

ECOSYSTEM IMPACTS OF FISHING FORAGE FISHES:
AN ANALYSIS OF HARVEST STRATEGIES FOR THE
BRAZILIAN SARDINE

by

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Abstract

The ecosystem impacts of fisheries have become an important concern in fisheries management and one of the most important issues in fisheries science. The objectives of this thesis were i) to evaluate the use of trophic models in the analysis of the ecosystem responses to fishing small pelagic forage fish; ii) to forecast the 'fishing down marine food web' phenomenon in Brazil; and iii) to conduct an in-depth analysis of the sardine, *Sardinella brasiliensis*, fishery off southeastern Brazil to examine hypotheses of ecosystem changes following stock collapse, and to evaluate how uncertainties of ecological processes influence the choice of harvest strategies and controls in this fishery. Dynamic simulations of mass-balance trophic models were used to compare the ecosystem responses to fishing forage fishes across different types of marine ecosystems, and to examine the stability characteristics of ecosystems when impacted by fisheries. The comparative analysis among trophic models indicated that as 'wasp-waist' species in upwelling ecosystems, small pelagics will only sustain much more conservative exploitation rates than the levels that have brought about historical stock-collapses. In the upwelling ecosystem off southeastern Brazil, sardine has been historically the main target of commercial fisheries, although 'fishing down marine food webs' for small pelagic fish species is not yet an overall observed phenomenon in Brazil. The collapse of the sardine fishery in the late 1980s has apparently favored a competing small pelagic fish (anchovy, *Engraulis anchoita*) in the ecosystem. The combined effect of fishing and environmental effects makes it difficult, however, to characterize the changes in the sardine population and the ecosystem, and to predict the results of rehabilitation measures for the stock. On the other hand, the explicit recognition of these ecological uncertainties allows a sound choice of precautionary strategies for the fishery, and a better scrutiny of research programs to improve management. In this context, trophic models will have a complementary role to single-species models in the analysis of the broad consequences of fishing policies, and in the test and formulation of hypotheses about the causes of observed changes in marine ecosystems.

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Chapter 1. Introduction

One of the major challenges of natural resources management centers on the science-policy interface (Cicin-Sain and Kenecht, 1998; Walters, 1998). The main reason to relate science and policy is to improve the information available for making management decisions. Improvements in the management of natural resources is largely dependent on improvements in the understanding of the processes involved in the resource problem. Many resource management situations have been aggravated because of inadequate information or lack of foresight in anticipating unexpected problems; yet, good information does not always guarantee reliable decisions, since very often information is available but no appropriate management choices are implemented. Still, there is a perceived strong political benefit for grounding decisions on science (Jasanoff, 1990; Cicin-Sain and Kenecht, 1998). This thesis focuses on the use of scientific ecological information in the management of fisheries for small pelagic fish resources.

Fisheries for small pelagic fish resources

Since the advent of large-scale industrialized fisheries, small pelagic fishes have dominated world landings. Out of the five leading species in world catches between 1980 and 1990, four were either small or mid-size pelagics: the Peruvian anchoveta, *Engraulis ringens*, the Japanese and South American pilchards (*Sardinops melanosticta*, *S. sagax*) and the Chilean horse mackerel, *Trachurus murphyi* (Csirke, 1995). The term 'small pelagic' is used to refer to species such as anchovies, sardines, pilchards and herrings, which share common biological characteristics, such as strong shoaling behavior, planktonic feeders, fast growth and short lives. These characteristics lead to stocks with large biomasses, a key role in the transfer of energy in marine food webs, substantial temporal variability in abundance and to their potential as target of fisheries exploiting a cheap protein source for human use (Glantz, 1983; Csirke, 1995; Bakun, 1996).

Biological, economic and technological factors have played a role in the development of small pelagic fisheries under an 'unlimited resources' paradigm, in which the stocks were considered not prone to be overfished. Shoaling pelagic fish have highly aggregated distributions which makes them relatively easy to capture with modern and efficient fishing technologies, depriving

stock assessment and management of early warnings of overfishing and stock collapse. On the other hand, their life history strategies often make small pelagic fish stocks appear to be among the most productive and abundant marine fisheries resources. The Peruvian anchoveta, for instance, once supported the largest fishery ever recorded, accounting alone for over 10% of total world fish production. Fishmeal production is the main objective of pelagic fisheries worldwide. The increase in world demand for fishmeal to the feed industry following the World War II created economic conditions for the fast development of reduction fisheries for small pelagics. One of the best documented cases of rapid economically-driven development was that of the Peruvian anchoveta fishery in the early 1950s, when U.S. factories for fishmeal production were built in Peru following the collapse of the California Pacific sardine, *Sardinops sagax* (Glantz, 1983). Today, pelagic catches used worldwide by the reduction industry represents roughly one third of world marine catches and about 80% of total world pelagic catches (Durand, 1998).

The history of many pelagic fisheries worldwide reveals, however, a different reality. Small pelagic stocks were depleted to the point of collapse, in some cases repeatedly, and often in alternating 'regimes' between anchovy and sardine species (Lluch-Belda et al., 1989). The depletions caused not only economic and social difficulties but also undesirable and unexpected ecological disruptions, such as massive mortality of guano birds after the collapse of the Peruvian anchoveta (Tovar *et al.*, 1987), and an increasing dominance of jellyfishes after heavy exploitation of small pelagics and intense eutrophication in the Black Sea (Mee, 1992). Today, cyclic 'boom and bust' dynamics of pelagic fisheries is an widely recognized characteristic that is explained by alternative (but non-exclusive) hypotheses concerning climatic effects on recruitment, trophic interactions, and overfishing (Radovich, 1982; Caddy and Gulland, 1983; Lluch-Belda et al., 1989; Csirke, 1995; Bakun, 1996). In fact, vigorous debate on the extent that fisheries and environmental processes have contributed to cyclic regimes still persist (Radovich, 1982; Bakun, 1996; Steele, 1996). A metanalysis carried by Patterson (1992) showed, for instance, that most cases of small pelagic stock collapse occurred when F (fishing mortality) was higher than $0.6 M$ (natural mortality).

The demise of many small pelagic fisheries rouses a more fundamental rationale - that stock assessment research has not been providing adequate advice to managers, specially through the design of fishery control systems that can respond to the types of variability and uncertainties observed in nature. Scientific debate around the causes of collapses, recoveries and species shifts

in many ecosystems and the relatively short time series of data for most fisheries, have been historically responsible for the lack of a comprehensive framework for scientific advice to fisheries management. Debate on the causes of fisheries collapse has always permeated the philosophies, research activities and conclusions of fisheries scientists on different agencies, as portrayed by Radovich (1982) for the case of the Pacific sardine:

“The Federal scientists, working for an agency whose fundamental charter was to assist the development and maintenance of U.S. commercial fisheries, looked for reasons other than fishing, for the sardine’s declining condition, while the scientists employed by the State (whose basic role was protector of the State’s resources) supported the premise that overfishing was having a detrimental effect on the standing stock. These were capable, competent scientists using the same data and coming up with different conclusions in part because they were employed by agencies whose fundamental goals were different.”

On the other hand, a perceived need for scientific consensus is present in many resource management occasions, and in some of the most disastrous examples of fisheries mismanagement. For instance, in the case of the Atlantic cod, *Gadus morhua*, the insistence on consensus has led a government-administered assessment framework that suppresses scientific uncertainties and fails to document important differences in scientific opinion regarding the risks of stock collapse (Hutchings et al., 1997). Two types of responses to the lack of scientific consensus are commonly encountered in fisheries management: first to completely ignore uncertainties when making decisions; and second to direct more research efforts to better understand the nature of processes affecting fish stocks before changes in the *status quo* policies take place. More often, however, uncertainties have impeded scientific inputs into management decisions, which end up obeying strictly economic and political forces.

Ludwig *et al.* (1993) asserted that we shall never attain scientific consensus concerning the systems that are being exploited because controlled and replicated experiments are impossible to perform in large-scale systems. Therefore there will be always ample scope for differing interpretations of natural events. In this context, fisheries management should acknowledge the uncertain nature of ecological processes and seek for robust strategies for exploiting populations

and ecosystems. Moreover, it is necessary to recognize that science and management must be coupled to better understand the nature of processes affecting fish populations (Walters, 1986).

Guidelines for Fisheries Management

Complications arising from the uncertain nature of fisheries management, and the common realization of the need for a broader, ecosystem perspective on natural resources management has lead to the development of many principles and guidelines for effective fisheries management throughout the world (e.g. FAO, 1997; GESPE, 1997; Canadian Ocean Act).

With respect to uncertainties, the FAO Code of Conduct for Responsible Fisheries (FAO, 1995) adopts the precautionary approach which states that

“...where there are threats of serious or irreversible damage, lack of full scientific certainty shall not be used as a reason for postponing cost-effective measures to prevent environmental degradation”.

The proper implementation of the precautionary approach will require, among other issues identified by FAO Technical Guidelines for Responsible Fisheries (FAO, 1997),

“-consideration of the needs of future generations and avoidance of changes that are not potentially reversible;

- prior identification of undesirable outcomes and of measures that will avoid them or correct them promptly;

- that where the likely impact of resource use is uncertain, priority should be given to conserving the productive capacity of the resource;

- that harvestable and processing capacity should be commensurate with estimated sustainable levels of resource, and that increases in capacity should be further contained when resource productivity is highly uncertain”.

The FAO Technical Guidelines for Responsible Fisheries (FAO, 1997) also recognizes the need to place fisheries in an ecosystem context;

“...harvesting any one species is almost certain to impact others,...The impact of ecological linkages (e.g. through the trophic chain) between species, may lead to changes in species dominance and affect the dynamic equilibria of the resource system, potentially affecting future

options. These multi-species effects need to be considered in responsible fishing, which should aim to ensure that no species, whether targeted, by-catch or indirectly affected by fishing, is reduced to below sustainable levels.” Moreover,

“ Responsible fisheries management should consider the impact of fisheries on the ecosystem as a whole, including its biodiversity, and should strive for sustainable use of whole ecosystems and biological communities.”

Mangel et al. (1996) proposed an independent set of principles for the conservation of wild living resources which summarized the point of view of 42 scientists. Three out of seven principles explicitly recognize the need to account for human impacts on ecosystems, e.g.

“The goal of conservation should be to secure present and future options by maintaining biological diversity at genetic, species, population, and ecosystem levels; as a general rule neither the resource nor other components of the ecosystem should be perturbed beyond natural boundaries of variation.”

“Assessment of the possible ecological and sociological effects of resource use should precede both proposed use and proposed restrictions or expansion of ongoing use of a resource.”

“Regulation of the use of living resources must be based on understanding the structure and dynamics of the ecosystem of which the resource is part and must take into account the ecological and sociological influences that directly and indirectly affect resource use.”

The adoption of these principles will challenge scientists and decision makers to consider the more diverse as possible consequences of fisheries to marine populations and ecosystems. Therefore, a critical re-examination of concepts, methods, tools, and regulatory measures commonly used in fisheries assessment and management is primarily needed.

1.1. Objectives

It is the overall goal of this thesis to evaluate fishing strategies for small pelagic fish stocks considering the inherent variability of the ocean environment and the ecological role of these species in marine food webs.

The specific objectives of the thesis are

- to make specific predictions about ecosystem responses to fishing small pelagic species, using dynamic trophic models;
- to analyze the characteristics of stability and resilience of exploited marine ecosystems when impacted by fisheries for mid-trophic level forage species; and
- to carry out a case study with the fishery for sardine, *Sardinella brasiliensis*, in the Southeastern Brazilian Bight to examine how the combined effect of environmental, behavioral and ecological processes, as captured by different modeling approaches, influence the choice of harvest strategies and controls.

Problems in managing small pelagic fisheries

The inability to predict the effect of harvest policies given the lack of understanding of the processes affecting fish stocks has led to major research initiatives into fisheries-oceanography, specially in the analysis of the effects of environmental variability on recruitment of commercially important marine populations. International initiatives were supported by the Intergovernmental Oceanographic Commission (IOC-UNESCO) program on Ocean Sciences in Support of Living Resources (OSRL), which aimed to promote the development of plans for major oceanographic studies of the physical-ecological interactions of importance to fishery resource-related problems (Bakun *et al.*, 1982). The rationale of the program was that many fisheries problems, such as recruitment, population availability and species interactions, could not be solved solely based on the analysis of fisheries data. The accumulated evidence derived

from deposits of fish scales in sediments (Soutar and Isaacs, 1974; Baumgartner *et al.*, 1992), and the global synchrony in the raising and falling of the large populations of anchovies and sardines in the major upwelling regions of the world (Kawasaki, 1983; Lluch-Belda *et al.*, 1989), indicated that radical fluctuations in abundance may be an intrinsic feature of many marine fish populations. Moreover it pointed to the existence of physical processes that teleconnect these widely separated systems. If so, then the hope for successful fisheries management would appear to rely in gaining scientific understanding of the natural factors determining reproductive success and population dynamics of fishery stocks. The rationale would have two main implications to fisheries management: first, it would show the need to develop robust strategies for fisheries viability under conditions of radically varying resources; second, and most importantly, that fisheries management would directly benefit from the increased scientific ability to identify and predict transition periods or 'regime shifts', when distinct levels of precautionary actions would be necessary (Bakun, 1998).

A research framework was proposed involving a combination of a rational (cause-effect) approach, based on the understanding of relevant physical and biological processes for the viability of marine populations, and an empirical approach, in which functional relationships between these processes were defined by analysis of available data. The difficulty in addressing some of the physical-biological processes experimentally called for the combination of a third approach based on the comparative method of analysis (Bakun, 1996). Results of the comparative studies of geographical climatology of fish reproductive habitats have tended to identify a triad of physical factors capable of exerting control on reproductive success of marine populations (Bakun, 1996; Bakun *et al.*, 1998). These are *enrichment processes* that lead to the production of the zooplankton upon which the young stages depend for food; *concentration processes* that aggregate food products and therefore increase their availability for the growing larvae; and *retention processes* that keep the young in favorable nursery habitats. In coastal upwelling areas enrichment is basically driven by persistent alongshore winds that forces water to move offshore and, in order to balance the superficial deficit, deep nutrient-rich water is forced into the surface illuminated layers where primary production is possible. Frontal structures (vertical and horizontal) are the main features responsible for the concentration of plankton in thin stable layers and for creating optimal larval feeding conditions. Retention involves mechanisms such as Taylor column, Ekman divergence and zones of stability (Bakun, 1996). Some corollaries of triad theory have been tested by Cury and Roy (1989) who showed that the

reproductive success in upwelling ecosystem is tightly associated to an optimum window of moderate wind stress, though weak winds are not sufficient to enrich the upper layers and winds too strong can otherwise disrupt stable structures in the ocean. The “triad framework” is being applied in diverse international programs aimed at identifying the links between climatic-oceanographic processes and marine fish populations (Box 1.1).

