impact is also strongly negative for resident killer whales, seals and sea lions (Figure 4.34).

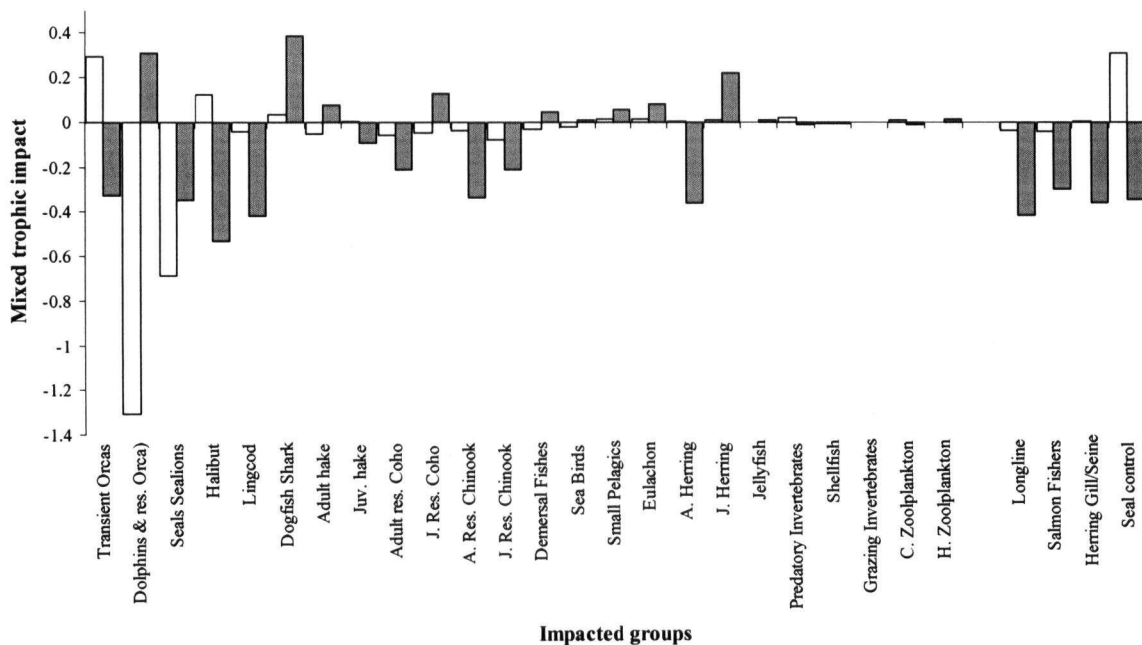


Figure 4.34. Mixed trophic impact of marine mammals (white) and fisheries (grey) on fish and fleet groups of the Strait of Georgia system.

The Strait of Georgia model was first analyzed with *Ecosim* with time series of fishing mortality to see which group decline or increase over time. The model covers eight sources of fishing mortality: longline; salmon fishers; herring gill/seine; 'seal control'; trawls; gill nets; seiners and industrial fleets. All fisheries were combined to test for their effect on the whole ecosystem. Time series cover a period of 50 years, from 1950 to 1999. At the end of the simulation with the original fishing effort, the juvenile resident coho salmon's biomass appears to explode; the zooplankton appears to show great variations, as well (Figure 4.35). Most groups stabilized after a slight decrease of biomass, and seals & sea lions, dolphins, juvenile resident coho salmon and adult herring stabilized after a slight increase. No groups had collapsed at the end of the simulation.

When all marine mammals were removed from the Strait of Georgia ecosystem, the ecosystem structure was altered (Figure 4.36). The extirpation of marine mammals lead to strong variation in halibut biomass, and drove the biomass of small pelagics, jellyfish, eulachon (*Thaleichthys pacificus*) and adult hake (*Urophycis tenuis*) close to zero. All other groups appeared to stabilize at lower levels at the end of the 50-years simulation. Over that period, there is no significant decrease in total biomass (543 *versus* 542 t·km⁻²; Table 4.12).

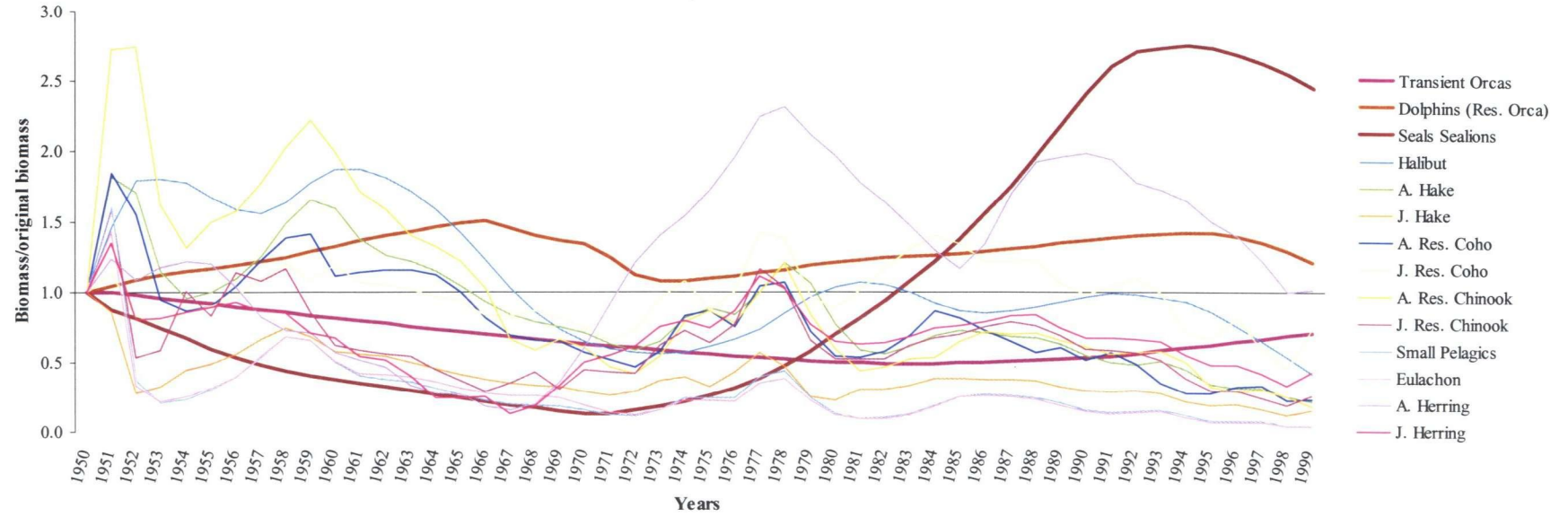


Figure 4.35. *Ecosim* results for the Strait of Georgia model with original fishing effort.

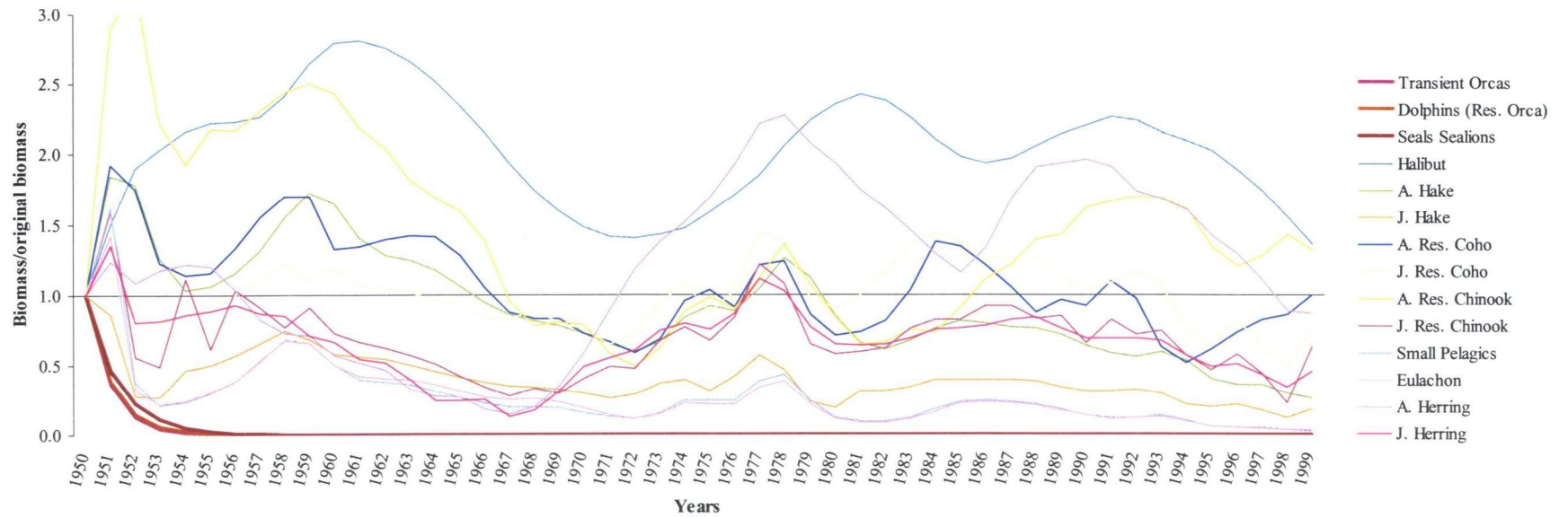


Figure 4.36. *Ecosim* results for the Strait of Georgia model after the extirpation of marine mammals.

Table 4.12. Biomass ($\text{t}\cdot\text{km}^{-2}\cdot\text{year}^{-1}$) change from the start (S) to the end (E) of the 50-year *Ecosim* simulation in the Strait of Georgia ecosystem, with and without marine mammals (MM). Groups in bold represent the commercially important species.

Group name	Ecosim with MM			Ecosim without MM			B change after MM extirpation
	Biomass (Start)	Biomass (End)	Biomass (E/S)	Biomass (Start)	Biomass (End)	Biomass (E/S)	
Transient Orcas	0.003	0.002	0.670	0.002	0.000	0.000	-100.0
Dolphins (Res. Orca)	0.060	0.072	1.190	0.047	0.002	0.030	-97.2
Seals & Sealions	0.381	0.842	2.210	0.322	0.007	0.020	-99.2
Halibut	0.004	0.002	0.470	0.004	0.006	1.450	200.0
Lingcod	5.415	1.708	0.320	5.416	2.517	0.460	47.4
Dogfish shark	6.528	4.888	0.750	6.528	5.957	0.910	21.9
Adult hake	7.807	1.865	0.240	7.814	2.224	0.280	19.2
Juvenile hake	2.546	0.586	0.230	2.548	0.640	0.250	9.2
Adult resident coho	0.186	0.047	0.250	0.187	0.211	1.130	348.9
Juv. Resident coho	0.910	0.865	0.950	0.911	0.909	1.000	5.1
Ad. Resident chinook	0.335	0.076	0.230	0.336	0.537	1.600	606.6
Juv. Resident chinook	1.283	0.518	0.400	1.286	0.766	0.600	47.9
Demersal fishes	12.781	4.099	0.320	12.791	5.024	0.390	22.6
Seabirds	0.020	0.008	0.390	0.020	0.008	0.410	0.0
Small pelagics	3.331	0.584	0.180	3.335	0.369	0.110	-36.8
Eulachon	2.495	0.464	0.190	2.495	0.308	0.120	-33.6
Adult herring	15.402	16.894	1.100	15.404	14.668	0.950	-13.2
Juvenile herring	3.635	1.944	0.530	3.635	1.956	0.540	0.6
Jellyfish	18.815	4.250	0.230	18.815	4.455	0.240	4.8
Pred. invertebrates	9.510	4.608	0.480	9.511	3.834	0.400	-16.8
Shellfish	231.457	123.610	0.530	231.457	126.475	0.550	2.3
Grazing invertebrates	491.271	228.769	0.470	491.273	224.623	0.460	-1.8
Carn. zooplankton	22.162	16.966	0.770	22.157	16.664	0.750	-1.8
Herb. zooplankton	39.683	33.429	0.840	39.684	34.289	0.860	2.6
Kelp / seagrass	29.465	13.151	0.450	29.465	13.154	0.450	0.0
Phytoplankton	101.806	81.893	0.800	101.807	81.079	0.800	-1.0
Detritus	1.382	1.127	0.820	1.382	1.119	0.810	-0.7
Total	1008.672	543.266	0.540	1008.631	541.800	0.540	-0.3

The main targeted species in the Strait of Georgia ecosystem are herring, resident Chinook salmon, lingcod and resident Coho salmon. When marine mammals are removed from the ecosystem, most of these commercially important fish end up with more biomass than in the initial ecosystem, except for herring, which decreases by 13% (Figure 4.37).

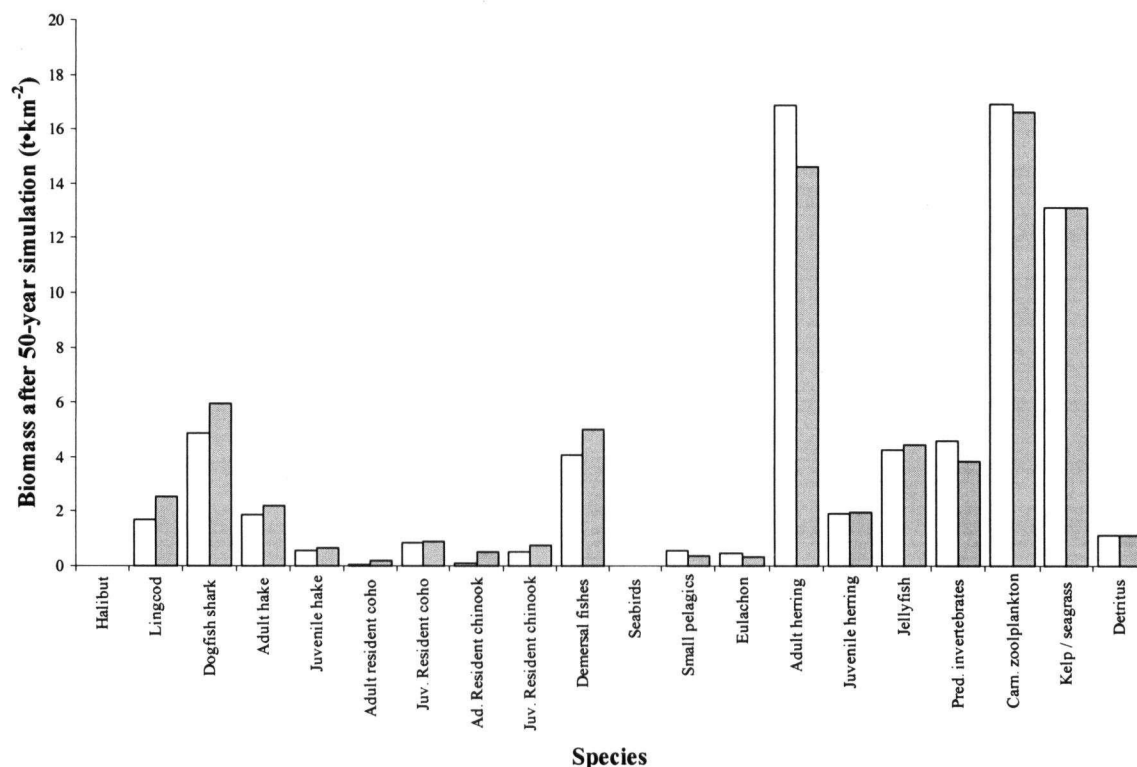


Figure 4.37. Biomass change after a 50-year simulation in the Strait of Georgia ecosystem, with (white) and without (grey) marine mammals (shellfish, grazing invertebrates, and phytoplankton [not shown] have very high and nearly identical biomasses with and with out marine mammals in the system, i.e., 124, 229, and 82 $\text{t}\cdot\text{km}^{-2}$, with marine mammals, and 126, 224, and 81 $\text{t}\cdot\text{km}^{-2}$ without marine mammals, respectively).

4.3.6 Mixed trophic impact versus catch or consumption

When mixed trophic impacts are plotted against consumption (for marine mammals) or catch (for fisheries), we see that marine mammals consume generally less than fisheries catch, and that their *TI* is less negative than that of fisheries for the same consumption or catch level (Figure 4.38). Moreover, the overall mixed trophic impacts of the marine mammals on the whole ecosystem becomes less negative with increasing consumption. This is a rather surprising result, to be discussed further below. Because of the exceptionally high level of consumption by large marine mammals (killer whales) in the Eastern Bering Sea, this ecosystem was considered as an outlier in the analysis.

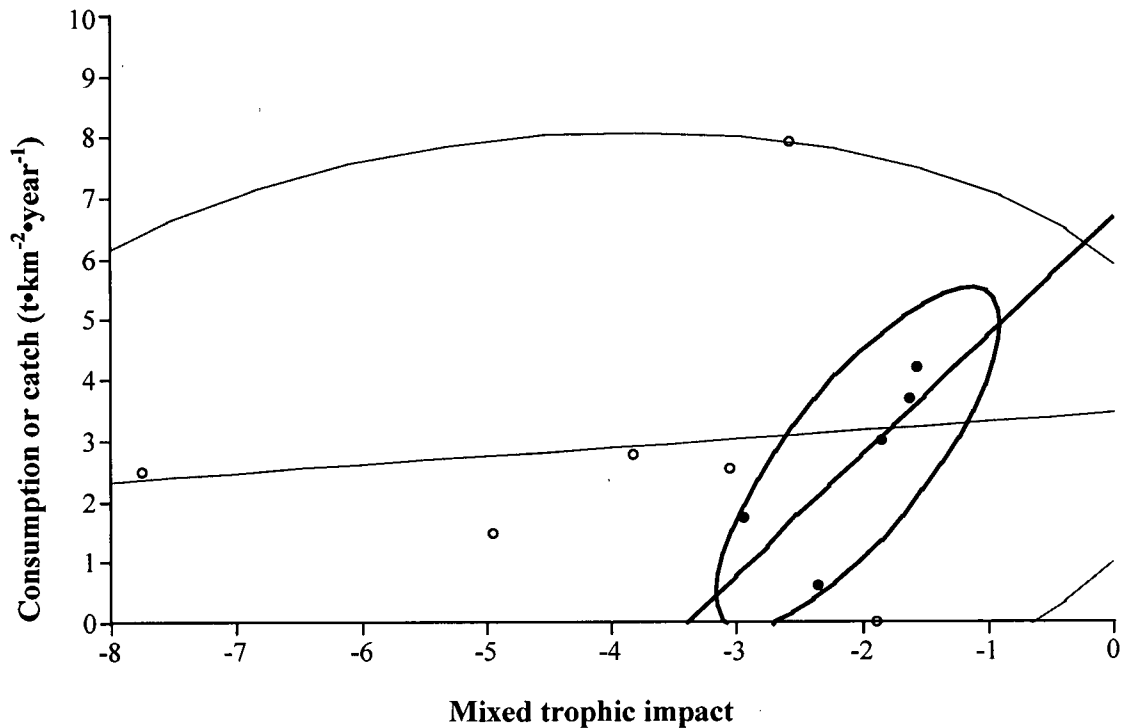


Figure 4.38. Total consumption by marine mammals (black dots) or total catch by fisheries (open dots) versus their respective overall mixed trophic impact for each studied ecosystem. Density ellipses represent the 90% confidence intervals.

Discussion

The trophic impact of marine mammals on food webs is generally seen as a direct relationship between the predators and their prey. Many studies (Parsons 1992; Kenney *et al.* 1995; Lesage *et al.* 2001; Tjelmeland and Lindstrøm 2005) have addressed the question of the trophic role of top predators without taking into account the indirect trophic effects that they can have on their prey. The results presented here suggest that marine mammals can have important indirect effects on trophic structure. Therefore, my analysis offers a new perspective on the function of these predators in marine food webs, and their interaction with fisheries.

We clearly see from results presented above that a change in marine mammal biomass can lead to important alterations in the structure of the ecosystem. In a time where marine ecosystems are overexploited (Pauly *et al.* 1998a; Lotze *et al.* 2006), polluted (Angel 1995; Sindermann 1995; Clark 2001) and subject to climate change

(Harley *et al.* 2006), improving our ability to understand ecological processes involving marine mammals and fisheries becomes crucial.