Box 1.1. International cooperative programs on oceanography and productivity of marine fish populations.

- IREP/SARP. The Sardine-Anchovy Recruitment Project (SARP) was established as the initial focus of the International Recruitment Project (IREP) component of the OSRL. The main objective of SARP was to promote a greater understanding of the biologic-oceanographic processes involved in controlling recruitment success in sardine and anchovy populations (Bakun et al., 1982).
- CEOS. The Climate and Eastern Ocean Systems (CEOS) project was a joint effort of the National Marine Fisheries Service (NMFS), the Institut Français de Recherche Scientifique pour le Développement en Coopération (ORSTOM), and the International Center for Living Aquatic Resources Management (ICLARM). The CEOS project was an international collaborative study of the potential effects of global climate change on the living resources of the highly productive eastern ocean upwelling ecosystems and on the ecological and economic issues directly associated with such effects. A major focus of the study were the clupeoid fishes (Durand et al., 1998).
- GLOBEC/SPACC. International Global Ocean Ecosystem Dynamics (GLOBEC) program on Small Pelagic Fishes and Climate Change (SPACC). The objective of SPACC is to identify how physical forces are linked with the growth of pelagic fish populations, which is believed to be mediated through the dynamics of zooplankton populations. The long-range goal of SPACC is to forecast how changes in ocean climate will alter the productivity of small pelagic fish populations. To address this goal, SPACC uses comparative retrospective and process studies (Hunter and Alheit, 1997).

The proposed improvement in management practice using climatic/oceanographic process studies has been fiercely criticized (Walters and Collie, 1988; Walters, 1998). As stated previously, one direct benefit of these studies would appear to be the improvement in the quality of decisions on harvest levels by allowing the adjustment of policies according with predicted environmental conditions. For instance, if short term variations could be accurately forecast, the best policy would be to adjust the target stock size so as to increase catch when positive variation is anticipated and to reduce when negative variation is anticipated. Conversely, it may involve allowing escapement to increase when good environmental conditions are forecast so as to take the maximum advantage of the optimum conditions (Parma, 1990; Walters and Parma, 1996).

Walters and Collie (1988) argued, however, that in most cases better understanding and predictive models are not that useful, since the same benefits could be met more cheaply by improved monitoring programs, i.e., recruitment and spawning biomass surveys, and existing feedback policies.

Better understanding of the processes controlling recruitment success seems to be mostly needed for situations in which the effects of long-term environmental factors are confounded with the effect of stock size and fishing (Walters and Collie, 1988). Environmental cycles of intermediate periods superimposed on stock production dynamics can obscure any underlying relationship between recruitment and spawning biomass (Armstrong and Shelton, 1988). In fact, most accounts of stock collapses during the last decades have at their core the endless debate about whether it was the result of fishing or of environmental effects. Among the best documented examples are the sardine/anchovy collapses in coastal upwelling systems (Pauly and Palomares, 1989; Barnes et al., 1992), the decline in recruitment of groundfish stocks off east coast of North America (Walters and Maguire, 1996) and the "Thompson-Burkenroad" debate on the causes of recruitment fluctuations in the stock of Pacific Halibut (Parma and Deriso, 1990). In these cases the understanding of how environmental changes affect fish productivity would be very valuable to fishery management. Yet, it is argued that such understanding will not be achieved by continued correlative and biological process studies and will instead require sound management experiments in which environmental studies are coupled with deliberate manipulation of stock sizes through changes in harvest policies (Walters and Collie, 1988; Walters, 1998).

A more fundamental criticism of the process-oriented studies is that they do not reflect necessarily the questions and information needs of managers. Walters (1998) stated that weak communication between scientists and managers have repeatedly resulted in the development of models based on variables and factors that do not consider policy options and values identified by managers, the allocation of scarce resources into research programs that are only vaguely related to policy questions, and, ultimately, the design of policies that most commonly fail when implemented because important details were not properly accounted for. Relating research and management will require a more thorough analysis of information needs for making management decisions, and a better scrutiny of research programs in which to allocate resources.

A framework for fisheries assessment

Fisheries stock assessment research has been recognized as a mean to provide some structured use of available information to estimate the nature of the tradeoffs when comparing fisheries management choices (Hilborn and Walters, 1992). Tradeoffs and choices are the core elements of fisheries assessment advice, and imply an active role of fisheries scientists in aiding managers understand the responses of fishery systems to alternative management choices, being the responses usually related to the impact of fishing on fish stock and ecosystem, social desirability of fishery regulations and economic returns to fishery sectors. The main scientific input to fisheries management is in the evaluation of the consequences of alternative harvest policies for marine resources. This advisory work should consider the consequences of fishing activities to marine populations and ecosystems, being ideally linked by a common framework (Mangel *et al.*, 1996). A framework for fisheries stock assessment must be able to provide managers with information on (Butterworth *et al.*, 1997; Cochrane *et al.*, 1998):

- tradeoffs among different regulatory mechanisms in the short, medium and long term;
- risks associated with each regulatory mechanism;
- outputs that could be easily understandable for all decision makers;
- guidance on what type of data to collect for the purpose of the chosen regulatory mechanism; and
- definition of a rank of research priorities, and a time frame for revision of both research and regulatory mechanisms, in light of any changes in understanding of resource/fishery.

The achievement of a basis for informed judgment on the costs of postponing or attenuating decisions demands an integrated strategy for fisheries management and research. Figure 1.1 outlines an integrated framework for fisheries assessment based on a set of interrelated questions.

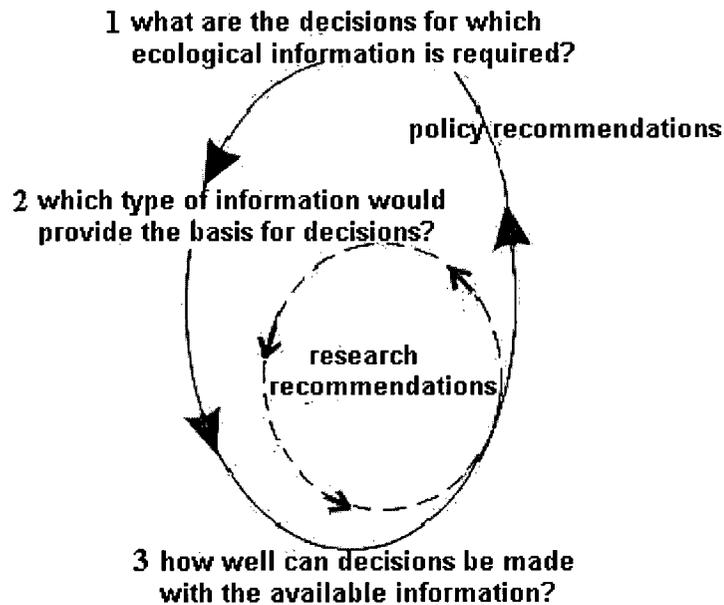


Figure 1.1. Analytical framework for integrating fisheries stock assessment and management (based on Dorcey and Hall, 1983).

The first step in the framework comprise the analysis of the management or decision context. The achievement of objectives is the sole reason for being interested in any decision. Yet, unfortunately, objectives are not adequately articulated and explicit in many management situations because of either a lack of involvement of all fisheries interests in the decision making process, or for the constant political pressure put on managers to produce short-term “tangible results” (Keeney, 1992). The values relevant to a decision context will indicate what type of information is important. In this respect, data will have value only if it will help lead to better consequences, either through the creation of better alternatives or through the wiser choice of alternatives (Keeney, 1992). For fisheries management, decisions normally involve the choice of harvest strategies, and ecological information will be used to estimate the impact of these regulatory mechanisms on the ecological sustainability of the fishery. The ecological criteria for sustainability may involve an array of indicators such as catch, the size (biomass) of the spawning stock, and/or indicators of fisheries impact on the ecosystem. Ecosystem impacts may include direct effects such as the catch of non-target species (by-catch) and the destruction of marine habitats, and indirect effects on non-target species due to trophic cascade effects through the food web.

Many possible combinations of harvest strategies and controls are possible, and it is the role of stock assessment to provide managers with advice on the possible consequences of each regulatory mechanism (management decisions). Once the decision context has been properly outlined it is then possible to analyze how well can the choice for management strategies be made, what are the sources of uncertainties and the opportunities for learning. At this stage decision analysis methodology can be used to provide an "heuristic aid" (*sensu* Rowen, 1976) for relating means to ends, for thinking about ends, as well as for identifying new management alternatives (Morgan and Herion, 1990). Decision analysis involve processes subsequent to the analysis of objectives, such as the identification of alternative hypothesis about the system been managed, inference of uncertainties on processes and states relevant for the decision context, and the assessment of the consequences and risks associated to each strategy using criteria defined by the objectives.

The completion of these steps will ultimately lead to policy and research recommendations (Figure 1.1). Research recommendations can be oriented for improving both descriptive and functional knowledge (Dorcey and Hall, 1983). Descriptive knowledge may include data on fish distribution and abundance, species diet compositions, fleet characteristics, oceanographic parameters, etc., and involves research activities such as inventorying and monitoring. Functional knowledge involves understanding system relationships such as how recruitment is affected by reducing the spawning stock, how catch rates change with oceanographic conditions, etc. New functional knowledge can only be developed by carrying out experiments to test hypotheses through either experimental research, experimental management or desk analysis (Dorcey and Hall, 1983). The later should precede experimental management or experimental research in order to develop new hypothesis and guide experimental design. Very often, when experimentation is difficult or unfeasible, the comparative method of analysis has been employed to acquire new functional knowledge of ecological processes (Mayr, 1997). The two types of knowledge are linked by the fact that new functional knowledge is only obtained when the data produced by inventorying and monitoring are used to test hypothesis about system processes. Characteristically, research recommendations will have a longer time frame for involving the understanding of processes operating at medium and long-term scales (e.g. oceanic regimes, recruitment variability, cycles of investment, technological changes, etc.).

Policy recommendations, on the other hand, require short-term responses from scientists who are compelled to explicitly confront and communicate uncertainties to decision makers. There are usually competing hypothesis about the dynamics of a natural resource, and the outcomes of a given management decision may differ considerably according to which of the alternatives come out to be true. Therefore when decisions are made under uncertainty, managers are bound in effect to consider the risks associated with their actions and the impacts of their choices on the 'legacy of uncertainty' that their successors will face. The emphasis on the need to account for uncertainties when making decisions is however not often transparent. Morgan and Herion (1990) describe situations in which accounting for uncertainties is crucial for a decision analysis, e.g., when people's attitude towards risk is likely to be important, such as in many health and environmental issues; when multiple information sources and uncertainties must be combined; when a decision must be made on the allocation of resources to obtain additional information on the problem being analyzed; and in situations where the process of decision making involve multiple actors making explicit and implicit decisions over an extended period. In these cases the analysis will be more useful if it treats the uncertainty explicitly allowing users to evaluate its conclusions and limitations better in the changing context of the ongoing decision process (Morgan and Herion, 1990). Taking account of uncertainties is on the other hand a fundamental requirement for the adoption of sound precautionary measures in fisheries management (FAO, 1997).

Fisheries stocks assessment is usually faced with uncertainties on the biological production, and on the expected outcomes of harvest strategies and controls. Uncertainties on the biological production, and hence in the relationship between current catches and the future state of the stock, frequently result from biases in fishery data as a descriptor of stock dynamics, sampling errors, and by process errors created by environmental effects on recruitment and production rates. Also, the ecosystems supporting small pelagic fish populations undergo productivity changes of decadal frequencies, often called 'regime shifts' (Steele, 1996; 1998). These systematic shifts in productivity can be driven by a variety of factors including climate changes, variability in the abundance of preys, competitors, predators as well as by changes in the internal structure of the stock (Walters, 1987). The lack of understanding of processes controlling biological production and the multi-interest nature of resources exploitation generates uncertainties in the choice for management strategies and in the expected outcomes of a chosen fishing strategy. Finally, the information required to achieve the objectives of a fishing strategy

may include data on spatial distribution, temporal distribution and abundance of the stock, and on fleet characteristics and movement on the fishing ground. The information requirements for harvest control are best remembered as the answers to the questions, “where, when and how many ?” (Mundy, 1985). Uncertainties in the outcomes of the implemented tactics arise whether the information on the state of the resource is poor or catch rates vary independently of stock size as a result of changes in catchability.

Fisheries advisory work can be based on two types of modeling approaches: single-species and ecosystem or multi-species models. Multi-species models are in their infancy and have been little used to date. Multi-species models have been proposed as tools for guiding the implementation of ecosystem principles in fisheries management, but exactly how the approach could be used, and also what should be the role of single-species approaches in this new paradigm is still unclear. Such comparisons have not been performed explicitly before.

This thesis is organized in four chapters.

Chapter 2 uses trophic models to examine the ecosystem impacts of harvesting small pelagic fishes in selected marine ecosystems. Results are used to discuss three main questions: i) what are the general predicted ecosystem responses to fishing small pelagics species?; ii) what is the role of trophic cascades in the replacement of species at the pelagic planktonic niche? and; iii) what are the characteristics of stability of marine ecosystems when impacted by fishing at the mid-trophic level groups? The validity of the predicted results is evaluated with published observations and limitations of the modeling approach.

Chapter 3 analyzes the carrying capacity of marine shelf ecosystems in southern Brazil for harvestable species by (1) quantifying the amount of available primary production appropriated by fisheries catches, (2) evaluating the trend in the mean trophic level of fisheries, and (3) simulating the ecosystem effects of ‘fishing down the food web’ in an intensively exploited shelf region. The analysis aims to forecast the ‘fishing down marine food web’ effects in Brazil, and to compare the footprint of fisheries in two of the most intensively exploited regions of Brazil: the southern and southeastern shelf ecosystems.