4.4.1 Resource overlap and trophic levels

On a global scale, most food consumed by marine mammals consists of prey types that are not the main target of fisheries (Figure 4.2), and whales seem to consume most of their food in areas where commercial vessels do not fish (Kaschner and Pauly 2005). In areas where competition between marine mammals and fisheries is evident (identified as hotspots of resource overlap by Kaschner and Pauly [2005]), my results show that the resource overlap is indeed higher than the global average presented in Kaschner and Pauly (2005). However, most overlap appears to occur between fisheries and larger, deep-diving toothed whales (Kaschner 2004), so when all marine mammals are analyzed as a whole, their overlap is not as strong as may be expected.

Depending on the ecosystem, the overlap between marine mammals and fisheries index involves different food types. In the North Sea, the Benguela, and the Strait of Georgia systems, marine mammals and fisheries compete mainly for the 'miscellaneous fish'. This group includes demersal, benthic, benthopelagic and bathydemersal fish that are less than 150 cm, and pelagic fish that are between 60 cm and 150 cm (Pauly *et al.* 1995; Kaschner 2004). For the purpose of this analysis, this prey group is clearly overaggregated; it represents too many different species. Thus, it is important to look at the different species composing the 'miscellaneous fish' group in different ecosystems. In the North Sea, the Benguela and the Strait of Georgia ecosystems, (and for the time periods they represent), there were important fisheries for larger fish (Christensen *et al.* 2002; Shannon *et al.* 2004; Wallace 1998), and the marine mammals species in these ecosystems are higher trophic-level predators, who mostly feed on these large fish (Christensen *et al.* 2002; Shannon *et al.* 2004; Dalsgaard *et al.* 1998). These ecosystems are quite different in terms of structure from the Gulf of St. Lawrence, where the intense fishing activity in the 1980s has led to the depletion of most groundfish stocks, leaving mainly smaller planktivorous fish and crustaceans for fisheries and marine mammals (Morissette *et al.* 2006; Savenkoff *et al.* in press; and see Chapter 5). Consequently, in this

ecosystem, small pelagics are the main overlapping resource. In the Gulf of Thailand, benthic invertebrates and miscellaneous fish are the food types that are most overlapping. Here again, the major development of trawl fishery in the 1960s has led to a shift to lower trophic levels such as 'trash fish' and shrimps (Gulland 1983), and most marine mammals are dolphins and whales that mainly eat smaller fish (Perrin *et al.* 2005). There may have been a time when fisheries and marine mammals did not overlap much in terms of food resources, but now that fisheries has moved down the food web (Pauly *et al.* 1998), the target food types might have become very similar. Finally, in the eastern tropical Pacific ocean, where the resource overlap is the lowest, there is not much competition between fisheries and marine mammal. Fisheries target mainly miscellaneous fish and large species such as tuna, and marine mammals feed mostly on small squids, mesopelagics and small pelagic fish. The number of trophic links in the ecosystem also has an effect on the resource overlap between marine mammal and fisheries. Indeed, food webs with lower connectance (less trophic links) tend to have higher overlap values.

Some ecosystems show an important overlap between marine mammals and fisheries when analyzed by food types: the North Sea, Benguela and Gulf of Thailand are the most important. When the same analysis is done per trophic group (using the complete structure of the catch and the consumption matrix of marine mammals), the overlap index is reduced, but most ecosystems showing important overlap between marine mammals and fisheries remain the same. However, in the case of the North Sea, the overlap index calculated per trophic group is very low compared to the index calculated by food type, suggesting that there is no overlap at the species level.

Overall, landings from global fisheries have shifted from large piscivorous fish toward smaller invertebrates and planktivorous fish (Pauly *et al.* 1998). The mean trophic level of fisheries catches calculated here is thus lower than it was 50 years ago. By contrast, nothing is known about the potential decline in trophic level of marine mammals' consumption over the last century. However, my results show that globally, the trophic level of marine mammals prey is lower than the trophic level of the catch (2.88 *versus* 3.42). As fisheries continue to move further down in terms of the trophic level of species caught, the competition for food resources with marine mammals might become more important. In ecosystems such as the Eastern tropical Pacific where the mean trophic level

of the catch is still high, the overlap with marine mammals is negligible. Interestingly, the Strait of Georgia represent a higher trophic level of marine mammals consumption than trophic level of the catch. This is due to the fact that in this ecosystem, an important marine mammal predator is the killer whale, who mainly feed on pinnipeds, at a very high trophic level. Their presence in the Strait of Georgia definitely increases the average trophic level of marine mammal consumption.

Lately, Japanese scientists have stressed that whales of the world consume annually some 3 to 5 times more marine fish and invertebrates than are fished for direct human consumption or for reduction into fish meal and oil (Anonymous 2001). This situation, it is alleged, is not “in balance” with the world’s increasing need for a stable food supply. Such arguments are used extensively to justify whaling activity, as it is shown in this citation of Mr. Masayuki Komatsu, executive director of the Japanese Marine Fisheries Research and Development Department, to BBC on “the forces that drive Japanese whaling”, 15 June 2006:

“Whale [are] abundant. The number of fish is falling while the number of whales is rising. Surely, the rapid increase in the whale population influences the level of fish stocks? We need to know more about it”.

, my results show that there is no clear and direct relationship between marine mammals’ predation and the potential fish catch in the world’s oceans. Many whales do eat fish, but the species that they eat are not necessarily targeted by fisheries. In fact the global overlap of food resources, representing the main ‘hotspots’ of competition between marine mammals and fisheries (Kaschner 2004; Kaschner and Pauly 2005), is relatively low and similar to ecosystems such as the Gulf of St. Lawrence or the Strait of Georgia. Moreover, as the simulation results showed, it is not that clear whether the extirpation of marine mammals in ecosystems would even increase the biomass of the fish targeted by most fisheries.

4.4.2 Primary production required to sustain marine mammals and fisheries

In the ecosystems studied, the primary production required to sustain marine mammals represents an average of 9.7% of total primary production, less than half the PPR to sustain fisheries catch (20.1%). The latter value represents nearly three times the estimate by Pauly and Christensen (2002) for global fisheries. This is probably due to the fact that my analysis focuses on zones where fishing activity is intense. Accounting for other ecosystems that are less fished would reduce that average PPR presented here.

In most ecosystems, PPR for marine mammals is smaller than PPR for the catch. However, this is not the case in the Eastern tropical Pacific Ocean. All my results show quite different results for this ecosystem. This is likely due to the fact that, indeed, marine mammals are more important than fisheries in the Eastern tropical Pacific Ocean. A second order effect may also be that this model represents a very large area, and that information about marine mammals (biomass, consumption rates, diet, production, etc.) is applied directly on the populations known to be within this area, while fisheries' effects might be more 'diluted' and less important in high sea.

The highest absolute PPR for fisheries catch is seen in the North Sea, and this is driven by very high PPR for sustaining the mackerel catch (1500 t·km⁻² for this single species early in the simulation). Fisheries in this ecosystem require 50% of the total primary production of the system. An even worse case is seen in the Eastern Bering Sea, where 54% of primary production is required to sustain fisheries. PPR required by marine mammals is also the highest in this ecosystem. On the opposite end of the spectrum, the Benguela ecosystem, with the lowest PPR values for both marine mammals and fisheries, is known to be a very productive ecosystem, due to the seasonal, wind-driven upwelling, which enrich the shelf waters and result in a very large productivity (Shannon *et al.* 2003).

4.4.3 Comparing the mixed trophic impact of marine mammals and fisheries

The effect of marine mammals on their prey and consequently on available resources for fisheries is not only a direct predator-prey relationship. Rather their effect is also indirect, for example through feeding both on a prey and the competitors of the prey.

Even if negative for all studied ecosystems, the overall trophic impact of marine mammals on the different trophic groups of the ecosystem was always less strong than that of fisheries, except in the Eastern tropical Pacific Ocean where fisheries target mainly large tunas (important predators of many trophic groups in the ecosystem), while marine mammals feed on a larger array of smaller prey (Olson and Watters 2003).

For marine mammals, there is a paradoxical trend suggesting that the more they consume, the less they tend to reduce overall biomass. This is possible due to the fact that if marine mammals have to increase their consumption, they will feed on a wider array of prey and induce beneficial predation (see below). In contrast, the mixed trophic impact of fisheries on the entire ecosystem is always strongly negative.

Finally, my results show that overall, when marine mammals have a positive impact on some trophic group, the impact of fisheries on the same group is usually negative.

4.4.4 What if marine mammals were not present in these ecosystems?

When the extirpation of marine mammals is simulated in the studied ecosystems, the biomass of other species of the food web also changes. In some ecosystems, commercially important species increase significantly after the eradication of marine mammals (e.g., halibut and large pelagics in the Gulf of St. Lawrence, tuna species in the Eastern tropical Pacific, tuna and pelagic species in the Gulf of Thailand, and cod and plaice in the North Sea). However, when all commercial species are considered, there is no obvious benefit for the fisheries. Indeed, total biomass, with no marine mammals in the ecosystem, remains generally and surprisingly similar, or even decrease (as it is the case with the Eastern Bering Sea and the Gulf of St. Lawrence). Indeed, the extirpation of marine mammals may lead to reduced abundances of commercial important fish in some ecosystems. Cape hake, sardine, redeye in the Benguela upwelling, and herring in the North Sea and in the Strait of Georgia decrease if marine mammals are removed from these systems. In the case of the Gulf of Thailand, the *Plectorhynchidae* group becomes totally depleted when marine mammals are absent. On the other hand, when species or groups increases as a result of the extirpation of marine mammals in the ecosystem, these

species or groups are not necessarily the most important commercially (deepwater fish, jellyfish and cephalopods in the Eastern Bering Sea; cephalopods, juvenile pelagics, or juvenile carangids in the Gulf of Thailand). Finally, when commercially important species increase following the extirpation of marine mammals, the instability that this new situation might lead to is not necessarily a stable equilibrium (Berkeley *et al.* 2004). There might be more fish to catch, but once overfished, these ecosystems could become unstable and at risk of severe losses in biodiversity.

In certain ecosystems (e.g., in Eastern Canada), there have been an important debate on culling marine mammals in an attempt to rebuild stocks of once commercially important fish species (e.g., cod) (Dwyer 1999, Fisheries Resource Conservation Council 2002). In that particular case, at least for the Gulf of St. Lawrence ecosystem, my results suggest that culling of marine mammals would not have led to recovery of the stocks of cods, nor otherwise benefited the commercial fishery. This corroborates the findings of Trzcinski *et al.* (2006), who suggested that even the complete removal of grey seal predation in the eastern Scotian Shelf (Northwest Atlantic) would not assure the recovery of the cod population, given the high levels of other sources of natural mortality.

4.4.5 Marine mammals and beneficial predation

The view that fewer marine mammals would mean more fish in the ocean and more fish for human consumption is often said to be based on “common sense” (Lavigne 2003). However, this view does not account for other components of the ecosystem, and ecological effects such as prey switching, competition, or cascading effects that may overall result in unintended outcomes, including beneficial predation.

I propose in the following conceptual model three types of beneficial predation that can occur between marine mammals and their prey (Figure 4.39). First, a predator (A) can have a positive impact on a prey (2) by also relying on another prey (3), which is a competitor of prey 2 (beneficial predation type 1 in Figure 4.39). An increase of predation from A on 3 would reduce its biomass and thus the level of competition with prey 2. If prey 3 is a preferred prey of predator A and that competition between prey 2 and prey 3 is strong, such a change in the biomass of prey 3 can create a positive effect that

encompasses or else exceed the effect of predation from A on prey 2, creating an overall positive effect of predator A on prey 2. This type of beneficial predation may occur for instance in the Gulf of St. Lawrence, where harp seals are major predators for capelin, but also for Arctic cod, a species that is potentially competing with capelin for the same resources. The overall mixed trophic impact of harp seals on capelin is a positive one (Morissette *et al.* 2006). When all marine mammal species are grouped, this effect is not visible, however. The same kind of phenomenon happens in the Strait of Georgia ecosystem with marine mammals (dolphins, resident killer whales, seals and sea lions) feeding on small pelagic fish and on the competing herring group (competition for zooplankton). The mixed trophic impact analysis clearly shows that even if marine mammals are predators of small pelagics, their presence in the ecosystem is beneficial to this group because they also feed on competing species. In that case, the *Ecosim* scenario with no marine mammal results in a decrease of small pelagic fish, which corroborates that beneficial predation was occurring.

Predator A can also have a positive effect on prey 2 by also feeding on prey 1, which is a predator of prey 2 (beneficial predation type 2 in Figure 4.39). When predator A feeds on prey 1, the predation level on prey 2 is decreased (less predation from prey 1 on prey 2). Once again, if the predation of predator on prey 1 is larger than on prey 2, the overall effect of having Predator A in the ecosystem would be beneficial for prey 2. This is the case, for example, in the Benguela ecosystem, where marine mammals (cetaceans and seals) are feeding on mesopelagic fish, but also on cephalopods, which are major predators of mesopelagic fish. The overall mixed trophic impact of marine mammals on mesopelagic fish is positive, even if they represent a source of predation for that trophic group. Furthermore, the *Ecosim* scenario with no marine mammal results in an important decrease of mesopelagic fish, which indicates that there may be an indirect effect of marine mammals on this trophic group.

Finally, predator A can have a positive effect on prey 3 by being itself a prey for another, larger marine mammal: predator B (type 3 in Figure 4.39). If predator A and prey 3 are both present in an ecosystem, even if predator A is eating prey 3, its presence can be beneficial if predator B has a diet preference for predator A. In this case, the presence of predator A redirected predation by predator B on prey 3. If the predator A becomes less

abundant, predator B can switch to prey 3 and thus this results in higher predation on prey 3. This seems to be the case in the Strait of Georgia ecosystem. Indeed, transient killer whales are predators of small pelagics, but also (and mainly) feed on seals and sea lions, who themselves are important predators of small pelagic fish. The overall mixed trophic impact of marine mammals on small pelagic fish is positive. In *Ecosim* a scenario with no marine mammal would result in a decrease of small pelagic fish.

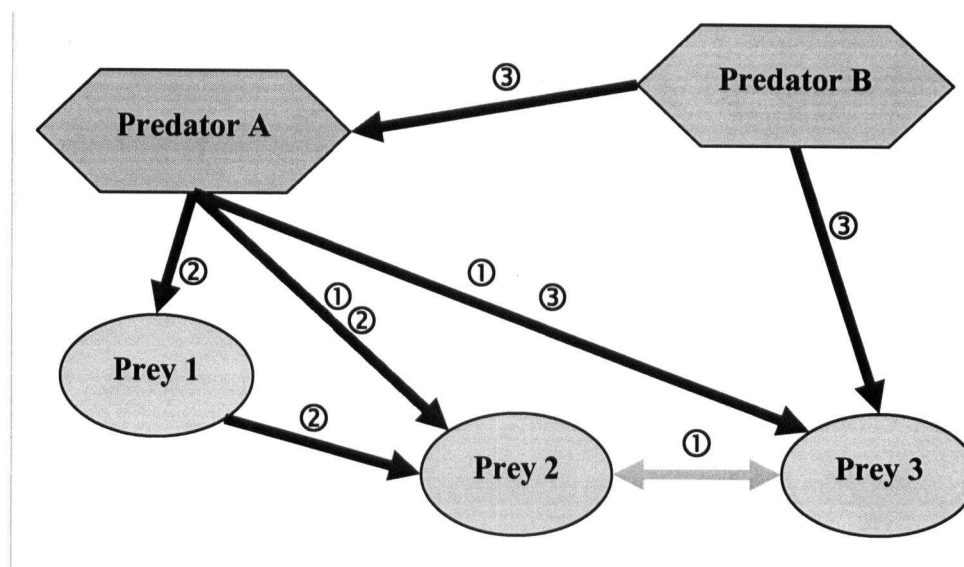


Figure 4.39. Trophic interactions (predation in black, competition in grey) between predators and their prey that can lead to beneficial predation. The numbers above arrows represent the different types of beneficial predation (see text).

4.4.6 Strengths and weaknesses of the modelling approach

My approach emphasized the use of ecosystem models to examine the outcomes of trophic interactions between marine mammals and fisheries. Studying this ecological problem through a modelling approach can enhance our understanding of effect of relationship that would otherwise be very difficult to study. The fact that I could compare and generalize from different ecosystems constructed using the *EwE* approach was one advantage of having comparable models, based on the same framework. The level of detail included in *Ecopath* model structure and equations is a real asset and represent a rigorous analytical framework (Plagányi and Butterworth 2004).

Some authors warn modelers that caution may be taken in applying *EwE* models to marine mammal populations, because their life history is very different from most fish (Plagányi and Butterworth 2004). However here, the simulations I performed consisted in removing all marine mammals, and thus releasing their predation on other trophic groups in the ecosystem. The temporal variation of marine mammals abundance itself was not addressed here (the simulated scenarios always presented how the system would react to the extirpation of marine mammals species, not with the possible causes and modalities of such extirpation). In *Ecosim* runs with original fishing effort (where marine mammals are present in ecosystems), I assume the vulnerabilities and the ecological reliability of each model is representative of the species dynamics and life cycles. These models have all been published and peer-reviewed, and the marine mammals groups present in the models are assumed to have realistic ecological parameters. However, the analysis done with these seven *Ecopath* models did not included any environmental effects that may affect ecosystem dynamics. I thus assumed that everything was explained by species interactions, which is definitely not the case. There are indeed strong evidences that climate change, for example, have an important impact on the availability of marine mammals' prey (Harwood 2001), as well as on their distribution and abundance (Simmonds and Isaac 2007).

One inconvenience of my approach is that I grouped all marine mammals together instead of analyzing pinnipeds, toothed whales, and baleen whales separately. Doing so, I masked the major differences in their feeding ecology. Also, analyzing marine mammals as a whole group could not show what effect their relative abundance have on the trophic impacts. The relative proportions of different marine mammals species would also affect the trophic level. For example, a large biomass of baleen whales, who would mainly consume krill, would significantly lower my estimate of trophic level of consumption.

The calculated overlap index has the disadvantage of representing very large categories of species. Aggregation into large functional groups does not well represents the dynamics of the ecosystem. Thus, while the overlap index represent a good way to have a global and simple representation of the interaction between fisheries and marine mammals, the in-depth analysis of the structure of ecosystems remains crucial. The overlap index calculated at the species level showed that in the case of the North Sea, this

can lead to opposite conclusions. Finally, the fact that the overlap index was calculated for marine mammals as a whole group present, once again, a difficulty. Indeed, as most overlap with fisheries occurs among pinnipeds and dolphins, our estimates of the global overlap between fisheries and marine mammals may be underestimated.

The use of mixed trophic impact analysis is not sufficient when analyzing the global impact of marine mammals on the foodweb. It is never enough to evaluate only the impact from an ecological snapshot that is fixed in time. Dynamic simulations, validated to reproduce reasonably well the past patterns of change in relative abundance of major species (Walters *et al.* 2005) remains the best option.

Conclusions

Our analysis identified that marine mammals are important top predators in marine ecosystems, and that they play an important role in structuring the trophic relationships among food webs. My results show that even in hotspots of competition between marine mammals and fisheries, the overlap for food resources is lower than earlier thought. My results confirm Kaschner and Pauly (2005), who suggested that even the complete eradication of all marine mammals, from all oceans, would likely not increase fisheries catches. Hence, large-scale cullings, as advocated by the Japanese studies (Anonymous 2001) would not increase catches.

This study has focused on the top-down influences of marine mammals and fisheries on the fish species in different ecosystems. Although 'bottom-up' changes were not investigated here, their effects might just be additive and alter even more the structure of the ecosystem. This is particularly true in the actual context of climate change, which can affect the productivity of the world's oceans (Loreng 2004; Sanae *et al.* 2006). There is still much debate about this idea and it will be important to find different ways of addressing this issue. The analysis presented here provided an insight into the problem, but further work on this needs to be pursued.