Chapter 4 reviews the status of fisheries assessment of the Brazilian sardine in the Southeastern shelf ecosystem. The fishery was chosen as a case study because it exhibits many similarities with other pelagic fisheries worldwide, notably for its history of development and collapse, as well as for its regional importance as one of the most productive and well studied marine fisheries resources in Brazil. Ecological and fisheries data are used to describe the changes in recruitment, stock catchability, and the structure of the Southeastern Brazilian Bight ecosystem. This information is used to formulate hypotheses about the resilience of the population and ecosystem when impacted by fisheries.

Chapter 5 centers on the assessment of risks of management decisions in the sardine fishery with currently available information and according to two modeling approaches: a single-species and a multi-species model. The analysis aims to evaluate the short and long term predictions of the impacts of harvest strategies and controls; to discuss the relative values of reducing current process uncertainties; to recommend the types of research that would most likely provide the information needed to improve the quality of decisions; and to suggest the precautionary measures that should be adopted in face of the ecological uncertainties.

Finally, Chapter 6 summarizes the general conclusions of this work.

The map in figure 1.2 identifies the trophic models used in each chapter to evaluate the ecosystem responses to fishing small pelagic fish species.

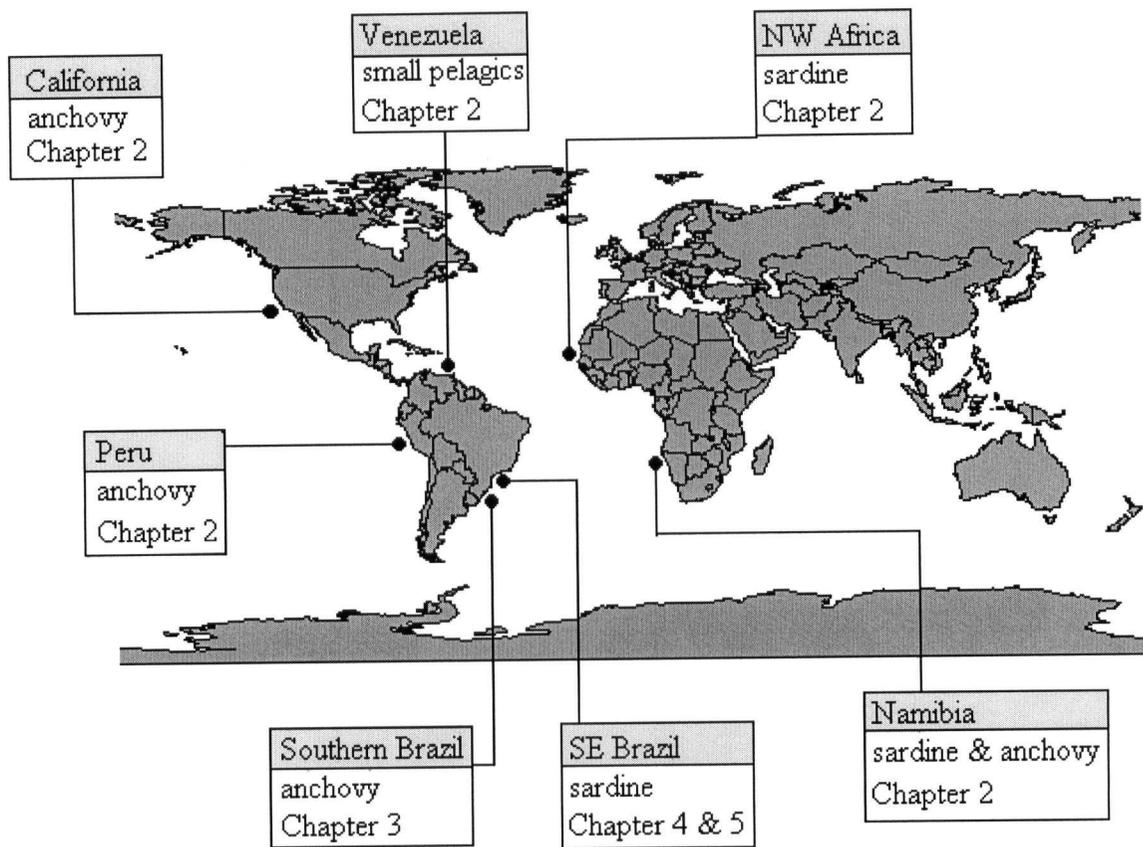


Figure 1.2. Ecosystems for which trophic models were used to evaluate the effects of fishing small pelagic fish species. The boxes indicate the species fished and the correspondent chapters where the models were used.

Chapter 2. Ecosystem impacts of harvesting small pelagic fishes. A comparative analysis using trophic mass-balance models¹

2.1. Introduction

Fisheries management has been urged to consider the ecosystem impacts of fishing activities, given the signs of human dominance and impact on the oceans. Recent assessments of the worldwide status of marine capture fisheries revealed for instance that, fisheries alone appropriate ca. 8% of the total marine primary production and up to one third of temperate shelf systems production (Pauly and Christensen, 1995); over 60% of the most important fish stocks are either overexploited or at the verge of becoming overexploited by current fishing intensity (Garcia and Newton, 1997); and that approximately 27 million tons of nontarget animals are discarded annually as “trash” fish (Alverson et al., 1994). Also, present exploitation patterns are resulting in a “fishing down marine food webs” phenomenon, by which heavy commercial fisheries are causing a progressive simplification of ecosystems in favor of smaller, high-turnover, lower-trophic-level fish and invertebrate species that are adapted to withstand disturbance and habitat degradation (Pauly et al., 1998; Pitcher and Pauly, 1998).

The effect of fisheries on ecosystems are usually classified in direct and indirect impacts (Botsford et al., 1997; Goni, 1998). Direct impacts include overfishing, by-catch and discard of non-target species, changes in genetic diversity of stocks, physical disturbances and habitat destruction by fishing gears. Fisheries, for instance, have the potential to affect the genetic diversity of populations by selectively removing older and larger individuals (Goni, 1998), and by depleting small reproductive stocks of metapopulations of species such as salmon and herring (Policansky and Magnuson, 1998). Ultimately, the decrease in genetic diversity by fishing can cause loss of resilience of fish populations to both human and natural impacts. Fisheries are also responsible for physically damaging important marine habitats, specially with towed gears (otter trawlers, beam trawlers, dredges). The effects of trawling on the sea bed vary from destruction of suitable habitats for the settlement of juvenile and adult phases of diverse marine organisms, changes in abundance and species composition of benthic communities, and concomitant changes in the fish species composition associated with the physical alterations of bottom structures (Goni, 1998).

Indirect ecosystem impacts of fisheries are at least partly mediated through the food web, where the effects of fishing 'cascade' to other components of the system. The ecosystem-wide effects of catching fish attracted little attention and probably had minor importance before the advent of large-scale industrialized fisheries. But, today, the scale of fish production can considerably alter the structure of marine food webs. Heavy commercial fishing has been often associated with drastic changes in species composition in marine communities. Examples of major changes in marine ecosystems with intense fishing are present in almost every region of the world (Goni, 1998), although in many cases it has proved difficult to separate the natural and anthropogenic causes of changes (Steele, 1998). Among the best documented examples are the cases of switches in dominance between sardines and anchovies in coastal upwelling systems after the activity of reduction fisheries (Lluch-Belda et al., 1989; Bakun, 1996). In the Bering Sea, human exploitation of whales and other top predators is thought to be responsible for cascading effects on other components of the ecosystem, such as declines in sea lions and seals, and the dominance of groundfish species such as pollock, *Theragra chalcogramma*, and large flatfishes (NRC, 1996; Trites et al., 1999). On Georges Bank, large scale disturbances caused by intense fishing and habitat destruction were also associated with apparent replacement of gadids and flounders by species of low commercial value, including dogfish sharks and skates (Fogarty and Murawski, 1998).

Over the last 70 years a dramatic catalogue of stock collapses have involved small pelagic forage fish, but despite some pioneering analyses (Beddington and May, 1977) there have been few rigorous attempts to model and predict the potentially devastating ecosystem consequences of overfishing. In the case of the Peruvian ecosystem there is clear belief, but little evidence, that the loss of ca. 5 million guano-producing birds with the collapse of the anchoveta stock will have had profound ecosystem impacts (Pauly and Tsukayama, 1987). Beverton (1990) warned against the subtle consequences to the ecosystem that may result from the collapse of major small pelagic populations. He suggested that there was "some inferential evidence that the disappearance of some 10 million tonnes of Norwegian spring spawning herring and 2 million tonnes from the North Sea may have resulted in reorientation of the flow of production into alternative stable states". Some believe this reorientation of flow was responsible for the "gadoid outburst" (Cushing, 1980). In a review of cases of species replacement, Daan (1980) concluded that for the North Sea some sort of replacement was likely. However, under his rather strict

criteria for replacement, only one out of nine candidate cases (Pacific sardine and anchovy) could be considered as true replacement rather than coincident changes.

While evidence of ecosystem impacts of fisheries accumulates throughout the world, we see the development of fisheries management principles and guidelines which acknowledge the need to place fisheries in an ecosystem context (e.g. Mangel et al., 1996; FAO, 1997). Scientific advisory work is now compelled to consider the more diverse as possible aspects or consequences of fishing activities to marine populations and ecosystems (Mangel et al., 1996). Although the need for ecosystem management has been widely recognized, scientific advice is still hampered by the lack of understanding of the complex dynamics of ecosystems, and the lack of consensus on which framework should be used to account for the ecosystem effects of fisheries. Despite the reality that fisheries are generally not restricted to affecting one species alone, the development of single species models for fisheries management has centered around that very assumption. And, due to our lack of ability to model complex systems, such methodology is still prevalent.

Attention during the last decades has been given to the development of tools that describe patterns of trophic interactions in the food web, mainly represented by multispecies virtual population analysis, MSVPA (Sparre, 1991), and ecosystem mass-balance models such as Ecopath (Polovina, 1984; Christensen and Pauly, 1992). The implementation of the first type of modeling tool has been hampered in part by the need for extensive time series of catch-at-age data, difficult parameterization, the high degree of expertise required from the modeller, and the overall lack of transparency in the estimation procedure (Walters et al., 1997). Ecopath offers, on the other hand, a simpler approach for the reconstruction of trophic interactions in fished ecosystems, and has been widely applied to aquatic ecosystems (more than 80 Ecopath models have been published world-wide describing upwelling, shelf, lake, river, open ocean, and terrestrial farming systems; see the Ecopath homepage at <http://www.ecopath.org>). The approach has some advantages over other existent trophic models viz., it includes all trophic levels in the analysis (from primary producers to top predators) as opposed to focusing only on the commercially important fish species; the emphasis on ecological relationships makes it intuitively simple; it incorporates and standardize large amounts of scattered information, from data routinely collected by fisheries scientists and marine biologists to the traditional ecological knowledge (Pauly et al., 1998); and, more importantly, the widespread use of the approach

creates opportunity for comparative studies of ecosystem's response to fisheries impact. Moreover, further developments of the mass-balance model, which originally focused on describing systems at steady-state conditions, has resulted in a dynamic ecosystem model called Ecosim (Walters et al., 1997) that is capable of answering "what-if" questions about policy and ecosystem changes that would cause shifts in the balance of trophic interactions.

This chapter uses Ecosim to examine the ecosystem impacts of harvesting small pelagic fishes in selected models of marine ecosystems. Many marine ecosystems share a similar configuration of their biological community structure, characterized by a crucial intermediate trophic level often occupied by a small plankton-feeding pelagic species (Rice, 1995; Bakun, 1996). Unlike typical food webs where different types of predators feed upon different types of prey, in these ecosystems one prey type usually dominates as the primary channel of energy from lower to higher trophic levels (Fig. 2.1). Trophic dynamics in these 'wasp-waist' ecosystems (sensu Rice, 1995) is thought to be largely dependent on this mid-trophic level species, often represented by important fisheries resources of anchovy, sardines and herrings. Results of model simulations are discussed around three main questions: i) what are the general predicted ecosystem responses to fishing small pelagic species?; ii) what is the role of trophic cascades in the replacement of species in the pelagic planktivore niche? and; iii) what are the characteristics of stability of exploited marine ecosystems when impacted at the 'wasp-waist' species? Finally, the validity of results is evaluated with published observations and the limitations of the model. The practical utility of the results and approach for defining ecosystem objectives in fisheries management is discussed.

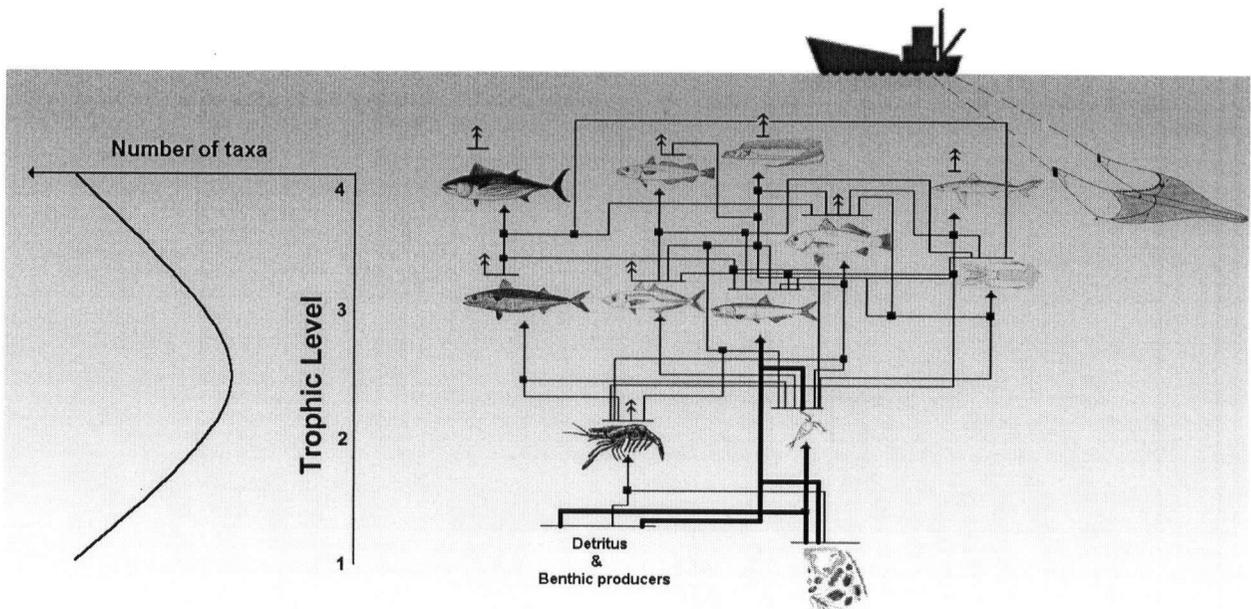


Figure 2.1. Schematic representation of marine food webs with waists at the mid-trophic level. A waist is characterized by a small number of taxa that transfer most of the energy between lower and higher trophic levels. In 'wasp-waist' ecosystems only one or a few species at the intermediate trophic level transfer most of the production from all lower levels to predators at the top of the food web. The flow diagram on the right shows a pelagic system where a small pelagic species (anchovy) is the 'wasp-waist' species. The thickness of lines is proportional to the biomass flow between species; double-head arrows indicate exports from the system.

2.2. Methods

Ecosystem impacts of harvesting small pelagic fishes were examined with a dynamic trophic model, Ecosim (Walters et al., 1997), structured from mass-balance assessments with Ecopath (Polovina, 1984; Christensen and Pauly, 1992). Ecopath provides a static picture of the ecosystem trophic structure by estimating trophic flows and biomasses which satisfy growth and mortality constraints. The model relies on the truism that for each group (i) in the system, and to any time period:

$$\text{Production by } (i) = \text{All predation on } (i) - \text{Fisheries catches} - \text{Other mortality} - \text{Losses to adjacent systems}$$

This can also be articulated as

$$B_i \cdot \left(\frac{P}{B}\right)_i \cdot EE_i - \sum_{j=1}^n B_j \cdot \left(\frac{Q}{B}\right)_j \cdot DC_{ji} - (Y + EX)_i = \Delta B_i \quad (1)$$

where in a system of $i=1, \dots, n$ functional groups; P/B_i is the production/biomass ratio of (i) (equal to the total mortality rate Z_i under the assumption of equilibrium); EE_i is the ecotrophic efficiency, i.e. the fraction of the production that is accounted for by consumption within the system (predation) or harvested; Y_i is the yield of (i), in weight, with $Y_i = F_i \cdot B_i$, where F_i is the fishing mortality; EX_i is other exports of (i) from the system; B_j is the biomass of the consumers or predators; $(Q/B)_j$ is food consumption per unit of biomass for consumer j , and DC_{ji} is the fraction of i in the diet of j . ΔB_i is biomass accumulation rate per time in cases where the analysis do not use data from an initial equilibrium situation.

By re-expressing the system of linear equations (1) as differential equations, Ecosim provides a dynamic model suitable for simulation of the effects of F varying in time on the biomass of each group in the system. The model provides dynamic biomass predictions of each (i) as affected directly by fishing and predation on (i), changes in food available to (i), and indirectly by fishing or predation on other groups with which (i) interacts (Walters *et al.*, 1997). Constructing a dynamic model from equation (1) involves three changes; a) replace the left side with a rate of change of biomass; b) provide a functional relationship to predict changes in P/B_i with biomass B_i and consumption, and c) provide a functional relationships predicting how the consumption will change with changes in the biomasses of B_i and B_j (Walters *et al.*, 1997). Thus equation (1) is re-expressed as

$$\frac{dB_i}{dt} = f(B_i) - M \cdot B_i - F_i \cdot B_i - \sum_{j=1}^n c_{ij}(B_i, B_j) \quad (2)$$

where $f(B_i)$ is a function of B_i if (i) is a primary producer or $f(B_i) = g_i \sum c_{ji}(B_i, B_j)$ if (i) is a consumer, where g_i is the net growth efficiency, and $c_{ij}(B_i, B_j)$ is the function used to predict consumption rates from B_i to B_j . Ecosim uses a function for c_{ij} derived from assuming possible spatial/behavioral limitations in predation rates

$$C_{ij} = \frac{v_{ij} a_{ij} B_i B_j}{v_{ij} + v'_{ij} + a_{ij} B_j} \quad (3)$$

where

C_{ij} is the trophic flow, biomass per time, between prey (i) and predator (j) pools;

B_i and B_j are the biomasses of prey and predators, respectively;
 a_{ij} is the rate of effective search for prey i by predator j ; and
 v_{ij} and v'_{ij} are prey vulnerability parameters

Parameters v_{ij} and v'_{ij} represent the rate of exchange of biomass between two prey behavioural states: a state vulnerable to predation and a state invulnerable to predation. The rationale of this representation is that at a given moment in time not all prey biomass is vulnerable to predators; predator-prey relationships in nature are often limited by behavioral and physical mechanisms, such as schooling behavior and diel vertical migration patterns in clupeid fish or spatial refuges used by many reef fish that considerably limit exposure to predation. The model is designed so that the user can specify the type of trophic control in the food web by hypothesizing the maximum consumption rates (and indirectly the rate of exchange of biomass v_{ij}) that a predator can ever exert on food resources. For low predator biomass or high exchange rates (v_{ij}) the functional relationship approximates a mass-action flow, or Lotka-Volterra type of model $c = a_{ij} B_i B_j$, implying a strong top-down effect. For high consumer biomass or low exchange rates the functional relationship approaches a donor-controlled (bottom-up) flow rate ($c = v_{ij} B_i$), so v_{ij} can be interpreted as the maximum possible instantaneous mortality rate that j can cause on i .

General Predicted Impacts

The impact of fisheries on upwelling ecosystems was examined by comparing equilibrium biomass predictions provided by Ecosim over a range of fishing mortality rates for a small pelagic species in five different upwelling ecosystems off California, Namibia, Northwest Africa, Peru and Venezuela. Details on each model are provided in table 2.1. Two contrasting trophic control hypotheses were tested by setting the maximum instantaneous mortality rate (v_{ij}) that consumer j could ever exert on food resource i . For a 'bottom-up' control v_{ij} was fixed as 4 times the baseline mortality rate; for a 'top-down' control v_{ij} was fixed as 20 times the baseline mortality rate.

Table 2.1. Trophic models of upwelling ecosystems used in the analysis of the impact of small pelagic fisheries. California: Horse mackerel, *Trachurus symmetricus*; Hake, *Merluccius productus*; Mackerel, *Scomber japonicus*. Namibia: Mackerel, *Scomber japonicus*; Horse mackerel, *Trachurus capensis*; Snoek, *Thyrsites atun*; Hake, *Merluccius capensis*, *M. paradoxus*. NW Africa: Anchovy, *Engraulis encrasicolus*; *Sardinella aurita*; Mackerel, *Scomber japonicus*; Horse mackerel, *Trachurus trachurus*; Hake, *Merluccius merluccius*. Peru: Sardine, *Sardinops sagax*; Mackerel, *Scomber japonicus*; Horse mackerel, *Trachurus murphyi*; Bonito, *Sarda chiliensis*; Hake, *Merluccius productus*; Pelican, *Pelecanus thagus*; Sea lion, *Otaria flavescens*. Venezuela: Small pelagics, Engualidids and Clupeids; Groupers, Serranids; Croakers, *Cynoscion* spp and *Micropogonias furnieri*; Squids, *Loligo* spp.

System/ Period	Fished group	N° of groups	Commercially exploited groups	Top predators	Reference
California 1965-1972	Anchovy, <i>Engraulis mordax</i>	17	Anchovy, Horse Mackerel, Hake, Demersals	Marine Mammals Marine Birds	Jarre-Teichman and Christensen, 1998
California 1978-1985	Anchovy, <i>Engraulis mordax</i>	17	Anchovy, Mackerel, Horse Mackerel, Hake, Demersals	Marine Mammals Marine Birds	Jarre-Teichman and Christensen, 1998
Monterey	Omniv. fish	16	Carnivorous nekton, Demersals, Omnivorous fish Micronekton	Sea Mammals Sea Birds	Oliviera et al., 1993
Namibia 1971-1977	Sardine, <i>Sardinops ocellatus</i>	17	Anchovy, Sardine, Mackerel, Horse Mackerel, Snoek /Tuna, Other pelagics, Hake, Other demersals	Marine birds Marine mammals	Jarre-Teichman and Christensen, 1998
Namibia 1978-1983	Anchovy, <i>Engraulis capensis</i>	17	Anchovy, Sardine Mackerel, Horse Mackerel, Snoek/ Tuna, Other pelagics, Hake, Other demersals	Marine birds Marine mammals	Jarre-Teichman and Christensen, 1998
NW Africa 1970-1979	Sardine, <i>Sardina pilchardus</i>	18	Anchovy, <i>Sardinella</i> sp, Sardine, Mackerel, Horse mackerel, Larg. Scombrids, Other pelagics, Hake, Demersals	Marine Birds Marine mammals	Jarre-Teichman and Christensen, 1998
Peru 1964-1971	Anchovy, <i>Engraulis ringens</i>	20	Macrobenthos, Anchovy, Sardine, Mackerel, Horse Mackerel, Bonito, Hake, Other pelagics, Other demersals Other mammals	Pelican Sea lion	Jarre-Teichman, 1991
Peru 1973-1981	Anchovy, <i>Engraulis ringens</i>	20	Macrobenthos, Anchovy, Sardine, Mackerel, Horse Mackerel, Bonito, Hake, Other pelagics, Other demersals, Fur seals Other mammals	Pelican Sea lion	Jarre et al., 1991
Venezuela	Small pelagics	16	Small pelagics, Small sharks, Scombrids, Carangids, Groupers, Squid, Croakers, Shrimps	Small sharks Scombrids Barracudas Snappers Groupers	Mendoza, 1993

Ecosystem Stability

Fisheries exploiting the 'wasp-waist' populations have a potential disrupting effect on marine ecosystems communities with direct impact on dynamic stability. There are three general views of ecosystem stability in the ecological literature (Holling, 1973; Peterman et al., 1978): one assumes that ecosystems are globally stable and tend to recover their original structure after disturbance; a second view is that ecosystems are highly unstable, and that disturbances will lead to system collapse; a third and intermediate view between the two extremes believes that ecosystems may have more than one equilibrium state which are separated by boundaries in the processes controlling the ability of the system to respond to disturbance. In this section ecosystem models are used to analyze the first type of stability, i.e., the ability of system to return to an equilibrium state after a temporary disturbance. The presence of narrow waists in food webs make it possible to compare the impact of disturbances on functionally similar groups in different ecosystems, which then allow us to derive stability properties from inter ecosystems comparisons.

Stability comparisons were carried out with 23 models of marine ecosystems (Table 2.2). In each model a group or species was selected using a set of criteria allowing direct comparison of results among ecosystems. The criteria define the characteristic role of wasp-waist species, which must: (i) occupy an intermediate trophic level; (ii) provide an important link between lower and higher trophic levels, indicated by a high energy throughput compared to other groups at similar trophic levels, as well as by the species importance in the diet of higher trophic level groups; and (iii) already be fished in the baseline Ecopath model.

A fishing pattern was chosen which generated a 5 fold increase in fishing mortality on the wasp-waist group. Simulations were run with a bottom-up control setting (mean $v_{ij} = 4.0$ over all $i \rightarrow j$ flows). Throughout the work we tested different levels of increase in F without noticing any substantial difference in results. We decided for a 5 fold increase to create a situation where the group is severely depleted or displaced from its original steady-state condition in a relatively short period of time. Such an extreme scenario is routinely applied to many small pelagic fish populations and very often associated with stock collapse (Patterson, 1992). The higher F values

were kept constant for 10 years, then returned to the baseline, with the model running for further 80 years (Fig. 2.2). This allows estimation of the time it took the system to return to its original state after having been impacted, that is, the time it takes the last impacted group to return to its baseline biomass level (Fig. 2.2). The recovery time was considered as a measure of the internal stability of the model and hence an index of ecosystem stability.

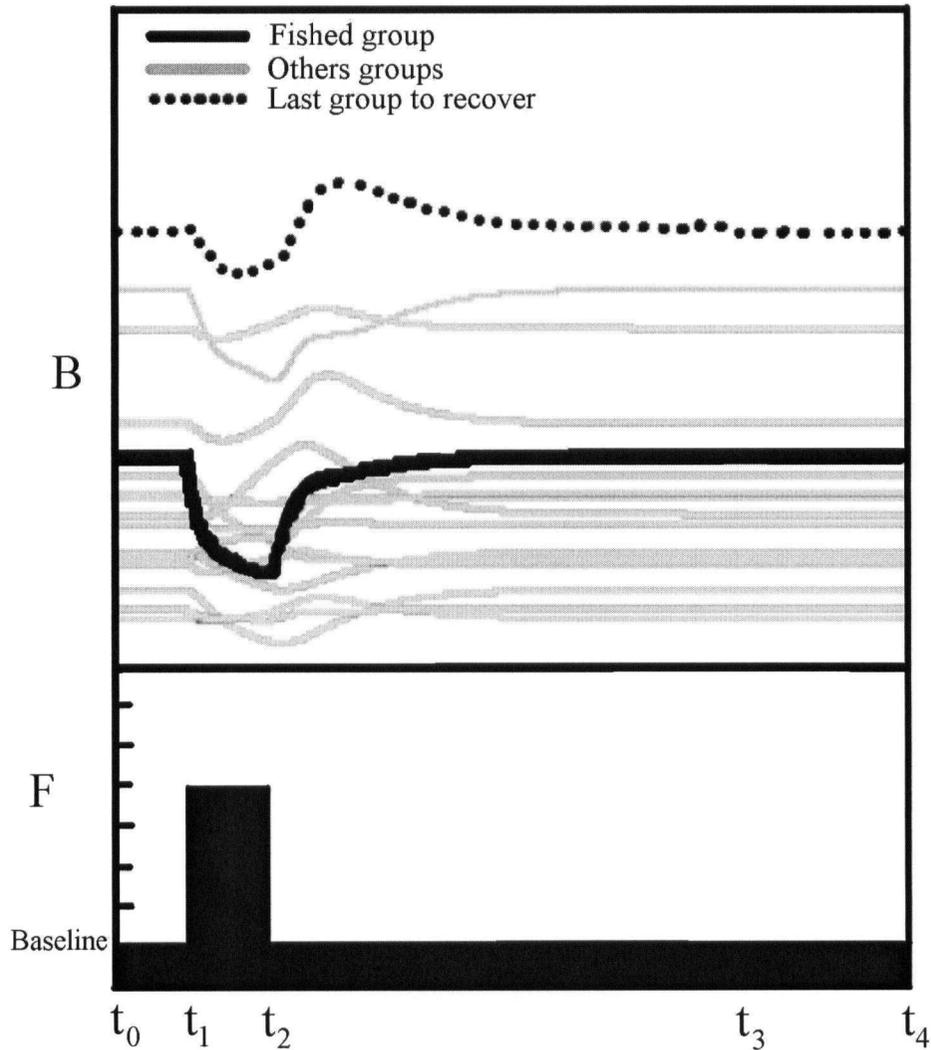


Figure 2.2. Simulation of system recovery of the Venezuela shelf model after fishing impact imposing a 5 times increase in fishing mortality. Top graph shows changes in biomass (B) by group; fished group: small pelagics (*Sardinella aurita*); last group to recover: croaker (*Cynoscion* spp. and *Micropogonias furnieri*); t_0 start of simulation with F baseline; interval $t_1 - t_2$ sets the time the system was kept under higher fishing mortality rates (here 10 years); interval $t_2 - t_3$ corresponds to the system recovery time or time it took the last impacted group to recover to its original biomass. Time t_4 equals 100 years.