Chapter summary

The competition between marine mammals and fisheries for marine resources is a major concern. I examined trophic interactions between marine mammals and fisheries

with a resource overlap index developed by Kaschner (2004), using seven *Ecopath* models including marine mammal groups. On a global scale, most food consumed by marine mammals consisted of prey types that were not the main target of fisheries. For each ecosystem, the primary production required (PPR) to sustain fisheries was compared to the PPR to sustain marine mammals groups. The PPR to sustain marine mammals was less than half the PPR to sustain fisheries catch. I also developed an index representing the mean trophic level of marine mammal's consumption (TL_Q) and compared it with the mean trophic level of fisheries catch. My results showed that globally, the trophic level of marine mammals prey was lower than the trophic level of the catch (2.88 *versus* 3.42). As fisheries continue to move further down in terms of the trophic level of species caught (Pauly *et al.* 1998), this competition for food resources with marine mammals might become more important. I also observed patterns of marine mammal consumption *versus* fisheries catches. I estimated the relative mix trophic impacts of a change in marine mammal's biomass on all other components of the ecosystem, including impacts on fisheries. This allowed me to show that marine mammals can have important indirect effects on trophic structure, even beneficial for some of their prey. Within the *Ecosim* framework, I assessed the change in the trophic structure of an ecosystem after the simulated extirpation of marine mammal populations in these seven ecosystems. Changes in marine mammal biomass lead to important alterations in the structure of the ecosystem. According to what I found, there was no clear and direct relationship between marine mammals' predation and the potential fish catch in the world's oceans. Many whales do eat fish, but the species that they eat are not necessarily targeted by fisheries. As the simulation results showed, it is not that clear whether the extirpation of marine mammals in ecosystems would even increase the biomass of the fish targeted by most fisheries. Indeed, total biomass, with no marine mammals in the ecosystem, remained generally and surprisingly similar, or even decreased.

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Chapter 5

A case study in ecosystem modelling:

Contrasting changes between the northern and southern Gulf of St. Lawrence ecosystems associated with the collapse of groundfish stocks.²

5.1 Introduction

In response to a steep decline in Atlantic cod (*Gadus morhua*) abundance in the late 1980s and early 1990s, a moratorium on commercial fishing in a number of stock management areas was imposed by the Canadian government in order to promote recovery of the depleted populations. The southern Gulf of St. Lawrence (SGSL) was closed to directed cod fishing in September 1993, followed by the closure of the northern Gulf of St. Lawrence (NGSL) fishery in January 1994 (Anonymous 1994). The NGSL moratorium was lifted in May 1997, and for the SGSL in 1999. During the three-year period that the moratorium was in place, differing effects were observed on cod stocks in the two regions. For example, a modest improvement in mature cod abundance was observed in the NGSL (Fréchet *et al.* 2005), while spawner abundance remained unchanged in the SGSL (Chouinard *et al.* 2003). Since the re-opening of directed cod fisheries in the two ecosystems, mature cod biomass has remained roughly constant in the NGSL (Fréchet *et al.* 2005), but has declined by nearly 20% in the SGSL (Chouinard *et al.* 2003).

In this study, mass-balance models (*Ecopath*) were developed for NGSL and SGSL ecosystems, for the periods before (mid-1980s) and after (mid-1990s) the collapse

² A version of this chapter has been submitted to *Deep Sea Research II* as Morissette, L., Castonguay, M., Savenkoff, C., Swain, D.P., Chabot, D., Bourdages, H., Hammill, M.O. and J.M. Hanson. Contrasting changes between the northern and southern Gulf of St. Lawrence ecosystems associated with the collapse of groundfish stocks.

of demersal fish stocks in the two areas. The objective was to determine if significant changes in ecosystem structure had occurred between the two time periods that might have contributed to the failure of the cod stocks to recover in the 1990s.

A major change in abundance of a species inevitably has consequences for its predators and prey. There is a need to integrate interactions between species (competition and predation) and the exploitation by fishing in a multispecific approach (Christensen *et al.* 2000; Morissette 2001). Moreover, changes in ecosystems are often studied by comparing models representing two different periods, without including parameter uncertainty and the ensuing uncertainty in the interpretation of the results. Here, we use a new approach towards analyzing the changes between two ecosystems over a period of 10 years by combining a multispecies approach with an in-depth analysis of uncertainty.

Materials and Methods

5.2.1 Study areas

The Gulf of St. Lawrence forms one of the most important estuarine shelves in the world (Therriault 1991). It is the outlet of the St. Lawrence River into the Atlantic Ocean via the Strait of Belle Isle, in the north between Newfoundland and Labrador, and Cabot Strait in the south (Figure 5.1). At its widest, the Gulf extends roughly 500 km from north to south. The northern and southern parts have very different bathymetric characteristics and, to some degree, different faunas. The SGSL (Northwest Atlantic Fishery Organization [NAFO] division 4T) is a relatively shallow shelf (generally < 60 m deep; maximum depth 130 m), with a total area of 64,075 km², and a permanent cold water layer that is in contact with the sediments in water 35 to 100 m deep (Gilbert and Pettigrew 1997) (Figure 5.1). In contrast, the NGSL (NAFO divisions 4RS) is characterized by channels as deep as 500 m: the Laurentian Channel, which extends nearly 1,000 km from the St. Lawrence Estuary to the Atlantic Ocean, in addition to the Esquiman Channel and the Anticosti Channel (Figure 5.1). In the NGSL, the study area covered 103,812 km². Depths shallower than 37 m were not included in the NGSL model. In the SGSL model, we defined the study area to include depths between 15 and the 200 m depth contour, where the deeper water included part of the sharp drop into the Laurentian Channel. The nearshore region was not included in the models because exchanges between infra-littoral

and pelagic zones are not well sampled by government scientific survey trawlers; consequently, the community structure of the shallow depth zones is poorly understood.

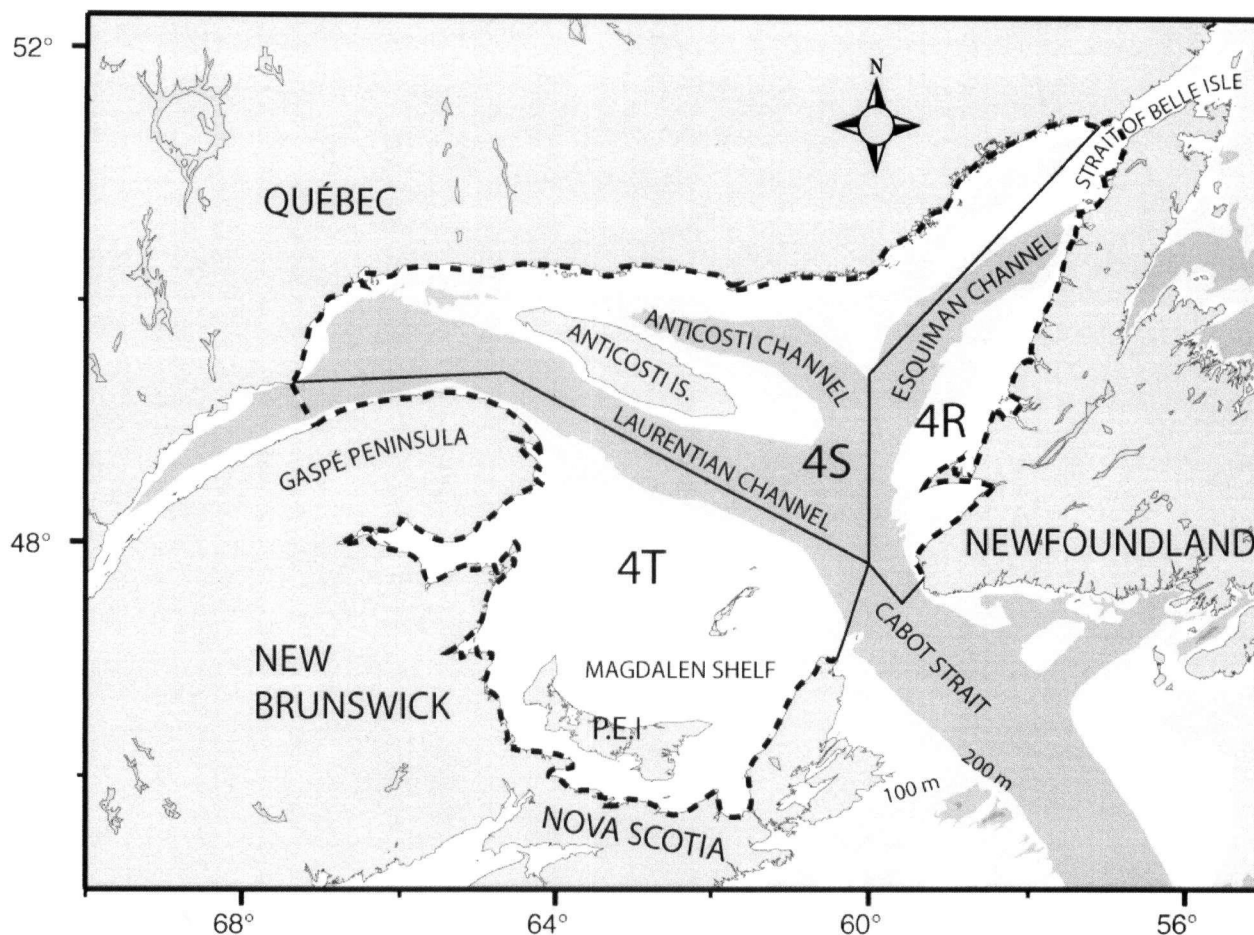


Figure 5.1. The regions of the northern (North Atlantic Fisheries Organisation divisions 4R and 4S) and southern (NAFO division 4T) Gulf of St. Lawrence.

5.2.2 Structure of the models

NGSL and SGSL models, for both periods, were divided into 32 and 30 trophic groups, respectively (Table 5.1). Species were grouped based on their commercial significance and importance as predators or prey. We distinguished five marine mammal groups, one seabird group, 14 (SGSL) or 16 (NGSL) fish groups, six invertebrate groups, two zooplankton groups, one phytoplankton group, and one detritus group (Table 5.1). Some compartments such as large pelagic feeders and large demersal feeders were aggregated on the basis of similarity of size and ecological role of their species. Atlantic

cod, Greenland halibut (*Reinhardtius hippoglossoides*) (in NGSL), and American plaice (*Hippoglossoides platessoides*) (in SGSL) were, for some models, separated into large and small individuals based on diet, age/size at first capture, and age/size at maturity. Smaller animals prey mainly on invertebrates whereas larger animals prey mainly on fish. These changes tend to occur gradually with increasing length, but for these models it was assumed that the change occurs at 35 cm for Atlantic cod (Lilly 1991), at 40 cm for Greenland halibut (Bowering and Lilly 1992), and at 35 cm for American plaice (Pitt 1973). Bacteria were assumed part of the detritus compartment.

Table 5.1. Trophic groups used in the models of the northern (NGSL) and southern (SGSL) Gulf of St. Lawrence ecosystems, for the 1985-1987 and the 1994-1996 periods.

Group Name	Main species	Comments
Cetaceans	<i>Balaenoptera physalus</i> , <i>Balaenoptera acutorostrata</i> , <i>Megaptera novaeangliae</i> , <i>Phocoena phocoena</i> , <i>Lagenorhynchus acutus</i> , <i>Lagenorhynchus albirostris</i>	
Harp seals	<i>Pagophilus groenlandica</i>	
Hooded seals	<i>Cystophora cristata</i>	
Grey seals	<i>Halichoerus grypus</i>	
Harbour seals	<i>Phoca vitulina</i>	
Seabirds	<i>Phalacrocorax carbo</i> , <i>Phalacrocorax auritus</i> , <i>Larus delawarensis</i> , <i>L. argentatus</i> , <i>L. marinus</i> , <i>Sterna hirundo</i> , <i>S. paradisaea</i> , <i>Cephus grylle</i> , <i>Oceanodroma leucorhoa</i> , <i>Morus bassanus</i> , <i>Rissa tridactyla</i> , <i>Uria aalge</i> , <i>Alca torda</i> , <i>Fratercula arctica</i>	
Large Atlantic cod (> 35 cm)	<i>Gadus morhua</i>	
Small Atlantic cod (\leq 35 cm)	<i>Gadus morhua</i>	
Large Greenland halibut (> 40 cm)	<i>Reinhardtius hippoglossoides</i>	Large and small Greenland halibuts were aggregated as Greenland halibut for the SGSL models
Small Greenland halibut (\leq 40 cm)	<i>Reinhardtius hippoglossoides</i>	
Large American plaice (> 35 cm)	<i>Hippoglossoides platessoides</i>	Large and small plaice were aggregated as American plaice for the NGSL models
Small American plaice (\leq 35 cm)	<i>Hippoglossoides platessoides</i>	
Flounders	<i>Limanda ferruginea</i> , <i>Glyptocephalus cynoglossus</i> , <i>Pseudopleuronectes americanus</i>	
Skates	<i>Amblyraja radiata</i> , <i>Malacoraja senta</i> , <i>Leucoraja ocellata</i>	
Redfish	<i>Sebastes mentella</i> , <i>Sebastes fasciatus</i>	
Large demersal feeders	<i>Urophycis tenuis</i> , <i>Melanogrammus aeglefinus</i> , <i>Centroscyllium fabricii</i> , <i>Anarhichas</i> spp., <i>Cyclopterus lumpus</i> , <i>lycodes</i> spp., <i>Macrouridae</i> , <i>Zoarcidae</i> , <i>Lophius americanus</i> , <i>Hippoglossus hippoglossus</i>	
Small demersal feeders	<i>Myoxocephalus</i> sp., <i>Tautoglabrus adspersus</i> , <i>Macrozoarces americanus</i> , juvenile large demersal feeders	
Capelin	<i>Mallotus villosus</i>	
Sand lance	<i>Ammodytes</i> spp.	Included in the planktivorous small pelagic feeder group for the SGSL models
Arctic cod	<i>Boreogadus saida</i>	Included in the capelin group for the SGSL models
Large pelagic feeders	<i>Squalus acanthias</i> , <i>Pollachius virens</i> , <i>Merluccius bilinearis</i> , <i>Cetorhinus maximus</i> , <i>Thunnus thynnus</i>	

Table 5.1: Cont.

Group Name	Main species	Comments
Piscivorous small pelagic feeders	<i>Scomber scombrus</i> , piscivorous myctophids and other mesopelagic species, <i>Illex illecebrosus</i> , piscivorous juvenile large pelagic feeders	
Planktivorous small pelagic feeders	<i>Clupea harengus harengus</i> , planktivorous myctophids and other mesopelagic species, <i>Scomberesox saurus</i> , <i>Gonatus</i> sp., planktivorous juvenile large pelagic feeders	
Shrimp	<i>Pandalus borealis</i> , <i>P. montagui</i> , <i>Argis dentata</i> , <i>Eualus macilentus</i> and <i>E. gaimardi</i>	
Large crustaceans	<i>Chionoecetes opilio</i> , other non-commercial crab species (<i>Hyas</i> spp)	
Echinoderms	<i>Echinarachnius parma</i> , <i>Stronglyocentrotus pallidus</i> , <i>Ophiura robusta</i>	
Molluscs	<i>Mesodesma deauratum</i> , <i>Cyrtodaria siliqua</i>	
Polychaetes	<i>Exogene hebes</i> , and other polychaetes species	
Other benthic invertebrates	Miscellaneous crustaceans, nematodes, other meiofauna	
Large zooplankton (> 5 mm)	Euphausiids, chaetognaths, hyperiid amphipods, cnidarians and ctenophores (jellyfish), mysids, tunicates >5 mm, ichthyoplankton	
Small zooplankton (< 5 mm)	Copepods (mainly <i>Calanus finmarchicus</i> , <i>C. hyperboreus</i> and <i>Oithona similis</i>), tunicates < 5 mm, meroplankton	
Phytoplankton	Diatom species, and a mixture of autotrophic and mixotrophic organisms including Cryptophytes, dinoflagellates, Prasinophytes, mixotrophic <i>Stombidium</i> spp., and Prymnesiophytes	
Detritus		

5.2.3 Data used for the models

Information on species, biomass, production, consumption, diet and catch for each trophic group of NGSL and SGSL models was obtained from various sources given in Morissette *et al.* (2003) and Savenkoff *et al.* (2004 *a, b*). Biomass estimates for demersal fishes were obtained from annual bottom trawl surveys in the two ecosystems. For both NGSL and SGSL models, biomass estimates from these surveys were adjusted to total biomass based on the catchability coefficients given by Harley and Myers (2001) and Savenkoff *et al.* (2004 *a, b*).

Overall, considerable effort was expended to obtain biomass, production, consumption, diet, and catch data that came from the study areas during the periods of interest. However, information on several groups (e.g., forage species, benthic invertebrates, and zooplankton) was sparse or non-existent for the areas and periods studied; in these situations, data were obtained either from the literature or from different period of the same area (Morissette *et al.* 2003; Savenkoff *et al.* 2004 *a, b*).

5.2.4 Modelling approaches

We used 31 balanced solutions obtained using inverse methodology for each ecosystem and period. These solutions corresponded to 31 random perturbations (including a response without perturbation) on each model input to a maximum of its standard deviation. The inverse approach was useful to obtain a first balanced solution by finding the solution that minimizes (objective least-square criterion) both the sum of squared flows (thus the total sum of flows through the food web) and the sum of squared residual errors (minimizes the imbalances between inputs and outputs) consistent with the constraints (Vézina and Platt 1988). A more complete description of these balanced scenarios is given in Savenkoff *et al.* (in press *a*) for the NGSL and in Savenkoff *et al.* (in press *b*) for the SGSL. Each of these 31 balanced inverse solutions were then transposed into *Ecopath* software to estimate mortality (due to fishing, predators, and other sources), the basic emergent properties and network analysis indices for the two time periods, and estimates of the associated uncertainties.

The emergent properties of the two systems were compared using a two-tailed t-test, with a significance level of 0.05. These t-tests verified the hypothesis that there was a significant difference, for a given emergent property and ecosystem, between the 31 balanced solutions obtained for the 1980s and the 1990s. Trophic levels of catches were also compared with a two-tailed t-test. Each value is presented with 95% confidence intervals around the mean (*CI*); if these *CI* do not overlap, the difference between the two values of a parameter is significant. The t-tests are fairly robust to lack of normality or to heteroscedasticity (Zar 1998). However, because our data sometimes departed markedly from the basic assumptions of the t-test, we also used the non-parametric test of Wilcoxon (also known as Mann-Whitney *U* test). The results were the same for most comparisons, but in case of conflict, we retained the non-parametric result. Only the latter are reported in the text or tables.

Assuming an equilibrium or steady state, model estimates of biomass, production, catch in fisheries and consumption by predators were used to derive estimates of total mortality (*Z*), and its components (fishing mortality *F*, predation mortality *M2*, and other mortality *M0*). Note that, in contrast to the usual notation in fisheries science (e.g., Ricker

1975), we use these symbols to refer to annual rates rather than instantaneous rates. These indices were compared for some important groups, and between similar trophic groups of each ecosystem. Four main trophic groups were studied here: (1) marine mammals and seabirds; (2) piscivorous fish including all fish species except forage species; (3) forage fish including capelin, sand lance, Arctic cod, and small pelagic fish (mostly herring and mackerel); and (4) shrimp and large crustaceans. The systems' emergent properties were also compared using emergent properties estimates and network analysis indices of the two models for the two time periods calculated by the *Ecopath with Ecosim* software (Christensen *et al.* 2000). The indices used include the sum of all consumption, exports, respiration, production, and flow to detritus (reported as $t \cdot km^{-2} \cdot year^{-1}$), the mean trophic level of the catch, gross efficiency of the catch (the catch divided by the net primary production; dimensionless), and the net system production (see Christensen [1995] and Christensen *et al.* [2000] for a description of the emergent properties indices). Network analysis indices were also analysed in terms of ascendancy (A), which is the product of the total systems throughput and the average mutual information of the flow structure (Ulanowicz and Puccia 1990), development capacity (C), which is a measure of the network's potential for competitive advantage over other real or presumed network configurations and is the upper bound to the ascendancy (Ulanowicz and Puccia 1990), and overhead (O), which is complementary to ascendancy and indicates the inefficiency and redundant degrees of freedom in the system (Ulanowicz 2000).

Ecopath methods also allow the calculation of many indices that can describe the complexity in the community structure (Christensen 1995). Attributes were selected according to a previous study by Vasconcellos *et al.* (1997), who identified ascendancy, connectance index, and system omnivory index as representative of Odum's attributes of ecosystem complexity (Odum 1971). Within these many indices, the system omnivory index (SOI) is the one that we favoured in our analyses. Pimm (1982) defined an omnivore as a species that feeds on more than one trophic level. The System Omnivory Index (SOI) is defined as the average Omnivory Index (OI) of all consumers weighted by the logarithm of the biomass consumed by each consumer (Christensen *et al.* 2000). In other words, the system omnivory index is a measure of how the feeding interactions are distributed

between trophic levels. This index is used to characterize the extent to which a system displays web-like features (Christensen *et al.* 2000).