To identify ecosystem attributes directly related to stability, a comparative analysis was carried out using a set of ecosystem goal functions previously identified as representative of Odum's attributes of ecosystem maturity (Christensen, 1995a). The attributes were chosen to represent

three different aspects of ecosystem development: i) complexity in community structure, ii) community energetics and iii) overall community homeostasis. A more detailed description of the indices listed below can be found in Christensen and Pauly (1992) and Christensen (1995a).

i) Complexity in community structure:

- *Total number of ECOPATH pools* (Npools);

- *Connectance Index* (CI): The connectance index represents the ratio between the number of actual trophic links to the number of possible links in the system. Ecosystems are expected to evolve from linear to weblike trophic relationships as they mature; the more complex is the trophic structure the higher is the connectance index.

- *System Omnivory Index* (SOI): The system omnivory is calculated as the average omnivory of all consumers in the system, omnivory being defined as the variance of the trophic level of preys of a consumer. The SOI measures how the feeding interactions are distributed between trophic levels and can be used along with the connectance index to describe the food web structure of a system.

ii) Community energetics: During the development of ecosystems towards a climax stage the relationship between three energetic properties, namely production, respiration and biomass, are expected to change. In the early stages of development, and hence in immature systems, the total primary production is expected to exceed respiration, leaving an excess net production to accumulate as biomass in the system. As the system matures biomass is expected to increase and production will tend to balance respiration. Five indices are used here to describe these changes in ecosystem energetics: the ratio between total primary production and total system biomass (Pp/B); system biomass and production (B/P); system respiration and biomass (R/B); the system throughput (SThr), which measures the size or total activity of the system; and the ratio between biomass and system throughput (B/T).

iii) Community overall homeostasis: Ecosystems will tend to attain during the different stages of succession large and diverse organic structures as a result of community actions such as symbiosis, nutrient conservation, and the increase in the information content of flows. These mechanisms also are thought to increase the ecosystem stability. Four indices are used in the analysis of community homeostasis. Ascendancy (Ascd) is a measure of the degree of development of an ecosystem, both in terms of size (throughput) and organization (mutual information) (Ulanowicz and Wulff, 1991; Baird et al., 1991). The system internal flow overhead (Iovh) measures the fraction of the development capacity that does not appear as organized structure due to the magnitude of an uncertainty in the imports, exports and

respiration flows, as well as to redundancies in the pathways between organisms in the system. The cycling index (FCI), developed by Finn (1976), measures the fraction of an ecosystem's throughput that is recycled. The degree of recycling of energy and nutrients in an ecosystem is assumed to increase as ecosystems mature and develop routes for nutrient conservation (Odum, 1969). The path length (Path) is defined as the average number of components or pools that a unit of flow passes through on its way from inflow to outflow (Finn, 1980). As diversity of flows and cycling is expected to increase with maturity, and as these tendencies should result in an increased path length it is assumed that the path length will be highest for more mature systems (Christensen, 1995a).

Table 2.2: Models used for analyses of ecosystem stability. Group trophic level is computed as 1+(the weighted average of the prey's trophic level) (Christensen and Pauly, 1992). F Baseline (year⁻¹) refers to the wasp-waist group's fishing mortality estimated from the corresponding mass-balanced ECOPATH model.

Model Code	Location	Species/Group Fished	Trophic Level	F Baseline	Source
Bru	Brunei, South China Sea	Pelagic fish	2.9	0.28	Silvestre <i>et al.</i> (1993)
Cmp	Campeche Bank, Gulf of Mexico	<i>Opisthonema oglinum</i>	2.9	0.89	Vega-Cendejas <i>et al.</i> (1993)
Cal65	California system, 1965 - 1972	<i>Engraulis mordax</i>	2.6	0.05	Jarre-Teichman and Christensen (1998)
Cal78	California system, 1978 - 1985	<i>Engraulis mordax</i>	2.6	0.09	Jarre-Teichman and Christensen (1998)
Cel	Celestun Lagoon, Gulf of Mexico	<i>Eucinostomus</i> spp	3.1	0.04	Chávez <i>et al.</i> (1993)
GMx	Northern shelf, Gulf of Mexico	Pelagic fish	2.0	0.11	Browder (1993)
Lng	Lingayen Gulf, Philippines	Sergestids	2.5	0.31	Pauly and Christensen (1993)
Mpt	Maputo Bay, Mozambique	Small pelagics	2.1	0.35	Paula e Silva <i>et al.</i> (1993)
Mrey	Monterey Bay, California	Omnivorous fish	2.5	0.16	Olivirei <i>et al.</i> (1993)
Nam71	Benguella system, 1971 - 1977	<i>Sardinops ocellatus</i>	2.4	0.29	Jarre-Teichman and Christensen (1998)
Nam78	Benguella system, 1978 - 1983	<i>Engraulis capensis</i>	2.4	0.56	Jarre-Teichman and Christensen (1998)
Nsea	North Sea	Sandeel, <i>Ammodytes</i> spp	3.7	0.45	Christensen (1995b)
NWAfrica	Northwest Africa, 1970 - 1979	<i>Sardina pilchardus</i>	2.2	0.13	Jarre-Teichman and Christensen (1998)
Peru 60	Peru upwelling, 1960 - 1969	<i>Engraulis ringens</i>	2.2	0.78	Jarre <i>et al.</i> (1991)
Peru 70	Peru upwelling, 1973 - 1979	<i>Engraulis ringens</i>	2.4	0.54	Jarre <i>et al.</i> (1991)
Sch	Schlei Fjord, Germany	Planktivorous fish	3.1	0.28	Christensen and Pauly (1992)
Thai10	Gulf of Thailand, 10 - 50 m.	Small demersal fish	3.3	3.86	Pauly and Christensen (1993)
Thai50	South China Sea	Small demersal fish	3.2	3.70	Pauly and Christensen (1993)
Thau	Etang de Thau, France	Atherinids	2.8	0.02	Palomares <i>et al.</i> (1993)
Trg	Kuala Trengganu, Malaysia	Pelagic fish	3.2	2.71	Christensen (1991)
Venz	Venezuela shelf, 10 - 50 m	Small pelagics	2.6	0.08	Mendoza (1993)
WMx	Western Gulf of Mexico	<i>Eucinostomus</i> spp	3.0	0.06	Arreguín-Sánchez <i>et al.</i> (1993a)
Yct	Yucatan shelf, Mexico	Herring, <i>Opisthonema oglinum</i>	3.2	0.01	Arreguín-Sánchez <i>et al.</i> (1993b)

2.3. Results and Discussion

Ecosystem responses to fishing

Figures 2.3 to 2.11 show the predicted equilibrium effects of fishing mortality rates on the biomass and yield of small pelagic species, and on the biomass of low, medium and high trophic level groups. Altering the ecosystem control mechanism between assumptions of top-down and bottom-up control results in marked difference of the predicted biomass changes in terms of both rate and magnitude; biomass changes are more extreme under assumptions of top-down control of trophic interactions. For all systems, corresponding with depletion of small pelagics, biomass of food groups (specially zooplankton) tend to increase. At the mid-trophic level, predictions of increase in biomass of a competing small pelagic species (e.g. sardine, anchovy or micronekton) occur in all but in the Peruvian system during the 1970s (Peru70 model; Fig. 2.10). The degree of replacement of one species by the other is more pronounced under assumptions of top-down control for the California system (Figures 2.3 and 2.4), the Namibian system (Figures 2.6 and 2.7), and the Northwest Africa system (Figure 2.8). In these cases it is the decrease in the biomass of a common predator, following the depletion of a forage species, that leads to a burst in the production of the competing mid-trophic level species. This is less apparent under bottom-up control, when competition for food resources were limiting interactions. Some of the models presented small oscillations in the predicted equilibrium biomasses, specially in the top-down cases (Figs 2.6 and 2.8). These types of responses do not correspond to 'real' predictions, as they result from an approximation problem caused by not running the model long enough to reach the actual equilibrium.

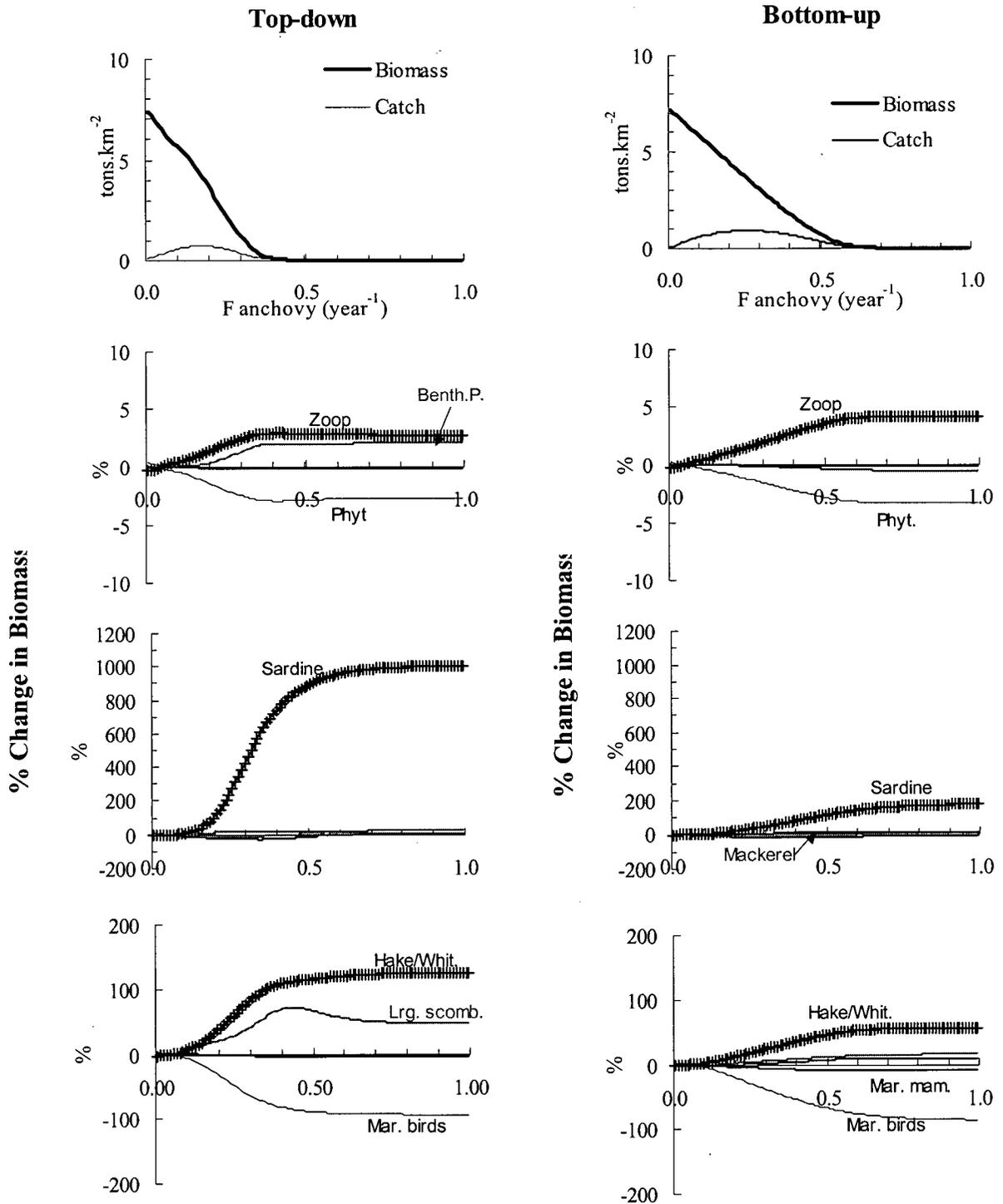


Figure 2.3. Predicted equilibrium biomass and catches of anchovy in the California System (1965-1972) under different fishing mortality rates (upper panel); lower panels show the predicted percent change in biomass (relative to the Ecopath baseline level) of all other groups in the system with the change in equilibrium fishing mortality rates for anchovy. Ecopath groups are organized according to their position in the food web (from lower to higher trophic levels).