Results

5.3.1 Biomass

The total catchability-corrected biomass of exploited fish and invertebrate species decreased by about 50% in NGSL (Figure 5.2) and about 30% in SGSL between the mid-1980s and the mid-1990s (Figure 5.3); on the other hand there was a significant increase in marine mammals biomass between the 1985-1987 and the 1994-1996 periods.

There was a significant decrease in the biomass of piscivorous fish in both NGSL and SGSL. Forage fish biomass also showed a downward trend, though the decline in their biomass was only slight in the SGSL. The total biomass of the shrimp and large crustaceans group changed little from the mid-1980s to the mid-1990s, except for shrimps, which doubled their biomass between these two periods in the SGSL.

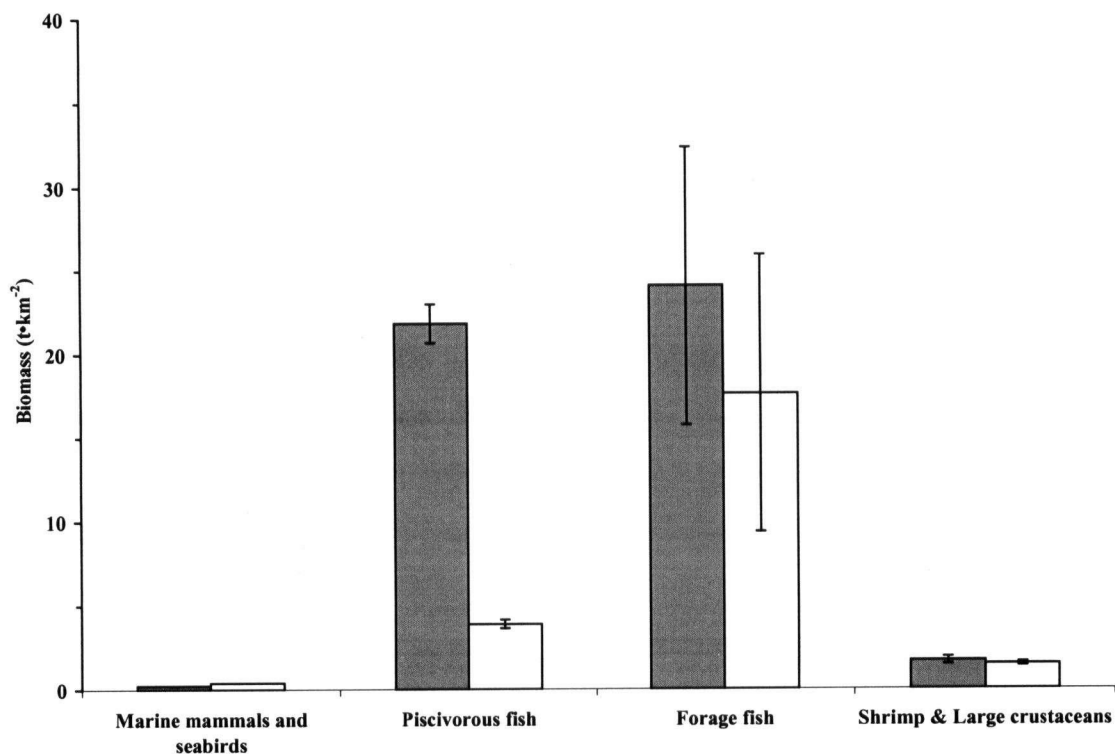


Figure 5.2. Biomass change for marine mammals and seabirds, piscivorous fish, forage fish, and shrimp and large crustaceans in the northern Gulf of St. Lawrence (NGSL) from the 1985-1987 (grey histogram; $B = 48 \pm 24 \text{ t} \cdot \text{km}^{-2}$) to the 1994-1996 (white histogram; $B = 23 \pm 23 \text{ t} \cdot \text{km}^{-2}$) periods. B = total biomass for the four

groups, or all commercial species. Error bars indicate the 95% confidence intervals of biomass for the 31 balanced scenarios.

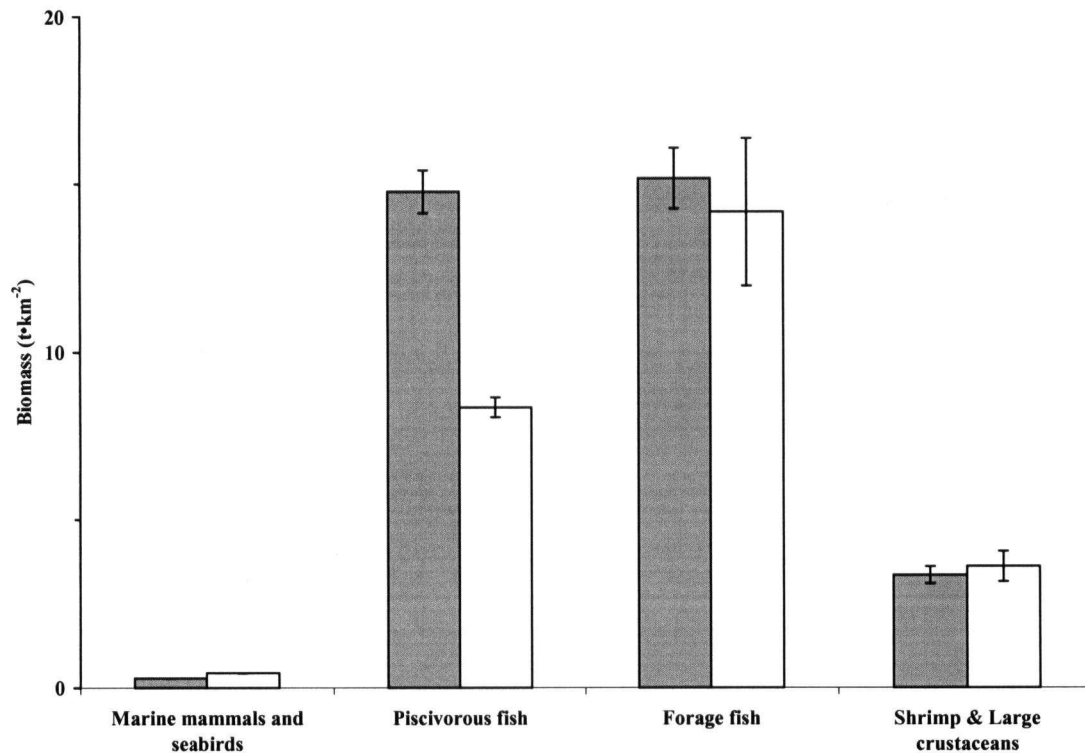


Figure 5.3. Biomass change for marine mammals and seabirds, piscivorous fish, forage fish, and shrimp and large crustaceans in the southern Gulf of St. Lawrence (SGSL) from the 1985-1987 ($B = 32 \pm 3 \text{ t} \cdot \text{km}^{-2}$) to the 1994-1996 ($B = 27 \pm 6 \text{ t} \cdot \text{km}^{-2}$) periods. B = total biomass for the four groups, or all commercial species. Error bars indicate the 95% confidence intervals of biomass for the 31 balanced scenarios.

5.3.2 Consumption

The major changes observed in the biomass structure also affected the total consumption (Q) of the different trophic groups on all their prey. In the NGSL, the total annual consumption by marine mammals significantly increased from the 1980s to the 1990s (Figure 5.4), while total consumption by piscivorous and forage fish, shrimp and large crustaceans showed a sharp significant decline (overall decrease $\approx 80\%$). The most important proportional decrease in consumption was attributed to the piscivorous fish group, for which Q decreased from 12.7 to $2.0 \text{ t} \cdot \text{km}^{-2} \cdot \text{year}^{-1}$ (84%), although the absolute decrease was much greater for forage fishes (a decrease of $27.4 \text{ t} \cdot \text{km}^{-2} \cdot \text{year}^{-1}$). In the SGSL, total consumption by piscivorous fish also decreased significantly from 11.3 to $6.3 \text{ t} \cdot \text{km}^{-2} \cdot \text{year}^{-1}$ (44%) (Figure 5.5). The consumption by marine mammals changed little

between the two time periods, while the consumption by both forage fish and shrimp and large crustaceans groups increased significantly. In both ecosystems, even in the 1990s, total consumption (i.e., predation) by marine mammals was always much smaller than consumption by any other trophic group examined (Figures 5.4 and 5.5).

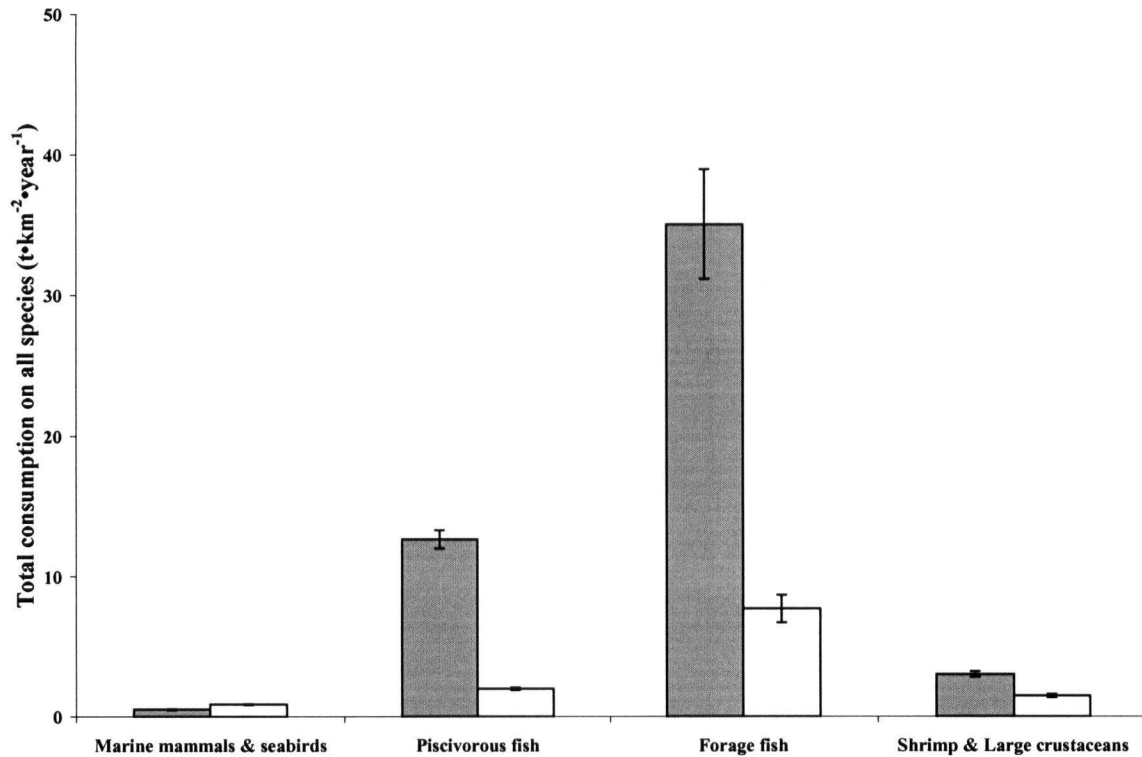


Figure 5.4. Total consumption (Q) on all prey by marine mammals, piscivorous fish, forage fish, shrimp and large crustaceans in the northern Gulf of St. Lawrence (NGSL) in the 1980s (grey) and the 1990s (white). Error bars indicate the 95% confidence intervals of total consumption for the 31 balanced scenarios.

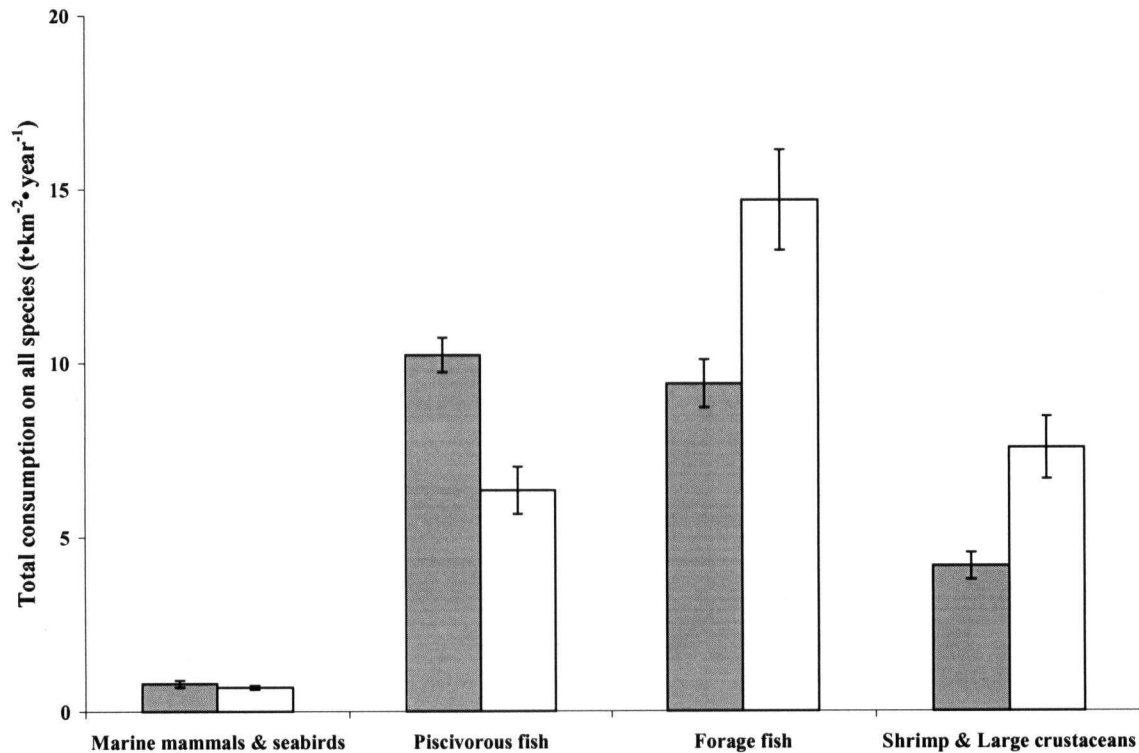


Figure 5.5. Total consumption (Q) on all prey by marine mammals, piscivorous fish, forage fish, shrimp and large crustaceans in the southern Gulf of St. Lawrence (SGSL) in the 1980s (grey) and the 1990s (white). Error bars indicate the 95% confidence intervals of total consumption for the 31 balanced scenarios.

In the NGSL, the overall consumption by all seal species increased significantly from the 1980s to the 1990s on all prey species except small cod for which consumption by seals significantly decreased, and for flounders and large crustaceans, where no significant difference was observed (Figure 5.6). In the SGSL, seal consumption significantly increased for half the prey groups (Greenland halibut, flounders, redfish, and capelin) (Figure 5.6). The increased consumption of capelin in the SGSL greatly exceeded the change in consumption of any other group. Overall, seals consumed more fish prey in the SGSL model than in the NGSL model, except for deep-water species such as Greenland halibut and redfish, consistent with the fact that they are not a major component of the SGSL ecosystem. Furthermore, seals consumed much more large cod in the SGSL than in the NGSL during both periods. In contrast, there was a sharp and significant decline in the consumption of small cod by seals in the SGSL in the 1990s model. Despite

increasing shrimp biomass, consumption of shrimp by seals actually dropped significantly in the SGSL model for the mid-1990s.

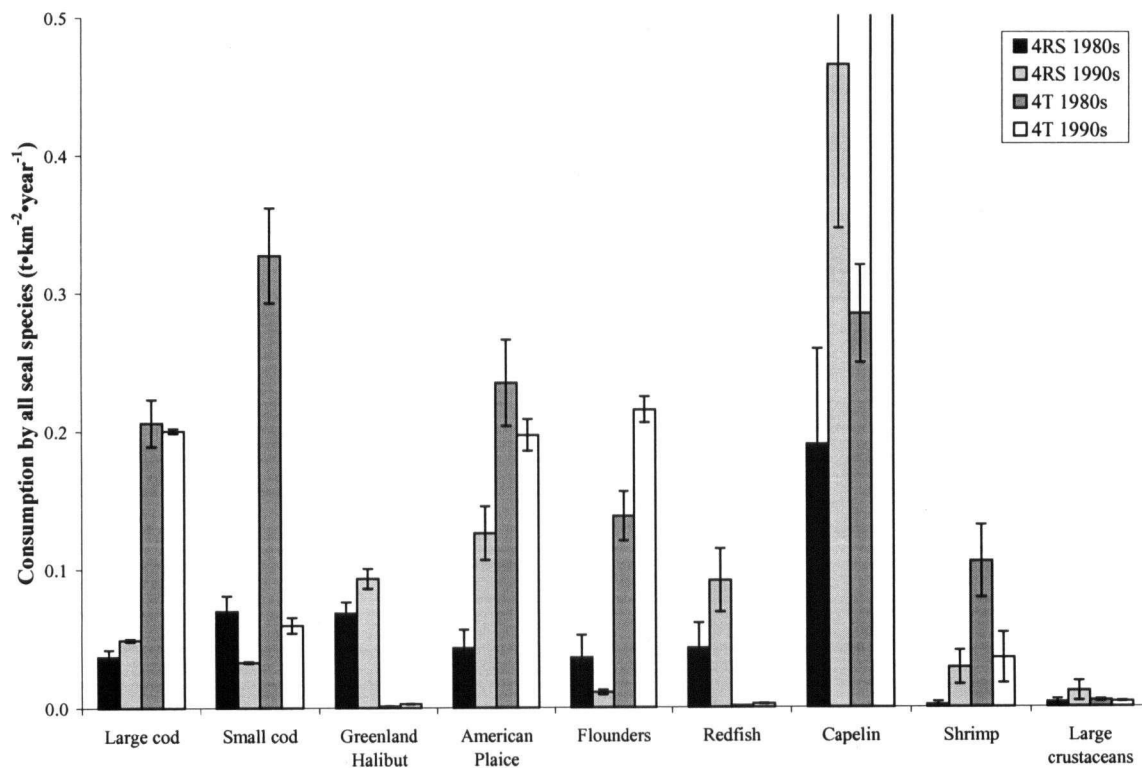


Figure 5.6. Seal consumption on various prey in the northern (NGSL) and southern (SGSL) Gulf of St. Lawrence in the 1980s and the 1990s. Error bars indicate the 95% confidence intervals of seals consumption for the 31 balanced scenarios. Q on capelin in NGSL 1990s = $0.47 \pm 0.12 \text{ t} \cdot \text{km}^{-2} \cdot \text{year}^{-1}$, Q on capelin in SGSL 1990s = $1.27 \pm 0.13 \text{ t} \cdot \text{km}^{-2} \cdot \text{year}^{-1}$.

5.3.3 Mortality

Three sources of mortality are distinguished by the *Ecopath* models: predation mortality ($M2$), fishing mortality (F), and other mortality (disease, other natural causes of death, and unexplained mortality, $M0$). At equilibrium, total mortality (Z) should be equivalent to the production to biomass ratio of each group. In the NGSL, small Greenland halibut had the highest significant increase in total mortality from the 1980s to the 1990s, while shrimp had the largest significant decrease (Table 5.2, Figure 5.7).

Table 5.2. Changes in predation mortality ($M2$), fishing mortality (F) and other mortality ($M0$) from the 1980s to the 1990s, for all trophic groups in the northern Gulf of St. Lawrence model.