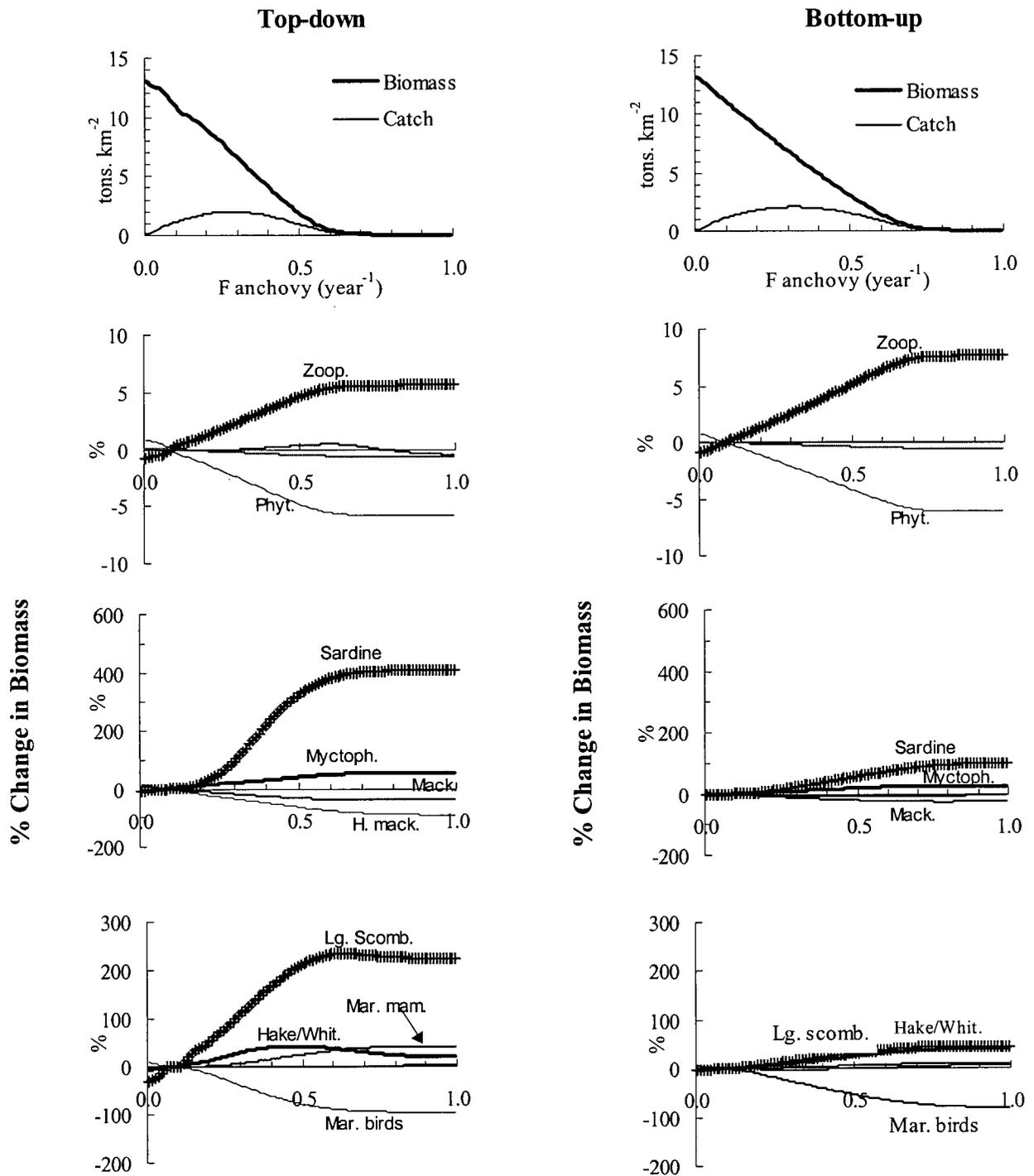


Figure 2.4. Predicted equilibrium biomass and catches of anchovy in the California System (1978-1985) under different fishing mortality rates (upper panel); lower panels show the predicted percent change in biomass (relative to the Ecopath baseline level) of all other groups in the system with the change in equilibrium fishing mortality rates for anchovy. Ecopath groups are organized according to their position in the food web (from lower to higher trophic levels).

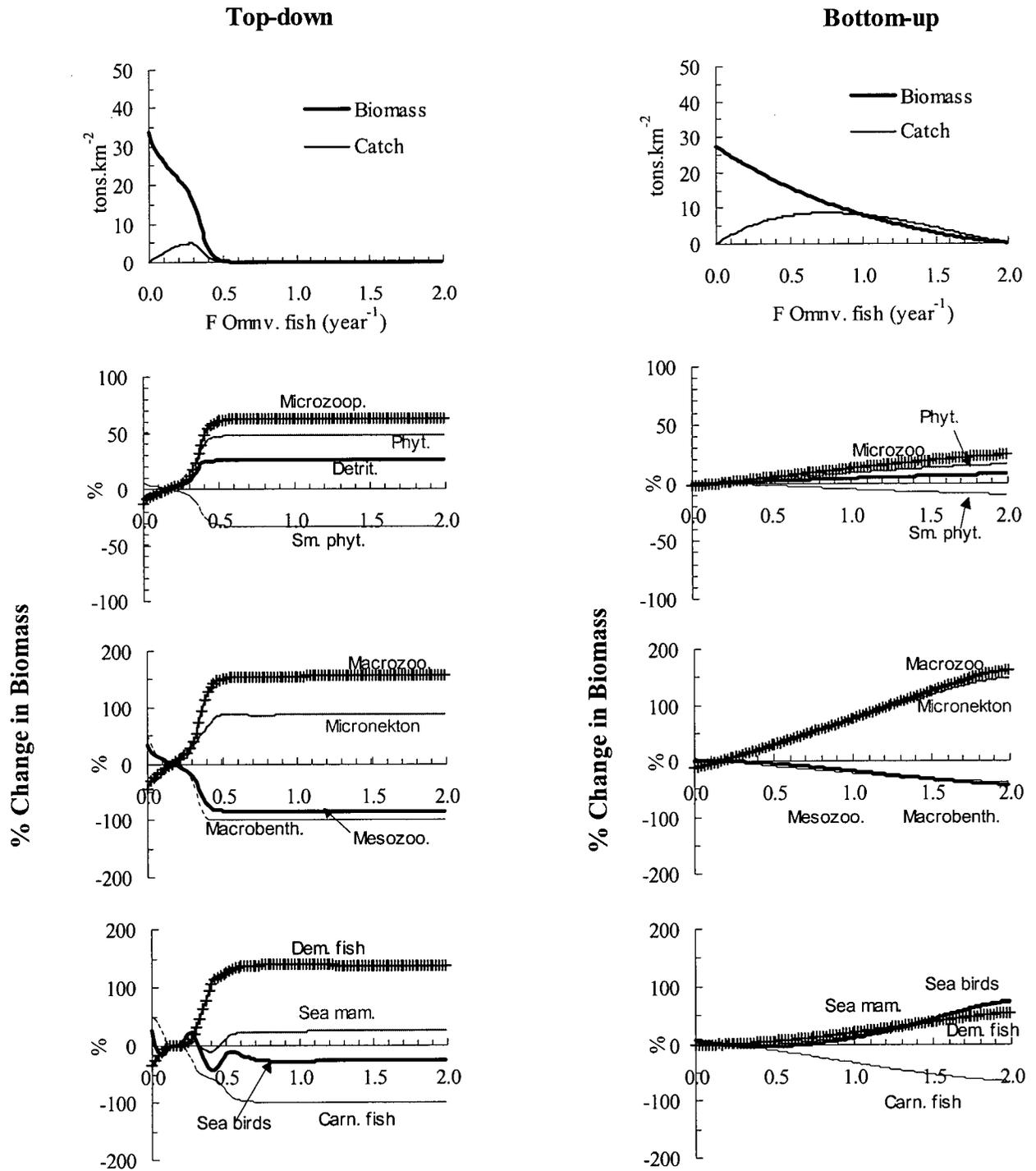


Figure 2.5. Predicted equilibrium biomass and catches of omnivorous fish in the Monterey System under different fishing mortality rates (upper panel); lower panels show the predicted percent change in biomass (relative to the Ecopath baseline level) of all other groups in the system with the change in equilibrium fishing mortality rates for omnivorous fish. Ecopath groups are organized according to their position in the food web (from lower to higher trophic levels).

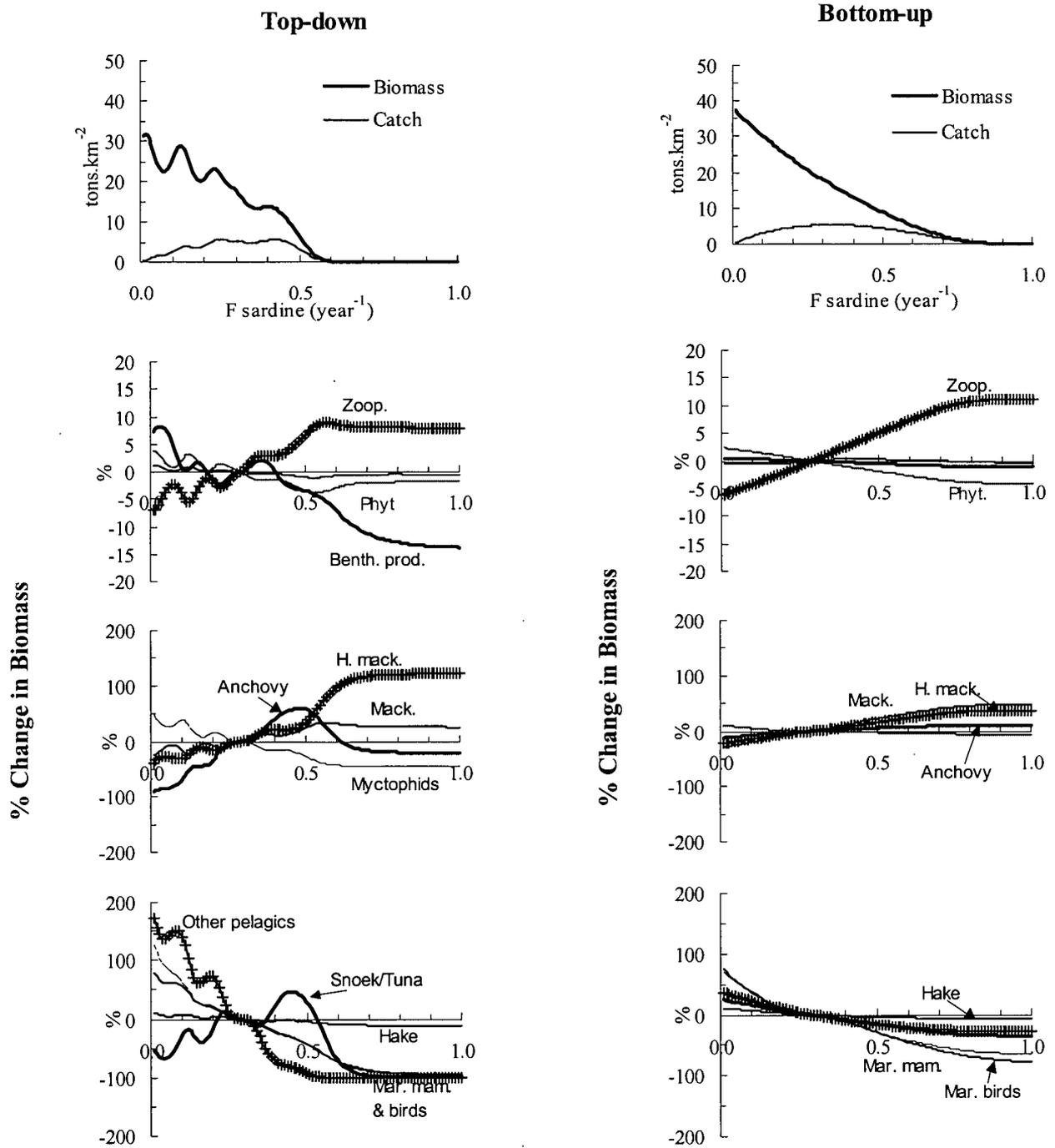


Figure 2.6. Predicted equilibrium biomass and catches of sardine in the Namibia System (1971-1977) under different fishing mortality rates (upper panel); lower panels show the predicted percent change in biomass (relative to the Ecopath baseline level) of all other groups in the system with the change in equilibrium fishing mortality rates for sardine. Ecopath groups are organized according to their position in the food web (from lower to higher trophic levels).

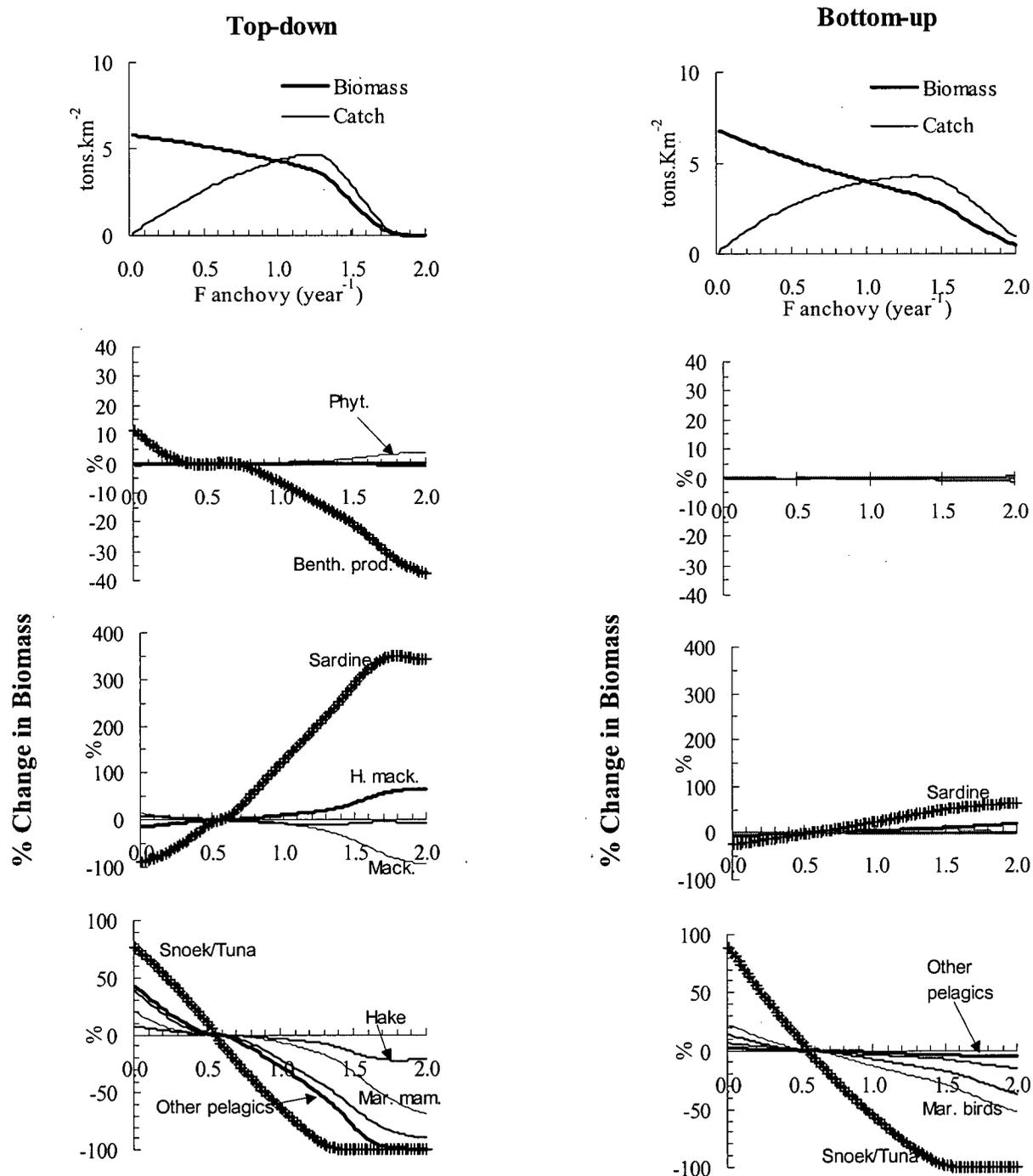


Figure 2.7. Predicted equilibrium biomass and catches of anchovy in the Namibia System (1978-1983) under different fishing mortality rates (upper panel); lower panels show the predicted percent change in biomass (relative to the Ecopath baseline level) of all other groups in the system with the change in equilibrium fishing mortality rates for anchovy. Ecopath groups are organized according to their position in the food web (from lower to higher trophic levels).