Species	M2			F			M0		
	1980s mean	1990s mean	P (U test) $\alpha = 0.05$	1980s mean	1990s mean	P (U test) $\alpha = 0.05$	1980s mean	1990s mean	P (U test) $\alpha = 0.05$
Cetaceans	-	-	-	0.003	0.002	<0.01	0.067	0.062	<0.01
Harp seals	-	-	-	0.078	0.053	<0.01	0.024	0.010	<0.01
Hooded seals	-	-	-	0.030	0.005	<0.01	0.042	0.085	<0.01
Grey seals	-	-	-	0.068	0.000	<0.01	0.038	0.045	<0.01
Harbour seals	-	-	-	0.000	0.000	-	0.069	0.051	<0.01
Seabirds	-	-	-	0.118	0.085	<0.01	0.240	0.289	0.02
Large cod	0.018	0.341	<0.01	0.349	0.019	<0.01	0.391	0.136	<0.01
Small cod	0.619	0.747	<0.01	0.001	0.000	<0.01	0.198	0.030	<0.01
L. Greenland halibut	0.086	0.099	0.46	0.098	0.048	<0.01	0.037	0.025	0.09
S. Greenland halibut	0.236	0.592	<0.01	0.000	0.000	-	0.059	0.103	0.11
American plaice	0.267	0.285	0.27	0.026	0.003	<0.01	0.039	0.032	0.24
Flounders	0.243	0.252	0.07	0.014	0.026	<0.01	0.029	0.035	0.06
Skates	0.226	0.250	0.80	0.000	0.008	<0.01	0.045	0.029	0.52
Redfish	0.158	0.181	<0.01	0.029	0.023	0.13	0.060	0.031	<0.01
L. demersal fish	0.113	0.164	<0.01	0.010	0.008	<0.01	0.028	0.013	0.03
S. demersal fish	0.423	0.278	<0.01	0.000	0.000	-	0.029	0.021	<0.01
Capelin	0.730	0.950	<0.01	0.002	0.013	<0.01	0.178	0.100	0.40
Sand lance	1.043	0.588	<0.01	0.000	0.000	-	0.250	0.035	<0.01
Arctic cod	0.431	0.628	<0.01	0.000	0.000	-	0.053	0.127	<0.01
L. pelagic fish	0.131	0.235	<0.01	0.056	0.001	<0.01	0.059	0.020	<0.01
S. pisciv. pel. fish	0.240	0.318	<0.01	0.007	0.060	<0.01	0.051	0.018	<0.01
S. plankt. pel. fish	0.315	0.316	0.21	0.111	0.144	<0.01	0.040	0.026	0.18
Shrimp	1.628	0.611	<0.01	0.116	0.166	<0.01	0.084	0.055	<0.01
Large crustaceans	0.194	0.192	0.04	0.053	0.083	<0.01	0.065	0.021	<0.01
Echinoderms	0.020	0.003	<0.01	0.000	0.000	-	0.321	0.390	<0.01
Molluscs	0.021	0.012	<0.01	0.001	0.000	<0.01	0.615	0.712	<0.01
Polychaetes	0.969	0.987	0.80	0.000	0.000	-	1.029	1.011	0.59
Other bent. invert.	0.401	0.220	<0.01	0.000	0.000	-	0.974	1.056	0.24
Large zooplankton	2.728	3.006	0.10	0.000	0.000	-	0.295	0.850	0.03
Small zooplankton	3.938	2.951	<0.01	0.000	0.000	-	1.011	2.496	<0.01
Phytoplankton	75.733	58.821	<0.01	0.000	0.000	-	29.302	34.530	0.96

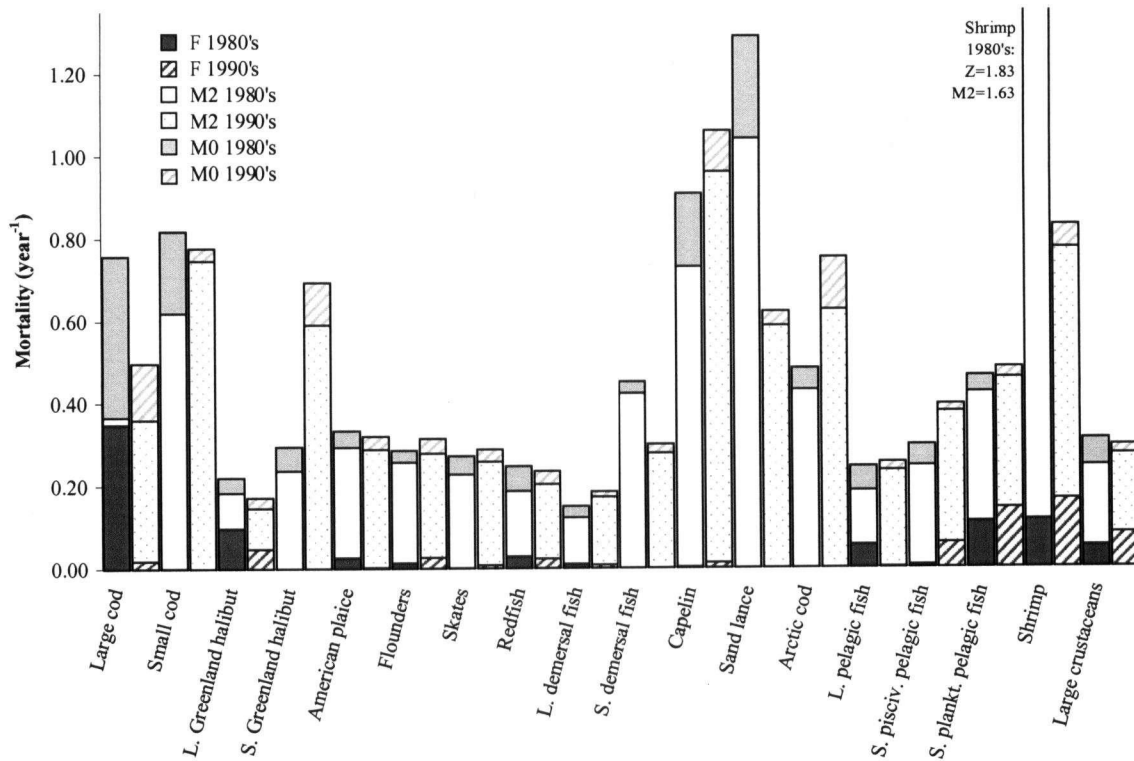


Figure 5.7. Breakdown of total mortality (Z) into fishing (F), predation ($M2$) and unexplained ($M0$) mortalities, in annual rate (year^{-1}), for commercial species of the northern Gulf of St. Lawrence (NGSL). Plain bars represent the 1980s while patterned bars represent the 1990s results. For clarity, 95% CI were excluded.

In the SGSL, small demersal fish had the highest significant increase in total mortality, while large cod had the steepest significant decline in total mortality (Table 5.3, Figure 5.8).

Table 5.3. Changes in predation mortality (*M2*), fishing mortality (*F*) and other mortality (*M0*) from the 1980s to the 1990s, for all trophic groups in the southern Gulf of St. Lawrence model.

Species	M2			F			M0		
	1980s mean	1990s mean	P (U test) $\alpha = 0.05$	1980s mean	1990s mean	P (U test) $\alpha = 0.05$	1980s mean	1990s mean	P (U test) $\alpha = 0.05$
Cetaceans	-	-	-	0.022	0.013	<0.01	0.048	0.075	<0.01
Harp seals	-	-	-	0.004	0.034	<0.01	0.065	0.041	<0.01
Hooded seals	-	-	-	0.000	0.000	-	0.109	0.085	<0.01
Grey seals	-	-	-	0.029	0.004	<0.01	0.101	0.112	<0.01
Harbour seals	-	-	-	0.000	0.000	-	0.119	0.109	0.10
Seabirds	-	-	-	0.097	0.119	0.12	0.246	0.258	0.85
Large cod	0.060	0.154	<0.01	0.318	0.024	<0.01	0.327	0.152	<0.01
Small cod	0.568	0.487	<0.01	0.000	0.000	-	0.051	0.063	0.16
Greenland Halibut	0.473	0.491	0.02	0.318	0.184	<0.01	0.189	0.120	0.03
S. American plaice	0.289	0.349	0.02	0.000	0.000	-	0.191	0.119	<0.01
L. American plaice	0.158	0.195	0.13	0.293	0.136	<0.01	0.066	0.028	<0.01
Flounders	0.236	0.211	0.01	0.028	0.012	<0.01	0.023	0.028	0.26
Skates	0.243	0.235	0.44	0.000	0.012	<0.01	0.031	0.046	<0.01
Redfish	0.209	0.223	0.36	0.104	0.049	<0.01	0.028	0.047	<0.01
L. demersal fish	0.188	0.401	<0.01	0.249	0.010	<0.01	0.020	0.026	0.01
S. demersal fish	0.298	0.779	<0.01	0.000	0.000	-	0.014	0.038	<0.01
Capelin	0.870	0.678	<0.01	0.005	0.001	<0.01	0.045	0.252	<0.01
L. pelagic fish	0.234	0.218	0.87	0.110	0.115	0.37	0.059	0.053	0.98
S. pisciv. pelagic fish	0.225	0.245	0.11	0.036	0.169	<0.01	0.072	0.057	0.44
S. plankt. pelagic fish	0.360	0.255	<0.01	0.157	0.270	<0.01	0.036	0.077	<0.01
Shrimp	3.172	2.639	0.27	0.005	0.010	0.01	0.527	0.685	0.97
Large crustaceans	0.204	0.191	0.03	0.137	0.140	0.85	0.019	0.034	0.30
Echinoderms	0.031	0.023	0.05	0.000	0.000	-	0.336	0.360	0.45
Molluscs	0.084	0.097	0.99	0.000	0.000	0.29	0.609	0.543	0.60
Polychaetes	1.838	1.728	0.11	0.000	0.000	-	0.242	0.241	0.18
Other bent. invert.	0.945	0.706	0.04	0.000	0.000	-	0.476	0.578	0.87
Large zooplankton	5.237	2.939	<0.01	0.000	0.000	-	0.687	0.970	0.22
Small zooplankton	3.214	3.994	<0.01	0.000	0.000	-	1.954	1.107	<0.01
Phytoplankton	74.568	62.756	0.13	0.000	0.000	-	23.227	35.040	0.13

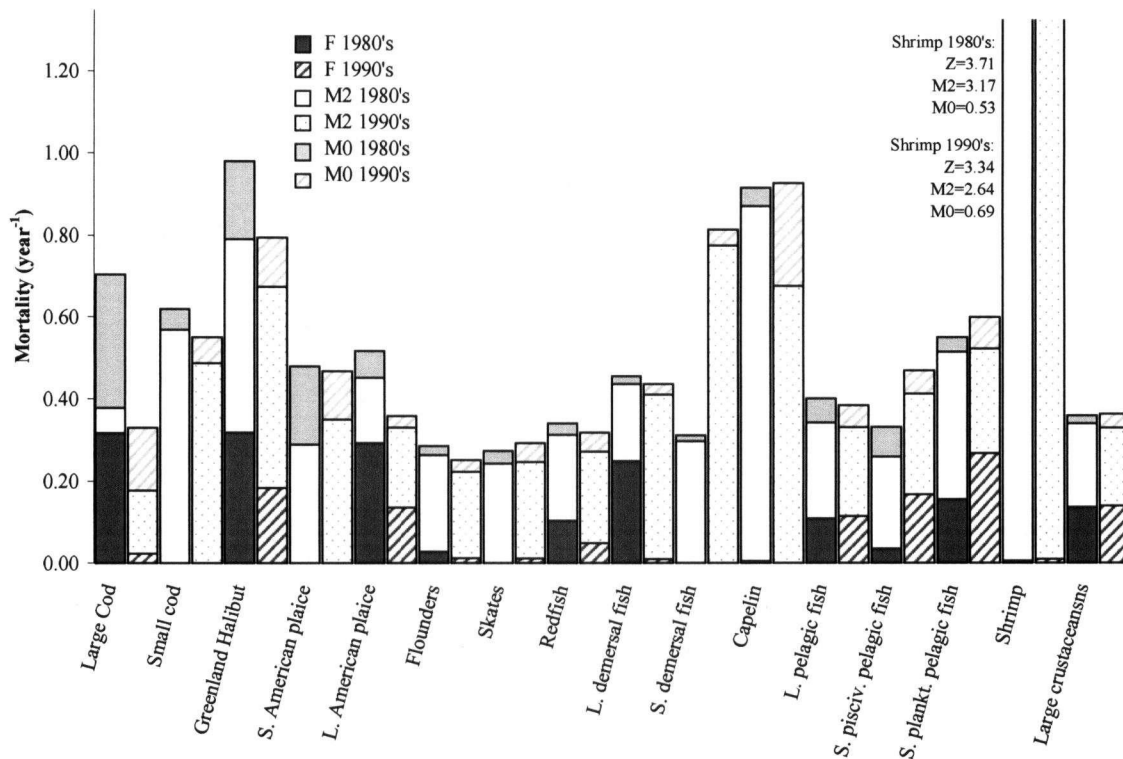


Figure 5.8. Breakdown of total mortality (Z) into fishing (F), predation ($M2$) and unexplained ($M0$) mortalities, in annual rate (year^{-1}), for commercial species of the southern Gulf of St. Lawrence (SGSL). Plain bars represent the 1980s while patterned bars represent the 1990s results. For clarity, 95% CI were excluded.

For both models in the 1990s, fishing mortality of the major piscivorous fish was significantly reduced (Tables 5.2 and 5.3), while it increased for species of lower trophic levels such as flounders (only in the NGSL), skates, capelin (only in the NGSL), large pelagic fish (only in the NGSL), small pelagic fish, shrimp and large crustaceans (only in NGSL). Overall fishing mortality decreased significantly in both ecosystems (from 1.17 to 0.75 year^{-1} in NGSL and from 1.91 to 1.30 year^{-1} in the SGSL). Also, predation mortality (excluding predation from benthic invertebrates and plankton) significantly decreased from 7.10 to 7.03 year^{-1} in the NGSL, and remained approximately the same from 7.79 to 7.75 year^{-1} in the SGSL. Predation mortality significantly increased from the 1980s to the 1990s for some species such as cod (large and small), small Greenland halibut, redfish, large demersal fish, capelin, Arctic cod, large pelagic fish, and piscivorous small pelagic fish in the NGSL, and for large cod, Greenland halibut, small American plaice, and demersal fish (large and small) and small zooplankton in the SGSL. Overall, other

mortality (excluding $M0$ on invertebrates and plankton) significantly decreased from the 1980s ($M0 = 2.17 \text{ year}^{-1}$) to the 1990s ($M0 = 1.40 \text{ year}^{-1}$) in the NGSL models, but was similar between the two periods in the SGSL models (2.39 year^{-1} in the 1980s and 2.51 year^{-1} in the 1990s). The most important level of $M0$ in proportion to total mortality was found for large cod in NGSL (51% in the 1980s. However $M0$ declined to 34% when 20% of misreported catches were included [Savenkoff *et al.* in press *a*]. In the 1990s, $M0$ was 28%). In the SGSL, the most important level of $M0$ in proportion to total mortality was also found for large cod (46% in the 1980s, 46% in the 1990s) (Tables 5.2 and 5.3, Figures 5.7 and 5.8).

In the specific case of large cod, total mortality was similar in NGSL and SGSL in the 1980s ($Z = 0.76 \text{ year}^{-1}$ in the NGSL and 0.71 year^{-1} in the SGSL), and decreased to lower values in 1990s ($Z = 0.50 \text{ year}^{-1}$ in NGSL and 0.32 year^{-1} in the SGSL) (Figures 5.7 and 5.8). Fishing mortality was also similar in both ecosystems in the 1980s ($F = 0.35 \text{ year}^{-1}$ in NGSL and 0.32 year^{-1} in the SGSL) and significantly decreased, to a value of 0.02 year^{-1} in the 1990s in both ecosystems. Predation mortality on large cod, $M2$, significantly increased in the NGSL, from 0.02 to 0.34 year^{-1} (Figure 5.7) but this increase was smaller (but still significant) in the SGSL (from 0.06 to 0.15 year^{-1}) (Figure 5.8). Finally, other mortality $M0$ decreased significantly from the 1980s to the 1990s, in both ecosystems (from 0.39 to 0.14 year^{-1} in NGSL, and from 0.33 to 0.15 year^{-1} in the SGSL).

5.3.4 Trophic levels

Among marine mammals, the trophic levels (TL) estimated by NGSL models significantly decreased from the 1980s to the 1990s for harp seals, but significantly increased for harbour seals. However, it remained about the same for cetaceans, hooded seals, and grey seals (Table 5.4). In the SGSL, trophic levels increased significantly for cetaceans, harp seals, and harbour seals but remained approximately the same for grey seals and hooded seals (Table 5.5). The most important decreases in TL were observed for large demersal fish in NGSL and skates in SGSL. The most important increases in TL were observed in piscivorous small pelagic fish in both ecosystems. Trophic levels did not change for skates, redfish, arctic cod, large crustaceans, benthic invertebrates, and small zooplankton in the NGSL, or for Greenland halibut, small American plaice, flounders,

redfish, demersal fish, capelin, shrimp, large crustaceans, and benthic invertebrates in the SGSL.

Table 5.4. Average trophic level of the 30 balanced scenarios for the Northern Gulf of St. Lawrence in the 1980s and the 1990s.

Species	Average TL 1980s	Average TL 1990s	% change	<i>p</i>
Cetacea	4.12	4.14	0.4	0.202
Harp seals	4.37	4.14	-5.6	0.000
Hooded seals	4.71	4.72	0.2	0.702
Grey seals	4.55	4.55	-0.2	0.823
Harbour seals	4.28	4.37	2.0	0.000
Seabirds	4.15	4.22	1.6	0.001
Large cod	4.20	4.08	-2.9	0.000
Small cod	3.65	3.83	4.8	0.000
L. Greenland halibut	4.08	4.18	2.5	0.000
S. Greenland halibut	4.08	4.03	-1.3	0.012
American plaice	3.53	3.13	-12.6	0.000
Flounders	3.18	3.12	-1.7	0.005
Skates	4.07	4.02	-1.1	0.167
Redfish	3.61	3.65	0.9	0.012
L. demersals	3.73	3.29	-13.1	0.000
S. demersals	3.12	3.33	6.3	0.000
Capelin	3.27	3.33	1.7	0.000
Sand lance	3.15	3.21	1.9	0.000
Arctic cod	3.26	3.30	1.1	0.274
L. pelagics	3.94	3.66	-7.8	0.000
S. pisciv. pelagics	3.18	3.43	7.3	0.000
S. plankt. pelagics	3.14	3.32	5.3	0.000
Shrimp	2.45	2.58	4.9	0.006
Large crustacea	3.04	3.02	-0.8	0.434
Echinoderms	2.00	2.00	0.0	-
Molluscs	2.00	2.00	0.0	-
Polychaetes	2.12	2.12	0.0	0.795
Other bent. invert.	2.00	2.00	0.0	-
Large zooplankton	2.44	2.50	2.4	0.001
Small zooplankton	2.10	2.13	1.1	0.015
Phytoplankton	1.00	1.00	0.0	-
Detritus	1.00	1.00	0.0	-

Table 5.5. Average trophic level of the 30 balanced scenarios for the southern Gulf of St. Lawrence in the 1980s and the 1990s.

Species	Average TL 1980s	Average TL 1990s	% change	<i>p</i>
Cetacea	4.23	4.35	2.8	0.000
Harp seal	4.01	4.15	3.3	0.000
Hooded seal	4.34	4.34	0.0	0.900
Grey seal	4.42	4.40	-0.4	0.223
Harbour seal	4.29	4.43	3.0	0.000
Seabirds	4.15	4.31	3.6	0.000
Large cod	3.50	3.69	5.2	0.000
Small cod	3.34	3.45	3.2	0.000
Greenland halibut	4.02	3.97	-1.4	0.053
Sm. american plaice	3.25	3.28	1.0	0.186
L. American plaice	3.14	3.22	2.4	0.034
Flounders	3.06	3.06	-0.3	0.244
Skates	4.25	4.01	-6.0	0.000
Redfish	3.62	3.62	-0.1	0.872
L. demersal feeders	4.20	4.23	0.6	0.191
Sm. demersal feeders	3.98	3.97	-0.1	0.887
Capelin	3.14	3.16	0.6	0.225
Large pelagic feeders	4.00	4.23	5.4	0.000
Pisc. sm. pel. feeders	3.29	3.55	7.4	0.000
Plank. sm. pel. feed.	3.22	3.28	1.7	0.001
Shrimp	2.45	2.50	2.1	0.392
Large crustaceans	2.83	2.79	-1.7	0.448
Echinoderms	2.00	2.00	0.0	-
Molluscs	2.00	2.00	0.0	-
Polychaetes	2.25	2.22	-1.4	0.213
OBI	2.00	2.00	0.0	-
Large zooplankton	2.43	2.50	2.6	0.001
Small zooplankton	2.12	2.14	1.0	0.218
Phytoplankton	1.00	1.00	0.0	-
Detritus	1.00	1.00	0.0	-

In both ecosystems, the mean trophic level of fishery landings over a 10-year period decreased significantly, from 3.30 to 3.08 in the NGSL, and from 3.33 to 3.21 in the SGSL (Figure 5.9). In the NGSL, landings changed from a predominance of large cod, redfish and planktivorous small pelagic fish (mainly herring) to a catch composition dominated by herring, shrimp and large crustaceans ten years later. In the SGSL, the fishery changed from a high proportion of large cod, planktivorous small pelagic fish (mainly herring), and large crustaceans to catches that were dominated by herring, large crustaceans, and piscivorous small pelagic fish (mainly mackerel) in the 1990s. Moreover,

the TL of landings in the 1980s was marginally higher in the SGSL than the NGSL (by about 1%), but this difference increased to 4% and became significant in the 1990s.