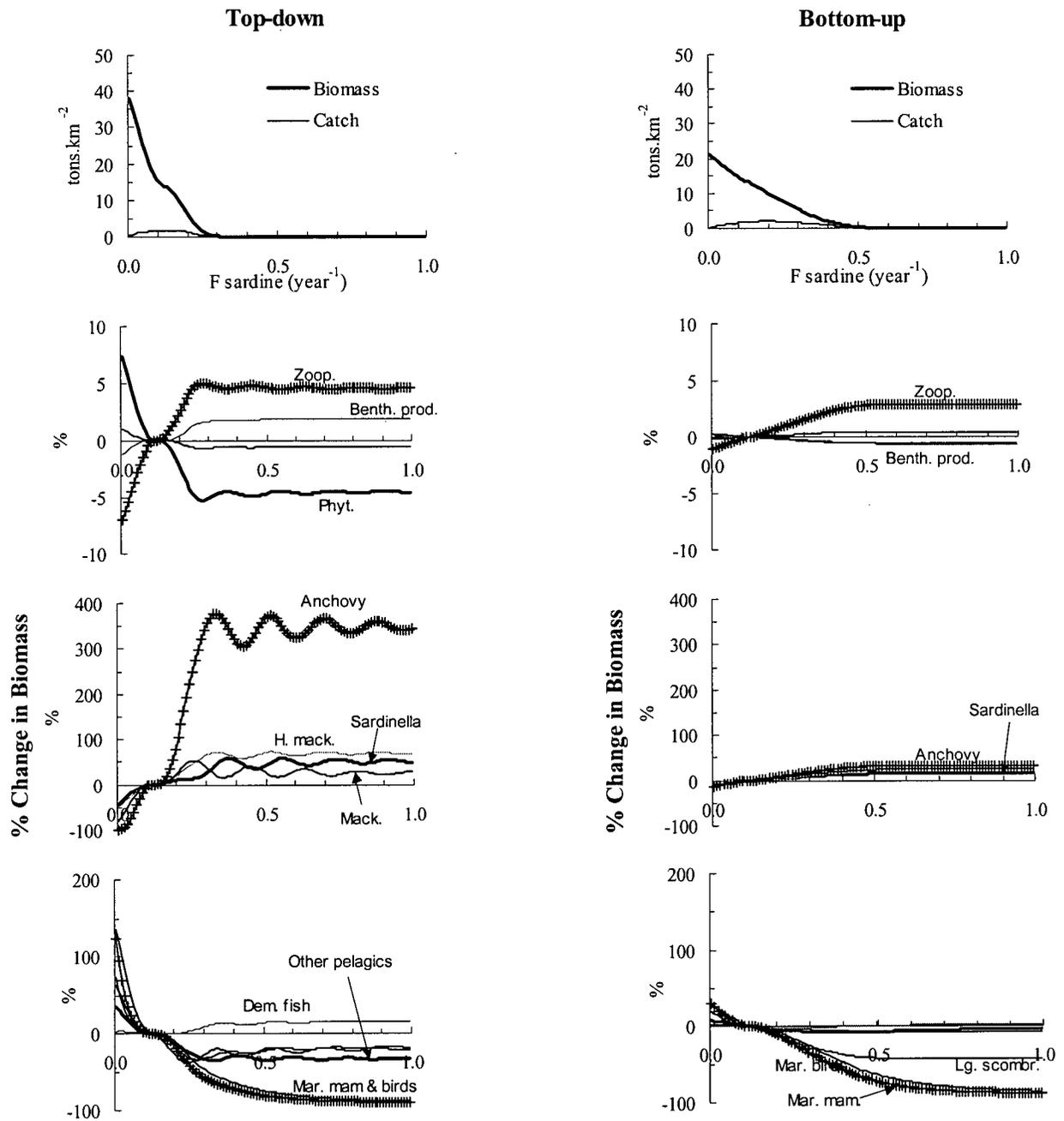


Figure 2.8. Predicted equilibrium biomass and catches of sardine in the Northwest Africa System (1970-1979) under different fishing mortality rates (upper panel); lower panels show the predicted percent change in biomass (relative to the Ecopath baseline level) of all other groups in the system with the change in equilibrium fishing mortality rates for sardine. Ecopath groups are organized according to their position in the food web (from lower to higher trophic levels).

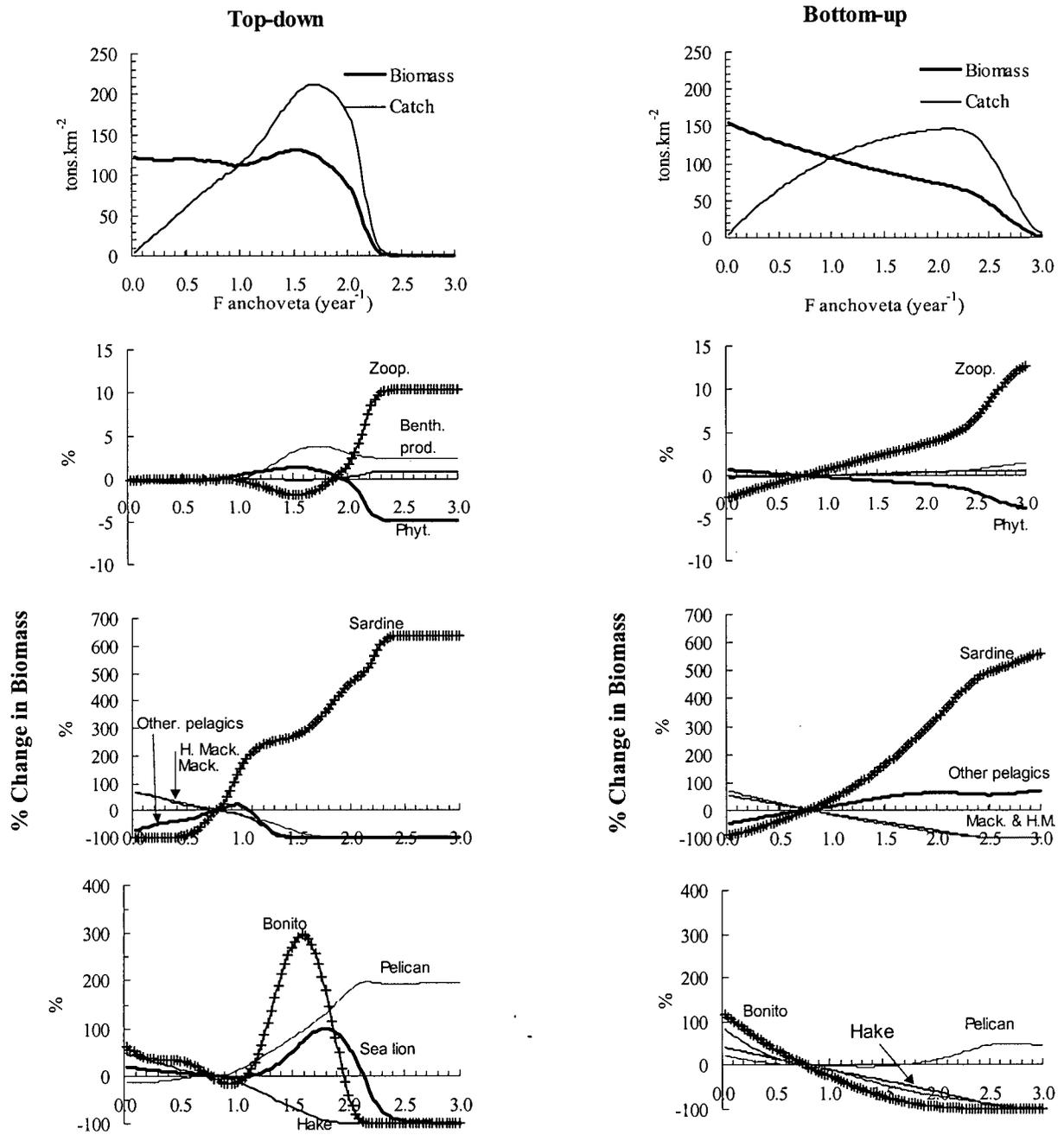


Figure 2.9. Predicted equilibrium biomass and catches of anchoveta in the Peruvian System (1964-1971) under different fishing mortality rates (upper panel); lower panels show the predicted percent change in biomass (relative to the Ecopath baseline level) of all other groups in the system with the change in equilibrium fishing mortality rates for anchoveta. Ecopath groups are organized according to their position in the food web (from lower to higher trophic levels).

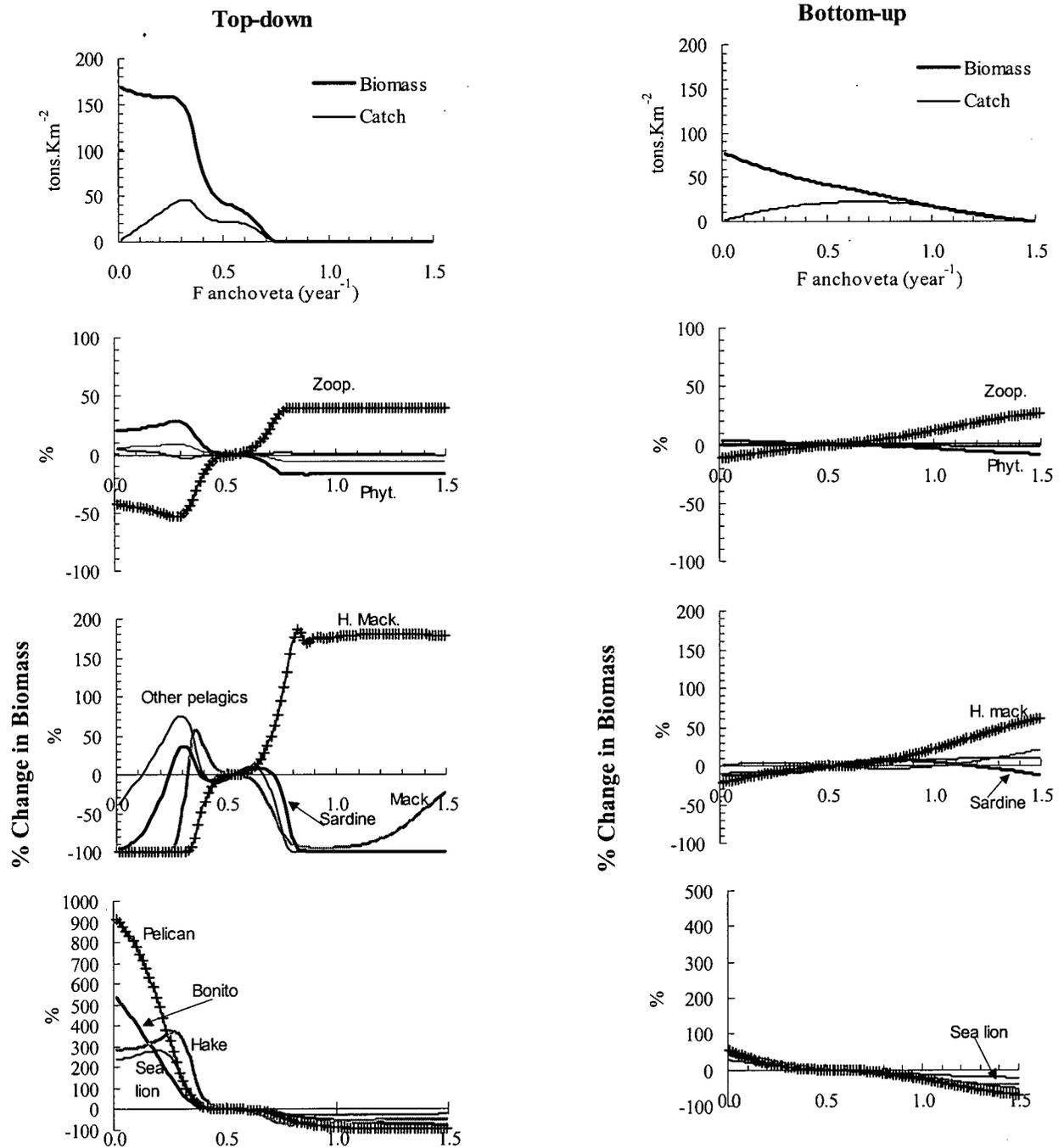


Figure 2.10. Predicted equilibrium biomass and catches of anchoveta in the Peruvian System (1973-1981) under different fishing mortality rates (upper panel); lower panels show the predicted percent change in biomass (relative to the Ecopath baseline level) of all other groups in the system with the change in equilibrium fishing mortality rates for anchoveta. Ecopath groups are organized according to their position in the food web (from lower to higher trophic levels).