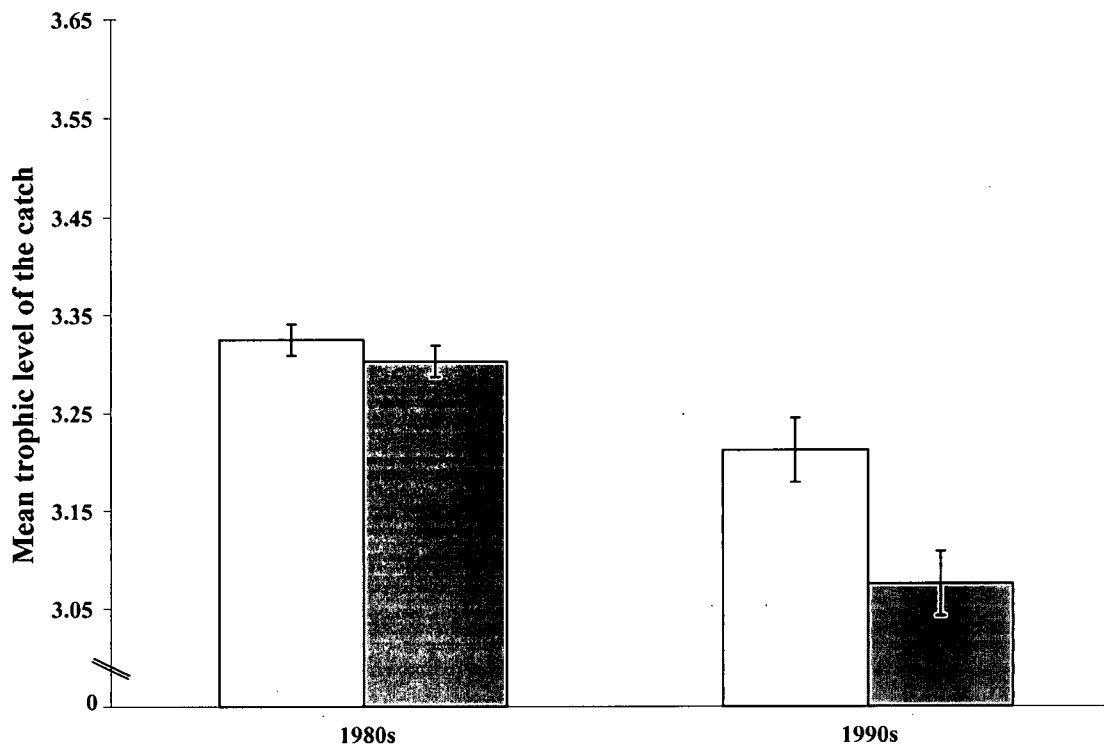


Figure 5.9. Mean trophic level of the catch change over a decade in the southern (SGSL, in grey) and northern (NGSL, in white) Gulf of St. Lawrence ecosystems. Error bars indicate the 95% confidence intervals of trophic level for the 31 balanced scenarios.

5.3.5 Emergent properties of ecosystems

Most of the emergent properties showed a significant difference from the 1980s to the 1990s (Table 5.6). The sum of all production, total system throughput, the ratio of total primary production to total production, ascendancy, overhead, capacity and throughput cycled (excluding detritus) significantly decreased in the NGSL, while they show a significant opposite change for the SGSL. In contrast, the ratio of total biomass to total throughput significantly increased in the NGSL while it decreased significantly in the SGSL. The mean trophic level of the catch, gross efficiency, total catches and connectance index decreased significantly for both ecosystems. There was also a significant change in the sum of all consumption in the NGSL, in addition to a significant change in the sum of all respiratory flows, sum of all flows into detritus, calculated net primary production, and

the ratio of total primary production to total respiration in the SGSL (Table 5.6). Most emergent properties that showed a significant change are indicators of a more productive ecosystem in the NGSL in the 1980s compared to the 1990s while, surprisingly, we see the opposite picture in SGSL (see Christensen *et al.* [2000] for a complete description of the indices).

Table 5.6. Emergent properties of the 1980s and 1990s models for the northern and southern Gulf of St. Lawrence.

Parameters	NGSL 1980s Mean	NGSL 1990s Mean	p (U test) $\alpha = 0.05$	SGSL 1980s Mean	SGSL 1990s Mean	p (U test) $\alpha = 0.05$
Sum of all consumption ^a	1861	1553	0.01	1832	2072	0.06
Sum of all exports ^a	12	10	0.77	14	14	0.06
Sum of all respiratory flows ^a	1297	1118	0.07	1293	1544	0.02
Sum of all flows into detritus ^a	1206	1220	0.28	1239	1504	<0.01
Sum of all production ^a	1788	1571	0.01	1780	2059	0.02
Total system throughput ^a	4377	3901	0.01	4378	5134	0.01
Mean trophic level of the catch	3.303	3.076	<0.01	3.325	3.212	<0.01
Gross efficiency (catch/net p.p.)	0.0023	0.0004	<0.01	0.0023	0.0014	<0.01
Calculated total net primary production ^a	1310	1128	0.07	1307	1558	0.02
Total primary production/total respiration	1.010	1.009	0.96	1.011	1.009	0.01
Net system production ^a	12.4	10.5	0.77	14.1	13.7	0.06
Total primary production/total biomass	4.6	4.2	0.01	4.7	5.1	<0.05
Total biomass/total throughput	0.066	0.071	<0.01	0.067	0.062	0.03
Total biomass (excluding detritus) ^a	285	276	0.74	284	308	0.16
Total catches ^a	2.794	0.471	<0.01	2.811	1.996	<0.01
Connectance Index	0.254	0.243	<0.01	0.258	0.235	<0.01
System Omnivory Index	0.121	0.126	0.35	0.130	0.126	0.09
Ascendancy ^d	3328	2958	0.02	3349	3873	0.03
Overhead ^d	14246	12246	0.01	14159	16770	0.01
Capacity ^d	17574	15204	0.01	17508	20642	0.01
Finn's cycling index ^b	15.03	16.57	0.08	14.97	14.73	0.88
Predatory cycling index ^c	7.32	7.56	0.25	7.20	8.41	0.55
Finn's mean path length	3.38	3.46	0.06	3.37	3.35	0.95
Throughput cycled excluding detritus ^a	142	113	0.04	137	173	0.01
Throughput cycled including detritus ^a	652	667	0.39	661	754	0.27

a = $\text{t}\cdot\text{km}^{-2}\cdot\text{year}^{-1}$; b = % of total throughput; c = % of throughput without detritus; d = flowbits (Ulanowicz and Puccia 1990)

Discussion

The comparison of SGSL and NGSL ecosystems and their changes over a 10-year period represents a step forward in the analysis of the Gulf of St. Lawrence ecosystem,

because of the areas covered, but also because of the thorough uncertainty analysis undertaken for the first time. All the results presented here were averaged from 31 balanced solutions obtained from inverse models, which represented possible stable states for the two ecosystems. Working with averages of many models (and their variation) is a much stronger approach than to only consider one balanced solution, and gives us more confidence in the results and their interpretation. Because it is the first time such an uncertainty analysis is coupled with *Ecopath* modelling, this work may represent an important step forward in such ecosystem investigations.

5.4.1 Biomass structure of ecosystems

In both the NGSL and SGSL ecosystems, the structure shifted dramatically from one previously dominated by piscivorous demersal fishes during the mid-1980s to one dominated by small-bodied pelagic species in the mid-1990s, with a significantly greater marine mammal biomass during the mid-1990s. For both ecosystems, there was an important decline in abundance and the predatory role of piscivorous fish between the two periods modelled. Changes in the biomass of forage fish and large crustaceans groups were not significant in either ecosystem. For the SGSL, an increase in capelin biomass during the mid-1990s offsets decreases in the biomass of piscivorous and planktivorous small pelagic species, while shrimp biomass doubled. In the NGSL models, capelin biomass (the main forage species) was assumed to be the same in both periods, but this may reflect the lack of information on this and other forage species (e.g., sandlance and Arctic cod) in the NGSL (Morissette *et al.* 2003). For the SGSL, the model results are supported by the trawl survey data that showed substantial increases in capelin and shrimp biomass between the two periods - by an even greater amount than is indicated in the models (Benoit and Swain 2003). Furthermore, changes in ecosystem structure may have been even greater than indicated by our models, because information on abundance and diet of zooplankton and many benthic invertebrate groups was lacking. Finally, the decline in abundance of large piscivorous fish in both these ecosystems was similar to the declines reported in many other ecosystems of the world (Pauly and Maclean 2003), including other regions of the Northwest Atlantic (Rice and Rivard 2003).

5.4.2 Changes in consumption

In the NGSL, the changes in the structure of the ecosystem were linked to a decrease in total consumption. Except for marine mammals, the consumption by all groups (excluding benthic invertebrates and plankton) decreased substantially. The main change in relative importance appears to be the decline in piscivorous fish, even though their importance relative to forage fish stayed about the same, i.e., they consumed about a third as much as forage fish in both periods. Interestingly, the consumption by shrimp and crabs decreased much more (about 50%, Figure 5.5) than their biomass (about 10%, Figure 5.2). This is mainly due to a substantial decrease in shrimp Q/B , (from 7.15 in the 1980s to 3.78 in the 1990s). This reduced Q/B was still within the range of possible values for shrimp, but was probably the maximum consumption the NGSL model could accept to reach a balanced solution.

In contrast to the NGSL, there was an increase in consumption in the SGSL. The system changed from one dominated by piscivorous and forage fish to one dominated by forage fish. The decline in total consumption by piscivorous fish was compensated by an increased consumption by shrimp (whose biomass at least doubled), large crustaceans, and forage fish. The increase in consumption by forage fish in the SGSL was mostly due to a large increase in capelin biomass. Although total forage fish biomass changed little between models for the two periods (Figure 5.3), biomass of capelin had to be increased, relative to the 1980s estimate, in order to meet predator demands and obtain a balanced model for the 1990s. As stated above, the empirical evidence from trawl surveys supports this result. Furthermore, the models indicated a diet switch for the forage species as well, with an increase in their trophic levels in both ecosystems from the 1980s to the 1990s. The increased importance of capelin biomass in the 1990s in the SGSL induced an increase of its proportion in the diet of its predators (mackerel and herring), and thus, an increase in their respective trophic levels.

These trophic level shifts could indicate either changes in prey eaten by the predator, or by one or more of its prey. If a species at a lower trophic level changes its diet (e.g., to benthic from pelagic prey, which results in increased trophic level of the prey species), then the predators feeding on this same prey would also show an increase in trophic level. For example, the observed decrease in the trophic level of marine mammals

(mainly harp seals) in the 1990s is consistent with the observed change in their diet. During the 1980s, small cod were important in the harp seal and grey seal diets but were replaced by a higher proportion of lower trophic level species in the 1990s. When planktonic prey were not considered, capelin was the most important prey during the 1990s and a large increase in the percent contribution of capelin to seal diets in the 1990s model was also observed. Thus, the increase in consumption by forage fish (i.e., capelin) could be explained by an increase in predation mortality, and then an increase in total mortality or production of capelin.

5.4.3 Predation by apex predators

The reduced biomass of large predatory fish such as cod, American plaice, flounders, and redfish in the 1990s resulted in an increased relative mortality on these species due to predation by seals. In the NGSL, the consumption by seals increased, perhaps due to the important increase in their biomass. Indeed, seal populations increased with annual rates ranging from 3.9% year⁻¹ (harp seal) to 9.7% year⁻¹ (grey seal) in Atlantic Canada during the last two decades (Hammill and Stenson 2000), and they are now among the top three predators for many important fish species.

However, despite their increase in biomass, total consumption by seals changed little in the SGSL, the increased consumption by grey seals being compensated by a substantial decline in consumption by harp seals. This decrease in consumption by seals coincides with a decrease in energy reserves (body condition) in the 1990s compared to the 1980s, and this has been documented for harp seals (Hammill *et al.* 1995; Chabot *et al.* 1996) and hooded seals off Newfoundland (Leblanc 2003). In the SGSL, seal consumption on large cod was much more important than in the NGSL. This is because grey seal abundance is higher in the SGSL (Hammill and Stenson 2000), and cod was its most common prey during the 1980s. Finally, the current level of consumption of cod and other prey by seals could actually represent an important source of competition for resources with the remaining fisheries (Trites *et al.* 1997).

The growing populations of seals in the Gulf of St. Lawrence could have a direct negative effect on cod recruitment through predation on prerecruit cod; but they could also have an indirect positive effect through predation on pelagic fishes, which are possible

predators of early life history stages of cod (Swain and Sinclair 2000). For example, in the NGSL, harp seals may have a positive impact on skates and small demersal fish, because even though they prey on these species, they also feed on species that are potentially competing with them for the same resources (e.g., capelin, Arctic cod, and sand lance), or on species that are also predators of skates and small demersal fish (e.g., large demersal fish, Atlantic cod). This beneficial effect could be even greater than the predation itself, leading to an overall positive impact of the predator for its prey (Morissette *et al.* 2006, and see Chapter 4).

5.4.4 Impact of fishing

In both ecosystems, fishing mortality was intentionally reduced by a 3-4 year groundfish moratorium in the mid 1990s. As expected, fishing mortality decreased significantly from the mid-1980s to mid-1990s. However, for cod in both areas, this part of total mortality was replaced by predation (Figures 5.7 and 5.8). Top predators such as cetaceans and seals became the only large predators left, and ended up occupying the place that was vacated by the fishery and large piscivorous fish. The large decrease in consumption by predator fish was not entirely compensated by an increase in consumption by marine mammals, and total consumption decreased in the NGSL, but not in the SGSL. The most important commercial species in both ecosystems in the 1980s was cod. These stocks suffered from a commercial collapse in the late 1980s, a phenomenon that has been well documented (see Harris [1998] for a review). There is no consensus on the causes of the collapse of cod stocks. Some authors argue that it is due to intensive exploitation combined with a period of reduced productivity of cod stocks, as evidenced by poor condition and growth, and increased natural mortality (Dutil *et al.* 1999; Dutil and Lambert 2000). Others conclude that the collapse of cod stocks was solely due to overfishing (e.g., Hutchings and Myers 1994, Hutchings 1996). This is supported by our models relying on nominal catches, which suggest that a large part of cod mortality remains unexplained (M0). Savenkoff *et al.* (2004c) concluded that much of the other mortality in the NGSL ecosystem in the 1980s might be the result of under-reporting and discarding of catches. As a result, fishing mortality was substantially underestimated in the mid 1980s, just before the demise of the cod stock. Even though all the factors stated

above may have contributed to the decline in cod stocks in the late 1980s and early 1990s, the modelling approaches used in Savenkoff *et al.* (in press *a*) and here provide support the conclusion that overexploitation was by far the leading cause of the collapse for the NGSL and SGSL stocks.

Pauly *et al.* (1998) called attention to the phenomenon of fishing down the food web. This occurs when large, relatively slow growing, piscivorous fishes are overfished and gradually replaced in fisheries landings by smaller, fast-growing, fish and invertebrates (Pauly and Maclean 2003). This phenomenon can be demonstrated through a decline in the mean trophic level of fisheries landings over time, a trend that has been frequently observed throughout the world. Slight declines in the mean trophic level of landings occurred between our models for the 1980s and 1990s, particularly in the NGSL. These decreases were mainly a reflection of the sharp declines in groundfish landings, i.e., high trophic level fishes, with little replacement by increased landings at lower trophic levels, as required for fishing “through” food webs (Essington *et al.* 2005).

5.4.5 Emergent properties of the models

Ecopath modelling allowed us to analyse a series of parameters on the systems’ emergent properties, which represented a useful way of comparing different ecosystems and to show important temporal or spatial trends. Even though the overall biomass and cycling (Finn’s cycling index, predatory cycling, throughput cycled) did not change significantly over the 10-year period we examined, there was a strong indication that the sum of flows changed in both ecosystems (significant decrease in respiratory flows, total system throughput, and total production in the NGSL, but significant increase of the same parameters in the SGSL). All these indices represent the size of the entire system in terms of flow (Ulanowicz 1986), meaning that less energy is flowing in the entire ecosystem in the 1990s compared to the 1980s in the NGSL; however, there was greater flow of energy for the 1990s compared to 1980s in the SGSL. Moreover, the ascendancy, the overhead and the capacity are indices based on thermodynamics and information theory representing ecosystem growth and development (Christensen 1995). They are other strong indicators that the NGSL ecosystem was closer to maturity in the 1980s than in the 1990s (these three indices decreased significantly over the 10 years period), while the

opposite is true in the SGSL. This change of flows certainly indicates that the overall structure of the NGSL and SGSL ecosystems changed through time. However, these indices need to be studied in more ecosystems before their interpretation in terms of maturity can be confirmed. The removal of cod in the SGSL can hardly be a sign of maturity, considering that historically cod was the dominant piscivorous fish in the ecosystem.

The lack of recovery of many important stocks of the GSL that underwent drastic declines leading to fishing moratoria clearly point to the need to understand how ecosystems react to perturbations. One argument is that more complex ecosystems will cope better with perturbations (McNaughton 1978). For example, major decreases in abundance of gadoid predators on the eastern shelf/Georges Bank ecosystem of the United States was offset by increased abundance of elasmobranchs and large demersal predators (i.e., various sculpins) such that total consumption of forage fishes changed remarkably little (Fogarty and Murawski 1998; Link and Garrison 2002). This concept of resilience is also linked to maturity, as ecosystems are thought to be more stable when they reach maturity. The connectance index, which reflects complexity, decreased significantly from the 1980s to the 1990s in both ecosystems. This may reflect that ecosystems were more perturbed in the 1990s than in the 1980s. In the NGSL, this loss in connectance is reflected by the loss in maturity (ascendancy, overhead and capacity), while in SGSL, even if the maturity seemed to increase over the 10-year period, the connectance decreased significantly. Also, since both ecosystems differed in their communities (NGSL was dominated by capelin and herring in the mid-1990s while SGSL was dominated by herring, capelin, mackerel, several flatfish species, and majiid crabs) and oceanographic features, we might predict that recovery from the current perturbation will also be different for each ecosystem.

In NGSL, the emergent properties suggested a less productive system for the 1990s than for the 1980s. In contrast, in the SGSL, productivity was similar to that of the NGSL in the 1980s, but actually increased in the 1990s. In the SGSL, there were also some higher trophic level fish such as cod whose biomass had not completely collapsed, which might increase the productivity of the system. In addition, biomasses of groups such as capelin and shrimp increased substantially during the 1990s. Moreover, the fact that there

was a large increase in consumption by forage fish in the SGSL in the 1990s, when their biomass showed no significant decline since the 1980s could reflect an increased consumption of forage fish by other groups, and hence increased productivity of forage fish (to keep biomass the same despite increased predation). This could explain the higher consumption by forage fish, linked to a greater abundance of high trophic level groups to prey on forage fish in the SGSL than in the NGSL. In the latter ecosystem, many species showed severely depleted abundance, which would explain the reduced productivity of the system in the 1990s.

Cury *et al.* (2003) defined a regime shift as a process of density compensation of some species after the removal of some other species in an ecosystem. As fisheries have removed extensive amounts of predatory fishes during the last decades, one must carefully consider the implications for the other components of these systems. However, our models suggest that in both NGSL and SGSL, fishing did not lead to clear compensatory of biomass or consumption of other species resulting from the removal of predatory fishes (except perhaps for capelin and shrimp, which increased in SGSL in the 1990s). In the SGSL case, the decrease in consumption by predatory fishes was more than offset by increases in consumption by forage fishes, shrimp and large crustaceans. For the SGSL, this increased importance of forage fishes, shrimp and crabs may reflect release from predation or competition, but it may also reflect other factors that are not examined here (e.g., favorable environmental conditions). Regardless of the cause, neither population of Atlantic cod has increased in abundance despite greatly reduced fishing pressure since 1993/94, and the failure of strong year-classes to develop is currently perplexing because both populations were able to increase due to strong pulses of recruitment during a similar population collapse in the 1970s (Chouinard and Fréchet 1994; Sinclair and Murawski 1997). Seals have also continued to increase at a relatively constant rate, but no species has yet had sufficient time to move in to occupy the role of large predator that was previously occupied by cod. More recent models would be useful in attempting to explain why cod has not recovered further nearly ten years after the 1990s models.

Chapter summary

In order to have a global view of ecosystem changes associated with the collapse of groundfish species in the Gulf of St. Lawrence during the early 1990s, four *Ecopath* mass-balance models were constructed that included an in-depth analysis of uncertainty. These models covered two ecosystems (northern and southern Gulf of St. Lawrence; NAFO divisions NGSL and SGSL), and two time periods (before the collapse, in the mid-1980s, and after it, in the mid-1990s). Our analyses revealed that the ecosystem structure shifted dramatically from one previously dominated by piscivorous groundfish during the mid-1980s to one now dominated by small-bodied pelagic species during the mid-1990s in both southern and northern Gulf. The species structure in NGSL versus SGSL was different, and that may explain why these two ecosystems did not recover the same way from the collapse in the early 1990s. Productivity declined in the northern Gulf after the collapse but increased in the southern Gulf. The collapse of groundfish stocks resulted in declines in the mean trophic level of the landings in both the northern and the southern Gulf. Even though fishing mortality was then intentionally reduced, this part of the total mortality was taken up by predation. The temporal changes in the internal structure of both ecosystems are reflected in their overall emergent properties.

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Chapter 6

Conclusion

If the ecological status of the world's marine ecosystems is to be evaluated, it could be as follows: at the global scale, fish populations are declining in abundance (Myers and Worm, 2003), and crashes of many large-scale fisheries around the world are occurring (Pauly *et al.* 1998). What was perceived for a long time as an inexhaustible resource now seems quite limited (Rosenberg *et al.* 1993).

To understand the nature and dynamics of exploited marine ecosystems, and more precisely the interactions of the species they are in, the development of an ecosystem approach is essential. In chapter 1, a database of *Ecopath* models of marine ecosystems was presented as a useful tool to investigate a wide range of scientific questions about the world's oceans. The database of models itself documents the great effort that is currently undertaken to describe the diversity of the world's ocean. Overall, this database assembled 393 *Ecopath* models that are now publicly available. As such, they can be put to more uses than the ones for which they were built. This thesis is one of these uses. It is based on a selection of ecosystem models representing the world's ocean, allowing three specific issues of marine ecology to be addressed. Thus, the use of several models simultaneously allowed me to address more general or global issues in marine ecology.

Ecosystem modelling is a useful tool to understand marine ecological processes, but there is a lot of uncertainty related to the models' structure and outcomes. In Chapter 2, I reviewed the different options available for uncertainty analyses in marine ecosystem models, and proposed some alternatives for a better investigation of uncertainty. Unfortunately, only few of the many published studies have gone so far as to examine uncertainty in their analyses. This chapter emphasized the importance of doing so. After discussing the strengths and weaknesses of the different ways to address uncertainty in the models, a new approach was proposed, combining *Ecopath* with other modelling techniques (inverse methods) in order to gain robustness.

Part of the uncertainty in ecosystem models is due to the quality of input data, and the trust we have in model parameters. Not only the quality of input data can influence model's uncertainty, but I also found out that it can affect importantly the way the model performs its simulations. In chapter 3, I used 50 *Ecopath* models to test the hypothesis that the quality of ecosystem models' inputs plays a significant role in predicting the relationship between complexity and stability. My secondary hypothesis was that there is, in ecosystems, a direct relationship between complexity and stability. Quality of input data has sometimes been questioned, but was never analysed as a factor that could affect the diversity-stability relationship, or the outcomes of modeling results. My results have shown that the quality of data used in ecosystems models, as well as the realism of the models used, were really important (and significant) factors to consider while attempting to describe the relation between complexity and stability, or to model any trophic interaction in ecosystems. Models of higher quality tend to perform better in predicting changes in species' biomasses, and they corroborated the hypothesis that stability of ecosystems tend to increase with complexity.

When changes in species biomass are analysed for a whole ecosystem, some of the most important groups to observe are the top-predators. Indeed, their overall impact on the ecosystem structure can be significant. In many ecosystems, marine mammals and fisheries represent the top-predators of the food web, and there is a growing concern to know if they compete for the same food resources. In chapter 4, a set of seven models presenting some competition between fisheries and marine mammal consumption was used to test the hypotheses that the presence of marine mammals in ecosystems and their overlap with fisheries for food resources does not have a significant effect on the overall productivity of the ecosystem, and that their extirpation can decrease this productivity because of beneficial predation effects marine mammals can have on their prey. Marine mammals are a very important component of marine ecosystems, and as top predators, they may compete with fishery for the same target species. However, in most ecosystems, the primary production required (PPR) to sustain marine mammals' consumption was smaller than the PPR for the catch. As for their mixed indirect trophic impact, it was always less important, even if also negative, than the impact of fishing on ecosystems compartments. Finally, when the extirpation of marine mammals was simulated, the

biomass of other species in the ecosystem was largely unaffected. Moreover, the impact of these top predators in marine ecosystems was not always negative. In many cases, there was a positive predation effect from marine mammals on their prey. Thus, the notion that hunting of marine mammals would solve the fisheries problems is too simplistic. These animals are part of a foodweb involving many species and their effect on these other species is not always direct.

One ecosystem that suffered from such a major fisheries crisis is the Gulf of St. Lawrence. In that ecosystem, top-predators (mainly pinnipeds) are important, and so was the fisheries before the collapse of groundfish stocks in the early-1990s. Chapter 5 addressed this problem of collapsing fish stocks in the Northwest Atlantic. By comparing two ecosystems (Northern and Southern Gulf of St. Lawrence) and two time periods (pre- and post-collapse), I attempted to explain the collapse of important predatory fish with an ecosystem-based approach, implemented by environmental (climate variability) and anthropogenic (overfishing) factors. My analyses revealed that indeed, significant changes occurred in the ecosystem structure between the 1980s and the 1990s and have contributed to the failure of the cod stocks to recover in the 1990s. In both ecosystems, the structure shifted dramatically, from one previously dominated by piscivorous groundfish during the mid-1980s, to one now dominated by small-bodied pelagic species during the mid-1990s in both the southern and northern Gulf of St. Lawrence. The species structure was different between the northern Gulf and the southern Gulf, and this may explain why these two ecosystems did not collapse to the same degree in the early 1990s.

Having a global representation of a food web using a modelling tool such as *Ecopath* is definitely an asset in trying to understand the structure and function of marine ecosystem. This is even more useful when many models are used simultaneously to address more general or global issues. Definitely, the use of models allowed me to test and examine major issues in marine ecology, and in some cases find some interesting answer to them. However, models are only possible representations of marine systems, and they cannot answer all our ecological questions, solve all our scientific concerns.

Strengths and weaknesses of this thesis research

In order to address issues at the ecosystem level, scientists create models that they hope represent these ecosystems and simulate different scenarios to see how they will react to diverse situations. Ecosystem modelling has become very popular in applied ecology, and this is even more so for marine ecosystems, which are more difficult to investigate directly.

Different modelling approaches are available to the scientific community. One of them is the *Ecopath* approach, which has its weaknesses, but most importantly has the great advantage of being an approach previously applied to many ecosystems around the world, leading to lots of replicates for comparative analyses, including at the global scale.

The modelling approach presented in this thesis research is innovative in the sense that it proposed model quality as a new metric to consider in analyses of marine ecosystems. With the large database of *Ecopath* models that we created, we were able to create scenarios representing global responses of marine food webs to global issues.

Only a minority of ecosystem studies address the uncertainty of model results. Uncertainty and variability are inherent in the very nature of ecosystem modelling. Therefore we need to use appropriate tools to define, represent and analyze this uncertainty. *Ecopath* is only one of the many approaches that are used worldwide for ecosystem modelling. The *Ecopath* software includes several tools that have been used – more or less successfully – to address uncertainty. The optimum solution seems to be the use of these tools in combination with the inverse modelling approach, in order to use the strengths of each approach.

Future improvements and applications

Aquatic ecosystems are under enormous stress. A variety of disturbances, including overfishing, climate change and fish introductions, are threatening the species, their community and entire food webs. The ecosystem modelling approach, until now, dealt mainly with ecological issues such as predator-prey relationships, fisheries management, biodiversity, etc. Now that modelling is becoming more and more popular, there is a need to focus on merging different fields to better understand the structure and function of ecosystems. For example, it seems that the role of genetic diversity of populations is as important as the species diversity (Reusch *et al.* 2005). The evolution of the prey can also modify considerably predatory-prey relationships (Yoshida *et al.* 2003). In a context of climate change, oceanographic features are also to be considered when addressing ecosystem dynamics (Gilbert 2005). New approaches should integrate these different fields for even more representative models and analyses.

Final conclusions and recommendations

This thesis research ended up being a very collaborative approach, where *Ecopath* users helped by providing information about their models, and sharing their interest in understanding marine ecosystems. Having a large number of models to compare is definitely an asset. Comparing ecosystems can sometimes enlighten us on some ecological phenomena or management choices that are successful in one ecosystem, we can then apply it in another ecosystem. Now that these ecosystems are threatened by factors such as habitat degradation, climate change, invasive species, overexploitation, and pollution all around the world, such comparative analyses are urgently needed.

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Appendices

Appendix 1: Questionnaire sent to *Ecopath* users.

Appendix 2: List of *Ecopath* models (models highlighted in grey are the ones that were already available on the *Ecopath* website) and their respective reference, when published.

Appendix 1

Questionnaire sent to Ecopath users

Dear *Ecopath* user,

My name is Lyne Morissette, I am a Ph.D. student at UBC Fisheries Centre with Dr. Daniel Pauly. Part of my project consists in a census of all the models that have been constructed over the years with the *Ecopath with Ecosim* software. Our database indicates that you downloaded the software. We would really appreciate if you could send the following information:

1. If a model was constructed or not with this software
2. Geographic area modeled
3. Period of time modeled (year)
4. Purpose of the model (management, description of the ecosystem, modelling protected areas, fishing policy, addressing theoretical ecology questions, etc.)
5. Citations of published work based on the model (Authors, year, title, journal, pages)
6. Type of institution (university, government, industry, etc.) for which the model was constructed
7. Who constructed the model (student, post-doc, research associate, faculty, etc.)
- 8.

Please send your reply to (email address) as soon as possible, and hopefully before July 7th 2006.

Thanks a lot, your help is much appreciated!

Lyne Morissette

Ph.D. Candidate

Marine Ecosystem Modelling

Fisheries Centre, The University of British Columbia

Appendix 2

List of Ecopath models (models highlighted in grey are the one that were already available on the Ecopath website) and their respective reference, when published.

Geographic area	Model	Citation
Africa, Lake Chad	Completed	Palomares <i>et al.</i> 1993a
Alaska Gyre	Completed	Pauly <i>et al.</i> 1996
Aleutian Islands	Completed	Aydin <i>et al.</i> (submitted)
Aleutian Islands	Completed	Heymans 2005b
Antartica	In progress	
Antartica, Antartic peninsula	Completed	Erfan and Pitcher 2005
Antartica, Falkland Islands	Completed	Cheung and Pitcher 2005
Antartica, Weddell Sea	Completed	Jarre-Teichmann <i>et al.</i> 1997
Arctic ocean	Completed	Okey 2003
Argentina, Coastal marine zone	In progress	
Atlantic, Northeast (ICES area VIa)	In progress	
Atlantic, South Bight	Completed	Okey and Pugliese 2001
Australia, Darwin Harbour	Completed	Martin 2005
Australia, Great Barrier Reef	Completed	Gribble 2001
Australia, North West Shelf	Completed	Bulman <i>et al.</i> 2006
Australia, Northern South Wales, inshore	Completed	Forrest (PhD thesis in preparation)
Australia, Northern South Wales, offshore	Completed	Forrest (PhD thesis in preparation)
Australia, Port Phillip Bay	Completed	Fulton and Smith 2004
Australia, Southeast coast	In progress	Fulton (in preparation)
Australia, Southeast, Eastern Bass Strait	Completed	Bulman <i>et al.</i> 2006
Australia, Southeast, Eastern Bass Strait	Completed	Goldsworthy <i>et al.</i> 2003
Australia, Southern Tasmanian midslope	Completed	Bulman 2002
Australia, Southern Tasmanian Seamoutns Reserve	Completed	Bulman <i>et al.</i> 2002
Bahamas, Bimini	Completed	Grant 2001
Baltic Proper	Completed	Möllmann and Eero 2004
Baltic Proper, open water	Completed	Cardinale and Casini 2004
Baltic Sea	Completed	Harvey <i>et al.</i> 2003
Baltic Sea	Completed	Zabel <i>et al.</i> 2003
Baltic Sea, central	Completed	Jarre-Teichmann 1995
Baltic Sea, Curonian lagoon	Completed	Razinkovas 2004
Baltic Sea, Gulf of Riga, Dzeni Retion, Ainazi	Completed	Strake <i>et al.</i> 2004

Baltic Sea, Kaliningrad region	In progress	
Baltic Sea, South (2)	In progress	In preparation
Baltic Sea, Southern, Gulf of Gdansk, Puck Bay	Completed	Tomczak <i>et al.</i> 2005
Bangladesh, Bay of Bengal	Completed	Mustafa 2003
Barents Sea	Completed	Blanchard <i>et al.</i> 2002
Barents Sea	Completed	Skaret and Pitcher, in press
Barents Sea	Completed	Falk-Petersen, (in preparation)
Belize, Turneffe Atoll, Calabash Caye, Mangrove-seagrass-coral reef	In progress	Model completed, but no publication
Benin, Lake Nokoué	Completed	Ph.D. thesis in preparation
Black sea	Completed	Orek 2000
Brazil, Abrolhos	Completed	Telles 1998
Brazil, Amazon basin	Completed	Angelini <i>et al.</i> 2006
Brazil, Caeté Mangrove estuary	Completed	Wolff <i>et al.</i> 2000
Brazil, East	Completed	Ph.D. thesis in preparation
Brazil, Itamaraca Estuarine System	In progress	Model completed, but no publication
Brazil, Rio de Janeiro, Cabo Frio	In progress	In preparation
Brazil, Rio de Janeiro, Guanabara Bay	In progress	Model completed, but no publication
Brazil, Rio de Janeiro, Itaipu coastal zone	In progress	Model completed, but no publication
Brazil, São Paulo State, Broa Reservoir	Completed	Angelini and Petrere 1996; Angelini 2002
Brazil, South Bight	Completed	Gasalla and Rossi-Wongtschowski 2004
Brunei, Darussalam, Borneo coast	Completed	Silvestre <i>et al.</i> 1993
Burkina Faso, Bagré reservoir	Completed	Villanueva <i>et al.</i> (in press a)
Burundi, Lake Tanganyika (2)	Completed	Moreau <i>et al.</i> 1993a
Cambodia, Tonle Sap Lake	In progress	Model completed, but no publication
Canada, Arctic (terrestrial)	Completed	Krebs <i>et al.</i> 2003
Canada, British Columbia, Northern coast (4)	Completed	Ainsworth <i>et al.</i> 2002
Canada, British Columbia, Strait of Georgia	Completed	Martell <i>et al.</i> 2002
Canada, Eastern Scotian Shelf	Completed	Bundy 2005; Bundy and Fanning

		2005; Bundy 2004a; Bundy 2002
Canada, Eastern Scotian Shelf	Completed	Bundy 2005; Bundy and Fanning 2005; Bundy 2004a; Bundy 2003
Canada, Gwaii Haanas	Completed	Salomon <i>et al.</i> 2002
Canada, Hecate Strait	Completed	Beattie 2001
Canada, Hecate Strait	Completed	Haggan <i>et al.</i> 1999
Canada, Kootenay Lake	Completed	Thompson 1999
Canada, Lancaster Sound	Completed	Mohammed 2001
Canada, Newfoundland (4)	Completed	Heymans and Pitcher 2002a,b; Heymans 2003
Canada, Newfoundland-Labrador Shelf	Completed	Bundy 2001; Bundy 2002; Vasconcellos <i>et al.</i> 2002; Savenkoff <i>et al.</i> 2001; Bundy <i>et al.</i> 2000
Canada, Northern British Columbia	Completed	Ainsworth <i>et al.</i> 2002
Canada, Northern Gulf of St. Lawrence (3)	Completed	Morissette <i>et al.</i> 2003, Savenkoff <i>et al.</i> 2004a,b; Savenkoff and Morissette(in prep.)
Canada, Puget Sound	Completed	Preikshop and Beattie 2001
Canada, Rivers Inlet of British Columbia	Completed	Watkinson and Pauly 1999
Canada, Southern Gulf of St. Lawrence (2)	Completed	Savenkoff <i>et al.</i> 2004c
Canari Islands, Gran Canaria, Maspalomas Lagoon	Completed	Moreno and Castro 1998
Cap Verde	Completed	Stobberup <i>et al.</i> 2003
Caribbean, British Virgin Island, Puerto Rico	Completed	Searles 2004
Caribbean, Grenada and Grenadines	Completed	Mohammed 2003
Caribbean, Southern Mexican, Coral reef	Completed	Alvarez-Hernández 2003
Caribbean Sea, coral reefs	Completed	Opitz 1996
Caribbean, BVI Puerto Rico	In progress	
Catalan Sea, South (2)	Completed	Coll <i>et al.</i> 2006; Coll <i>et al.</i> , in press b
Chile	Completed	Milessi 2005
Chile, Antofagasta Peninsula	Completed	Pavés and González, submitted
Chile, Central	Completed	Neira <i>et al.</i> 2004
Chile, Central	Completed	Ortiz and Wolff 2002a,b
Chile, central and south continental shelf	In progress	In preparation
Chile, Central MPA Central	In progress	In preparation

Chile, Northern coast	Completed	Medina <i>et al.</i> (submitted)
Chile, Tongoy Bay	Completed	Ortiz and Wolff 2002b
Chile, Tongoy Bay	Completed	Wolff 1993
China	Completed	Song <i>et al.</i> 2007
China, Beibu Gulf	Completed	Chen <i>et al.</i> 2006
China, Bohai Sea	Completed	Tong <i>et al.</i> 2000
China, Guangdong Province, Zhujiang Delta	Completed	Ruddle and Christensen 1993
China, Hong Kong	Completed	Pitcher <i>et al.</i> 1998; Pitcher <i>et al.</i> 2002a,b
China, Hong Kong	Completed	Sumalia <i>et al.</i> 2007
China, Yangtze River, Niushan Lake	Completed	Ph.D. thesis in preparation
China, Zhengjiao, Gougi Island, Seaweed beds	In progress	M.Sc thesis in preparation
China Sea, deep shelf	Completed	Pauly and Christensen 1993
China Sea, East	In progress	
China Sea, south, Cape Cambodia	Completed	Nguyen 1989; Pauly and Christensen 1993
China Sea, south, coral reefs	Completed	Pauly and Christensen 1993
China Sea, south, deep waters (50-200 m)	Completed	Pauly and Christensen 1993
China Sea, south, marine reserves	Completed	Pitcher <i>et al.</i> 2000
China Sea, south, ocean part (> 200 m)	Completed	Pauly and Christensen 1993
China Sea, south, shallow waters (< 10m)	Completed	Pauly and Christensen 1993
China Sea, southwest, eastern Malaysia and southeastern Sumatra	Completed	Liew and Chan 1987; Pauly and Christensen 1993
Colombia, Guarjira peninsula	Completed	Criales-Hernandez <i>et al.</i> 2006
Colombia, Gulf of Salamanca	Completed	Duarte and Garcia 2004
Congo, Lake Kivu	Completed	Villanueva <i>et al.</i> (in press b)
Costa Rica, Golfo de Nicoya	Completed	Wolff <i>et al.</i> 1998
Costa Rica, Golfo Dulce	Completed	Wolff <i>et al.</i> 1996
Cuba, Batabano ecosystem	In progress	Wolff <i>et al.</i> (in preparation a)
Denmark, coast	In progress	
Denmark, Faroe Islands	Completed	Booth and Zeller 2005
Denmark, Faroe Islands (1961)	Completed	Zeller and Reinert 2004
Denmark, Faroe Islands (1997)	Completed	Zeller and Freire 2002
Ethiopia, Lake Awassa	Completed	Fetahi 2005
Fantasy wonderland with seadragons, mermaids, etc	Completed	B. Fulton, educational purposes CSIRO

France, Bay of Biscay (2)	Completed	Ainsworth <i>et al.</i> 2001
France, Bay of Somme, Eastern Channel	Completed	Rybarczyk <i>et al.</i> 2003
France, Bretagne, Iroise Sea	Completed	M.Sc. thesis in preparation
France, Étang de Thau	Completed	Palomares <i>et al.</i> 1993b
France, Gironde Estuary	Completed	Lobry 2004
France, Golfe de Gascogne	In progress	
France, La Seine	Completed	Boët <i>et al.</i> 1999
France, Lake Aydat	Completed	Reyes-Marchant <i>et al.</i> 1993
France, Normandy, Seine Estuary Eastern Channel	Completed	Rybarczyk and Elkaim 2003
France, Toulouse, Garonne River	Completed	Palomares <i>et al.</i> 1993c
French Frigate Shoals	Completed	Polovina 1984
French Polynesia, Moorea Island, Tiahura Reef (2)	Completed	Arias- González <i>et al.</i> 1997
Galapagos, Floreana rocky reef	Completed	Okey <i>et al.</i> 2004a
Gambia, coast	Completed	Mendy 2003
Gambia estuary, Africa	Completed	Ph.D. thesis in preparation
Generic demersal system	Completed	Christensen <i>et al.</i> 2005
Generic pelagic system	Completed	Christensen <i>et al.</i> 2005
Ghana, Sakumo Lagoon	Completed	Pauly 2002
Greece, Eastern central Ionian Sea	In progress	M.Sc. thesis in preparation
Greenland, West coast	Completed	Pedersen 1994; Pedersen and Zeller 2001
Guinea	Completed	Dillao <i>et al.</i> 2003
Guinea (2)	Completed	Guénette and Dillao 2004; Guénette and Dillao (in press)
Guinea Bissau, coast	Completed	Amorim <i>et al.</i> 2003
Gulf of Thailand	Completed	Christensen 1998
Gulf of Thailand	Completed	FAO/FISHCODE 2001
Gulf of Thailand, coast	Completed	Vibunpant <i>et al.</i> 2003
Iceland	Completed	Buchary 2001
Iceland	Completed	Natoumbi Mendy 1999
Iceland, Shelf	Completed	Mendy (unpublished data)
Iceland, Shelf	Completed	Mendy and Buchary 2001
India, Arabian Sea off Karnataka (2)	Completed	Mohamed <i>et al.</i> 2006
India, Pullavali Brackishwater	Completed	Santhanam <i>et al.</i> 1993
India, Southwest coast	Completed	Vivekanandan <i>et al.</i> 2003
India, Veli Lake	Completed	Aravindan 1993

Indian Ocean, West-central	Completed	Ph.D. thesis in preparation
Indonesia, Eastern	In progress	
Indonesia, Papua, Raja Ampat, Kabui Bay	Completed	Bailey <i>et al.</i> 2007
Indonesia, Papua, Raja Ampat Islands	Completed	Ainsworth <i>et al.</i> 2007
Ireland, North, Lough Neagh	In progress	Ph.D. thesis in preparation
Irish Sea	Completed	Lees and Mackinson 2007
Irish Sea	Completed	Ph.D. thesis in preparation
Israel, Lake Kinneret	Completed	Walline <i>et al.</i> 1993
Italy, Adriatic Sea, North	Completed	Zucchetta <i>et al.</i> 2003
Italy, Adriatic Sea, North and Central	In progress	Coll <i>et al.</i> (in preparation a, b)
Italy, Adriatic Sea, North and Central (2)	Completed	Coll <i>et al.</i> 2006; Coll <i>et al.</i> (in press a, b)
Italy, Adriatic Sea, Upper, Miramare marine reserve	Completed	Libralato <i>et al.</i> (2006)
Italy, Orbetello Lagoon	Completed	Ceccarelli <i>et al.</i> 2005
Italy, Orbetello Lagoon (2)	Completed	Brando <i>et al.</i> 2004
Italy, Venice Lagoon	Completed	Pranovi <i>et al.</i> 2003; Libralato <i>et al.</i> 2002; Granzotto <i>et al.</i> 2004
Ivory Coast, Lagoon Ébrié	Completed	McNamara 2004
Ivory Coast, Lagoon Ébrié	Completed	Ph.D. thesis in preparation
Japan	Completed	Okamura <i>et al.</i> 2002
Japan, Hokkaido, Lake Toya	Completed	Matsuishi <i>et al.</i> 2005
Japan, Nagasaki, Lake Kawahara-oike	Completed	Matsuishi <i>et al.</i> 2005
Japan, Northern Pacific coast	Completed	Hamatsu, internal report (unpublished)
Japan, Seto Inland Sea	In progress	Model completed, but no publication
Kenya, Lake Naivasha	Completed	Mavuti <i>et al.</i> 1996
Kenya, Lake Nakuru (2)	Completed	Moreau <i>et al.</i> 2001a
Kenya, Lake Turkana	Completed	Kolding 1993
Kenya, Lake Victoria	Completed	Moreau <i>et al.</i> 1993b
Kenya, Lake Victoria	Completed	Kipkemboi 2006
Kerguelen Island	Completed	Pruvost <i>et al.</i> 2005
Korea, Gwangyang bay	Completed	Kang 2005
Lake Erie (2)	In progress	In preparation (Ecological Modelling)
Lake Huron	Completed	Mason <i>et al.</i> 2004

Lake Michigan	In progress	In preparation
Lake Ontario	Completed	Halfon and Schito 1993
Lake Ontario, Bay of Quinte (2)	Completed	Koops <i>et al.</i> 2006; Koops <i>et al.</i> (in press)
Lake Superior	Completed	Hoff <i>et al.</i> 2000
Lake Superior	Completed	Kitchell <i>et al.</i> 2000
Laos, Nam Ngum	Completed	Jutagate <i>et al.</i> 2002
Lesser Antilles, Pelagic ecosystem	In progress	
Lithuania, coastal zone	Completed	Bucas 2004
Madagascar, Antongil Bay	Completed	Ph.D. thesis in preparation
Madagascar, Coastal stations	Completed	Ph.D. thesis in preparation
Malawi, Lake Malawi	Completed	Degnbol 1993
Malawi, Lake Malawi	Completed	Nsiku 1999; Nsiku 2002
Malaysia, east coast	Completed	Alias 2003
Malaysia, Sabah	Completed	M.Sc. thesis in preparation
Malaysia, Sabah	Completed	Garces <i>et al.</i> 2003
Malaysia, Sarawak	Completed	Garces <i>et al.</i> 2003
Malaysia, Terengganu	Completed	Liew and Chan 1987
Malaysia, west coast	Completed	Christensen <i>et al.</i> 2003
Mauritania, EEZ	Completed	Sidi and Guénette 2004
Mauritania, Banc d'Arguin	Completed	Sidi and Samba 2003
Mediterranean Sea, Corsica, Bay of Calvi	Completed	Pinnegar and Polunin 2004
Mediterranean Sea, Northwest (2)	Completed	Coll <i>et al.</i> (in press b)
Mexico, Baja California Sur, La Paz Bay	Completed	Arreguín-Sánchez <i>et al.</i> 2004a
Mexico, Baja California tip, Central zone	In progress	
Mexico, Baja California, La Paz Bay	Completed	Ph.D. thesis in preparation
Mexico, Central Gulf of California	Completed	Arreguín-Sánchez and Calderón-Aguilera 2002
Mexico, Continental shelf of Tabasco	Completed	M.Sc. thesis in preparation
Mexico, Gulf of California, benthic ecosystem	Completed	Arreguín-Sánchez <i>et al.</i> 2002a, b
Mexico, Gulf of Mexico, Ecosystem management	Completed	Walters <i>et al.</i> 2006
Mexico, Gulf of Mexico, North Continental Shelf	Completed	Arreguín-Sánchez and Manickchand-Heileman 1998
Mexico, Gulf of Mexico, Southwestern	Completed	Manickchand-Heileman <i>et al.</i> 1998a
Mexico, Gulf of Mexico, Southwestern Campeche	Completed	Arreguín-Sánchez <i>et al.</i> 2004b

Mexico, Gulf of Mexico, Terminos Lagoon	Completed	Manickchand-Heileman <i>et al.</i> 1998b
Mexico, Gulf of Ulloa	Completed	del Monte-Luna 2004
Mexico, Huizache-Caimanero Lagoon	Completed	Zetina-Rejón <i>et al.</i> 2004
Mexico, Magdalena Bay, Channels zone	In progress	Model completed, but no publication
Mexico, Mexican Caribbean fringing coral reefs	Completed	Ph.D. thesis in preparation
Mexico, Northern Gulf of California	Completed	Morales-Zárate <i>et al.</i> 2004
Mexico, Oaxaca, Tonameca catchment	Completed	Avila-Foucat <i>et al.</i> 2004
Mexico, Quintana Roo, Bahía de la Ascensión	Completed	Vidal and Basurto 2003
Mexico, South Caribbean	Completed	Arias- González <i>et al.</i> 1998
Mexico, South Sinaloa	In progress	Salcido-Guevara (in preparation)
Mexico, Southern Gulf of Mexico, Términos Lagoon	Completed	Rivera-Arriaga <i>et al.</i> 2003
Mexico, Southwestern Gulf of Mexico, reef lagoon	In progress	Model completed, but no publication
Mexico, Tamiahua Lagoon	Completed	Abarca-Arenas and Valero-Pacheco 1993
Mexico, Veracruz, Alvarado lagoon system	Completed	Abarca-Arenas and Valero-Pacheco 1993; Abarca-Arenas <i>et al.</i> 2004; Arreguín-Sánchez and Valero 1996
Mexico, Veracruz, Alvarado lagoon system	In progress	Model completed, but no publication
Mexico, Veracruz, Mandinga Lagoon	Completed	De La Cruz-Aguero 1993
Mexico, Veracruz, Tampamachoco lagoon	Completed	Rosado-Solorzano and Guzman del Proo 1998
Mexico, Yucatan Peninsula, Boca Paila-Tampalam-Mah	Completed	Arias-González <i>et al.</i> 2004
Mexico, Yucatan Peninsula, Celestun Lagoon	Completed	Chavez <i>et al.</i> 1993
Mexico, Yucatan Peninsula, Mangroves (2)	Completed	Vega-Cendejas and Arreguín-Sánchez 2001; Vega-Cendejas 2003
Mexico, Yucatan, Northern Continental Shelf	Completed	Vega-Cendejas and Arreguín-Sánchez 2001
Micronesia, Enewetak Atoll	Completed	Dalsgaard 1998

Morocco, coast	Completed	Stanford <i>et al.</i> 2001
Mozambique, Maputo Bay	Completed	De Paula <i>et al.</i> 1993
Mozambique, Mozambique channel	Completed	Ph.D. thesis in preparation
Netherlands, IJsselmeer Lake	Completed	Buijse <i>et al.</i> 1993
New Caledonia, Coral reef lagoon	Completed	Bozec <i>et al.</i> 2004
New Caledonia, Loyalty Islands, Uvea	Completed	Bozec <i>et al.</i> 2004
New Caledonia, western tropical Pacific	Completed	Godinot and Allain 2003
New Zealand, Small coastal region	In progress	
New Zealand, Southeast, Southern plateau	Completed	Bradford-Grieve <i>et al.</i> 2003
North Sea	Completed	Christensen 1995; Christensen <i>et al.</i> 2002
North Sea	Completed	Silvert <i>et al.</i> , submitted
Norway, Sør fjord	Completed	Pedersen <i>et al.</i> (submitted)
Norwegian Sea	Completed	Skaret and pitcher, in press
Norwegian Sea & Barents Sea	Completed	Dommasnes <i>et al.</i> 2001
Pacific Basin, Subarctic	Completed	Aydin <i>et al.</i> 2003
Pacific coast mangrove	Completed	Cunningham 2003
Pacific Ocean, Central	Completed	Cox <i>et al.</i> 2002
Pacific Ocean, Eastern	Completed	Preikshot 2005
Pacific Ocean, North Central	Completed	Kitchell <i>et al.</i> 2002
Pacific Ocean, Pelagic eastern tropical	Completed	Olson and Watters 2003; Olson and Watters 2003; Hinke <i>et al.</i> 2004; Olson <i>et al.</i> 2002; Watters <i>et al.</i> 2003
Peru, Independencia Bay	In progress	Wolff <i>et al.</i> (in preparation b)
Philippines, Central Visayas, Bohol Island	In progress	Model completed, but no publication
Philippines, Eastern Visayas, Leyte Gulf	In progress	Model completed, but no publication
Philippines, Central Java, north coast	Completed	Nurhakim 2003
Philippines, Laguna de Bay (2)	Completed	Delos Reyes and Martens 1993; Delos Reyes 1995
Philippines, Leyte, San Pedro Bay	Completed	Campos 2003
Philippines, Northwest coast, Lingayen Gulf	Completed	Guarin 1991; Pauly and Christensen 1993
Philippines, Pangasinan, Bolinao	Completed	Aliño <i>et al.</i> 1993

Philippines, San Miguel Bay	Completed	Bundy 1997; Bundy 2004b; Bundy and Pauly 2001
Philippines, Western Visayas, Panay Island, Sapián Bay	Completed	Armada and Bacalso, 2004
Philippines, wetland ricefield	Completed	Lightfoot <i>et al.</i> 1993
Poland, Gdansk basin	Completed	Wielgat 2004
Portugal, Azores archipelago	Completed	Guénette and Morato 2001
Portugal, South, Ria Formosa coastal lagoon, Water Reservoir	Completed	Gamito and Erzini 2005
Rwanda, Lake Ihema	Completed	Mavuti <i>et al.</i> 1996
Sahel, artificial lakes	Completed	Model completed, but no publication
Senega., coast	Completed	Samb and Mendy 2003
Senegal, Saloum estuary	Completed	Ph.D. thesis in preparation
Shanghai	In progress	
Sierra Leone	Completed	Heymans and Vakily 2002
South Africa, Benguela	Completed	Shannon <i>et al.</i> 2004a
South Africa, Kromme estuary	Completed	Heymans and Baird 1995
South Africa, Northern Benguela	Completed	Heymans and Baird 2000
South Africa, Northern Benguela	Completed	Jarre-teichmann 1998
South Africa, Northern Benguela	Completed	Shannon and Jarre-teichmann 1999
South Africa, Saldanha Bay	In progress	
South Africa, Southern Benguela	Completed	Shannon <i>et al.</i> 2004b
South Africa, Sundays beach	Completed	Heymans and McLachlan 1996
South Georgia, South Orkney Islands	Completed	Bredesen 2003
Southern hemisphere (diatoms)	In progress	Model completed, but no publication
Spain, Cantabrian Sea	Completed	Sánchez and Olaso 2004
Spain, Medes island	Completed	Ph.D. thesis in preparation
Sri Lanka, coast	Completed	Ph.D. thesis in preparation
Sri Lanka, Parakrama Samudra reservoir	Completed	Moreau <i>et al.</i> 2001b
Taiwan, Kuo Sheng Bay	Completed	Lin <i>et al.</i> 2004
Taiwan, Southwestern Chiku	Completed	Lin <i>et al.</i> 1999
Taiwan, Tsengwen estuary	Completed	Kup and Shao 1999
Thailand, Pasak Dam	In progress	

Thailand, Sirindhorn reservoir	Completed	Jutagate <i>et al.</i> 2002
Thailand, Ubol Ratana Reservoir	Completed	Chookajorn <i>et al.</i> 1994
Trinidad / Venezuela, Gulf of Paria	Completed	Manickchand-Heileman <i>et al.</i> 2004
Uganda, Lake George	Completed	Moreau <i>et al.</i> 1993c
United Kingdom, English Channel	Completed	Stanford and Pitcher 2004
United Kingdom, River Thames	Completed	Mathews 1993
United Kingdom, Scotland, East coast	Completed	Buchan 1997
United Kingdom, Scotland, West coast	Completed	Morissette and Pitcher 2005
Uruguay, Coastal lagoon (2)	In progress	
USA, Alabama, Week Bay	Completed	Althausen 2003
USA, Alaska, Bercharof Lake	Completed	Mathisen and Sands 1999
USA, Alaska, Bering Sea	Completed	Aydin <i>et al.</i> 2002
USA, Alaska, Bering Sea	Completed	Trites <i>et al.</i> 1999
USA, Alaska, Bering Sea, East	Completed	Livingston <i>et al.</i> 1999
USA, Alaska, Bering Sea, East	Completed	National Research Council 2003
USA, Alaska, Bering Sea, Southeast	Completed	Ciannelli <i>et al.</i> 2004
USA, Alaska, Bering Sea, West	Completed	Livingston <i>et al.</i> 1999
USA, Alaska, Lake Illiamma	Completed	Anonymous 2003
USA, Alaska, Prince William Sound	Completed	Okey and Pauly 1999
USA, Alaska, Prince William Sound (pre-oil spill)	Completed	Dalsgaard and Pauly 1997
USA, Alaska, South East (3)	Completed	Guénette 2005
USA, Atlantic continental shelf	Completed	Okey and Publiese 2001
USA, California, Monterey Bay	Completed	Olivieri <i>et al.</i> 1993
USA, California, Northern current	Completed	Field <i>et al.</i> 2001; Field and Francis 2005
USA, California, Pt. Reyes	In progress	
USA, Chesapeake Bay	In progress	
USA, Chesapeake Bay	In progress	
USA, Chesapeake Bay (4)	Completed	Hagy 2002
USA, Columbia River	Completed	Harvey and Kareiva 2005
USA, Delaware Bay	Completed	Frisk 2007
USA, Everglades	Completed	Heymans <i>et al.</i> 2002
USA, Florida freshwater lakes	In progress	
USA, Florida, Apalachicola Bay	Completed	Carlson, (in press)
USA, Florida, Looe Key	Completed	Venier and Pauly 1997

USA, Florida, St. Marks	Completed	Baird <i>et al.</i> 1998; Christian and Luczkovich 1999; Luczkovich <i>et al.</i> 2002
USA, Florida, west shelf	Completed	Okey and Mahmoudi 2002
USA, Florida, west shelf	Completed	Okey <i>et al.</i> 2004b
USA, Gulf of Alaska	Completed	Heymans 2005a
USA, Gulf of California (2)	Completed	Ph.D. thesis in preparation
USA, Gulf of California, North	Completed	Ph.D. thesis in preparation
USA, Gulf of California, South, Coastal lagoon	In progress	M.Sc. thesis in preparation
USA, Gulf of Maine	Completed	Heymans 2002
USA, Hawaiian Island chain	Completed	Papastamatiou <i>et al.</i> (in press)
USA, Iowa lakes (3)	In progress	Model completed, but no publication
USA, Iowa, Clear Lake	In progress	None (class project)
USA, Lake Michigan, Green Bay	In progress	
USA, Long Island Sound - nearshore	In progress	
USA, Long Island Sound - offshore	In progress	
USA, Mid-Atlantic bight	Completed	Okey 2001
USA, NC, Lower Neuse River Estuary	Completed	Christian <i>et al.</i> 2003; Dame and Christian 2006
USA, New York, Oneida Lake	Completed	Koops <i>et al.</i> 2006; Koops <i>et al.</i> , in prep.
USA, North Carolina	Completed	Butler 2007
USA, North Carolina Reservoir	In progress	
USA, North Carolina, Neuse River, Contentnea Creek	Completed	Pine and Kwak 2007
USA, Northern Wisconsin freshwater lakes	Completed	Fayram 2005; Fayram <i>et al.</i> , in press
USA, Oneida Lake	Completed	Irwin <i>et al.</i> 2003
USA, Salt marsh ponds, Virginia Coast reserve LTER site	Completed	Dame 2005
USA, South Carolina, Charleston watershed	In progress	
USA, Texas, Laguna Madre	In progress	
USA, Washington, Straight of Juan de Fuca	In progress	
Venezuela, Northeastern Shelf	Completed	Mendoza 1993
Vietnam, coast	Completed	Pauly and Christensen 1993

Vietnam, Dong Nai Province, Tri An Reservoir	Completed	Luong 2000
Vietnam, southwest	Completed	Christensen <i>et al.</i> 2003
Zimbabwe, Lake Kariba	Completed	Machena <i>et al.</i> 1993

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