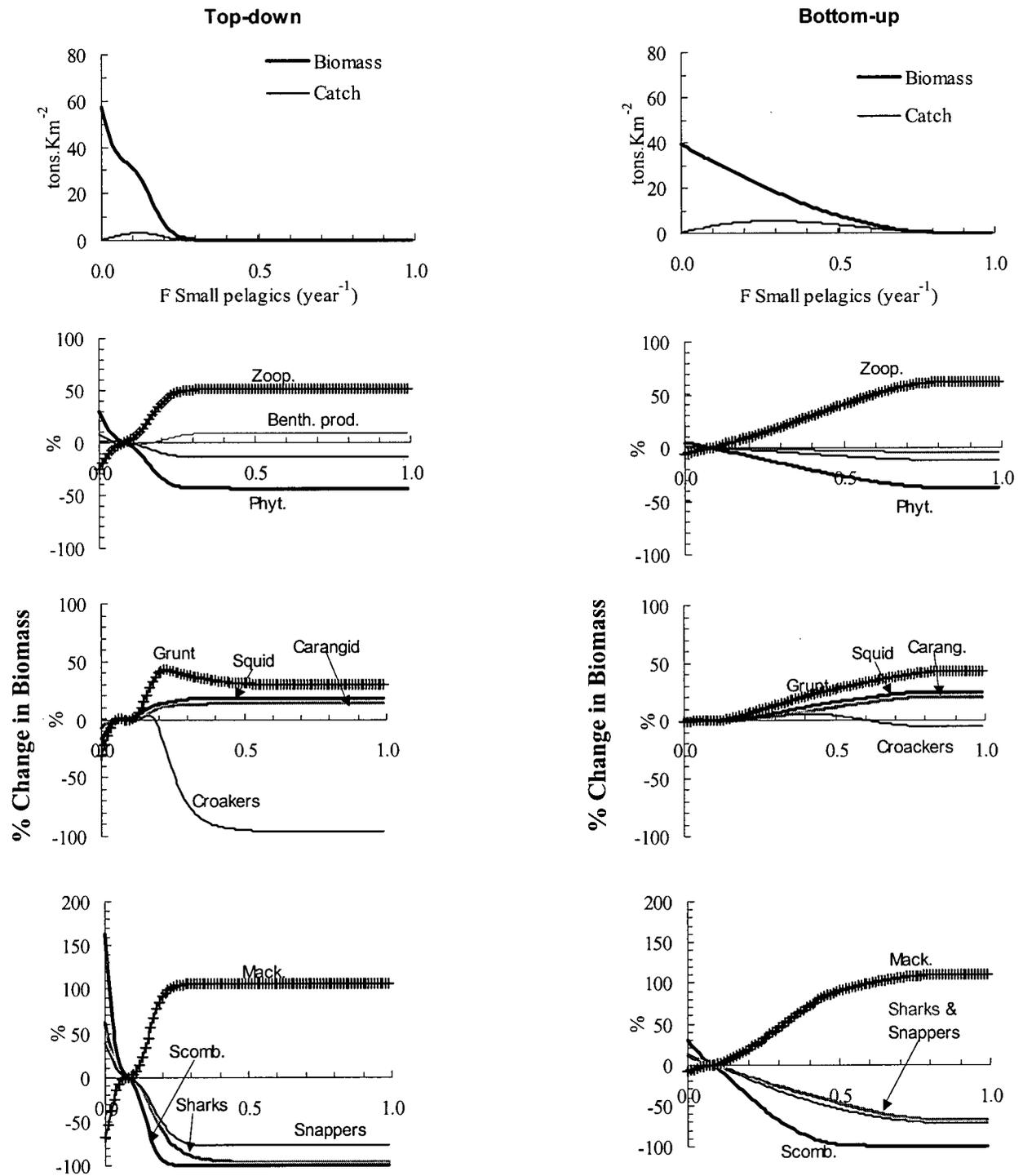


Figure 2.11. Predicted equilibrium biomass and catch of small pelagic fish in the Venezuela System under different fishing mortality rates (upper panel); lower panels show the predicted percent change in biomass (relative to the Ecopath baseline level) of all other groups in the system with the change in equilibrium fishing mortality rates for small pelagic fish. Ecopath groups are organized according to their position in the food web (from lower to higher trophic levels).

Responding to the depletion of small pelagic species, top predators display a decrease in biomass in all but in the California system models (Figures 2.3, 2.4 and 2.5). The degree to which predators are impacted further depends upon the relative importance of the small pelagic fish in their diet. As would be expected, those predators that rely solely upon small pelagics as their prey are impacted most heavily. On the other hand, predators that do not rely primarily on small pelagics, such as horse mackerel and mackerel in the Peruvian system of 1970s (Figures 2.10) and pelicans in the Peruvian system of 1960s (Figure 2.9), tend not to be heavily impacted, the increase in biomass of other species compensating their diet loss. In some systems, competitors of small pelagics represent important food items in the diet of top predators and hence there are close links between changes in biomass. For instance, while most top predators are negatively impacted by the depletion of small pelagics in the Peru, Namibia and Northwest Africa models (Figs. 2.6 to 2.10), sea mammals and predatory fish in the California system models appear to benefit (Figs. 2.3 to 2.5), probably as a result of the increased biomass of other prey groups. Evidence does exist of top predators, specially seabirds, that have been able to successfully shift their diet between sardine and anchovy following collapse (Velarde et al., 1994). But, experience gained in the Peruvian and Northwest Africa systems show undoubting evidence of drastic impacts on predatory fish, marine mammals and birds following the collapse of forage resources (Pauly and Tsukayama, 1987; Cury et al., in press). Cury et al. (in press) used this information to infer that the dominant relationship between top-predator and prey in upwelling ecosystems is bottom-up. Small pelagics evolved life-history strategies in the form of schooling and shoaling behavior to reduce mortality risks by predation, so it is expected that aggregation in the pelagic environment does limit predation. In all cases analyzed here, model simulations suggest that changes in the biomass of top-predators following the collapse of their prey occurs under both assumptions, and are in fact more pronounced under assumptions of top-down control.

Much scientific debate on the causes of shifts in species composition in many marine ecosystems has focused on a 'bottom-up' perspective in which the effect of physical forcing, mediated through climatic-oceanographic processes, leads to changes in primary production and reproductive success of fish populations which in turn will trigger changes in the food web (Beamish, 1995; Bakun, 1996). An alternative 'top-down' perspective, mostly applied in the study of lakes, asserts that predation affects directly and indirectly the structure of populations and communities, and production processes at all trophic levels in the food web (Kitchell et al.,

1994). Model simulations allowed us to explore the effects of both assumptions on predicting the changes in the food web accompanying the exploitation of small pelagic fish. Under top-down control the system responded with a marked increase in the biomass of a competitor species due to cascade effects up and down the food web. These results differ from the early emphasis placed on food competition as the driven force of species replacement (Cushing, 1980; Daan, 1980), and reinforce the potential role of predation mechanisms and trophic cascades effects in shaping the dynamics of mid-trophic level, forage species. The fact that in the four major upwelling ecosystems analyzed, natural mortality of small pelagic fish due to predation is much higher than their fishing mortality (Jarre-Teichman and Christensen, 1998) corroborates the above hypothesis.

The observed dynamics demonstrate that small pelagics play a central role in upwelling ecosystems. Their high throughput of energy, their intermediate trophic level, and the high connectivity to other components in the ecosystem indicate that depleting stocks of small pelagics through fishing is expected to have important consequences for other ecosystem components and for fisheries on other commercially important species. Where these other species are dominant predators of the small pelagics the likely outcome is a reduction in their biomass and catch. The converse may be true when the target species is a competitor, the increased biomass of food sustaining greater biomass of the competitor. If validated, these results indicate that one of the long term effects of intensive fisheries for small pelagics might be the intensification of the observed downward trend in the mean trophic level of fisheries (Pauly et al., 1998), by both accelerating the decline of species at the top of the food chain and favoring the outburst of other mid-trophic level forage species.

Predicted equilibrium yields and fishing mortality at maximum sustainable yield (F_{msy}) also vary significantly between the two control scenarios (upper panels in Figs. 2.3 to 2.11). Bottom-up control generally produces a catch curve that achieves an asymptote at higher F_s , predicting that stock can sustain much higher fishing pressure before it begins to decline. This occurs because under bottom-up control, predation mortality rate ($M_{ij} = C_{ij}/B_i$) tends to remain more stable, while the consumption rate (C_i/B_i) of small pelagics increases more, to make them more productive per biomass due to donor control of total food eaten (C_i). Strong predation control generally prevents higher yields under top-down control. F_{msy} values predicted under the two control scenarios are compared in Figure 2.12. As stated before, using a bottom-up control predicted

higher F_{msy} values. With the exception of two models (Namibia78-83 and Peru 64-71), predicted F_{msy} values fall in a conservative range of fishing mortality rates, below the sustainable exploitation rate of 0.4 suggested for small pelagic fish stocks by Patterson (1992).

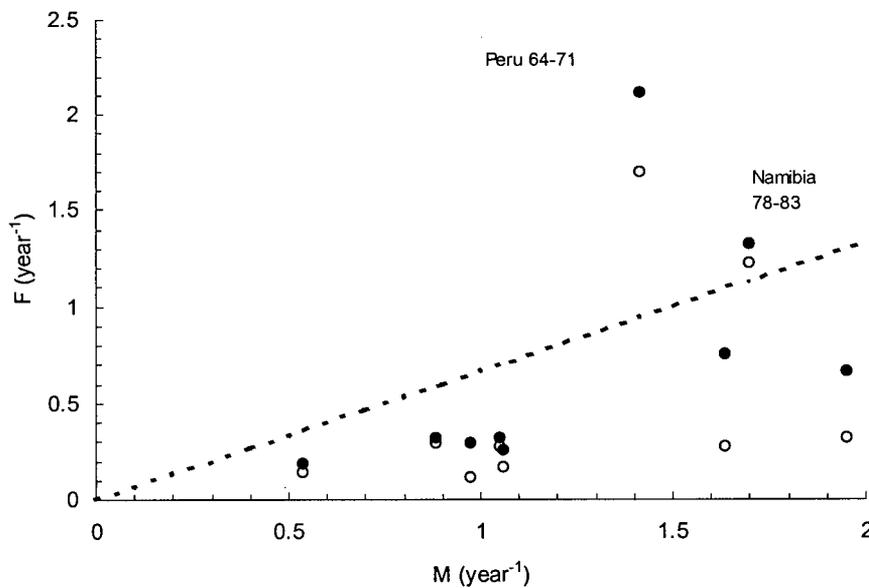
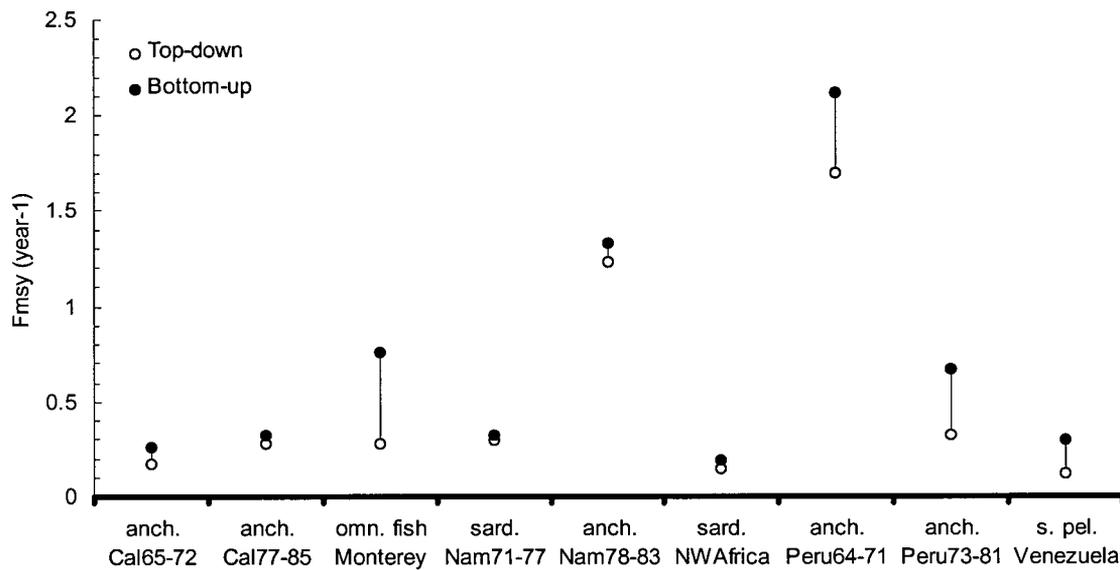


Figure 2.12. Upper panel: Predicted fishing mortality at maximum yield (F_{msy}) under two contrasting assumptions on the dominant type of trophic control in the food web. The x-axis indicates the species fished in the respective models. Lower panel: relationship between F_{msy} and the natural mortality rate of the small pelagic species fished in each model. The dotted line represent the exploitation rate (F/Z) of 0.4 suggested by Patterson (1992) as a sustainable fishing rate for small pelagic stocks.

Ecosystem stability and resilience

Of the 23 models analyzed, one (Thai10 model) did not recover the original stable state after being perturbed. Walters et al. (1997) suggested that such unstable behavior is expected when Ecosim is used to extrapolate to a state far away from that described by a given Ecopath model, or when diet composition data and group definitions are inadequate to represent actual trophic interactions among pools. Six out of the eight upwelling ecosystem models used in the analysis had not recovered completely their original biomass levels 80 years after the end of the perturbation (Figure 2.13). The low stability of these models must reflect some characteristics of upwelling ecosystems, either in terms of the importance of the impacted wasp-waist populations to other ecosystem components, or in terms of intrinsic properties of the food web captured in the models. One immediate conclusion from these results is that strategies of pulse fishing, historically applied to many small pelagics, have a potential destabilizing effect in upwelling ecosystems on time scale responses far from most projections customarily provided by conventional stock assessment research. On the other hand, results indicate an apparent lack of biological 'mechanisms' in these systems to cope with perturbations. That is explored below using ecosystem indexes calculated by Ecopath.

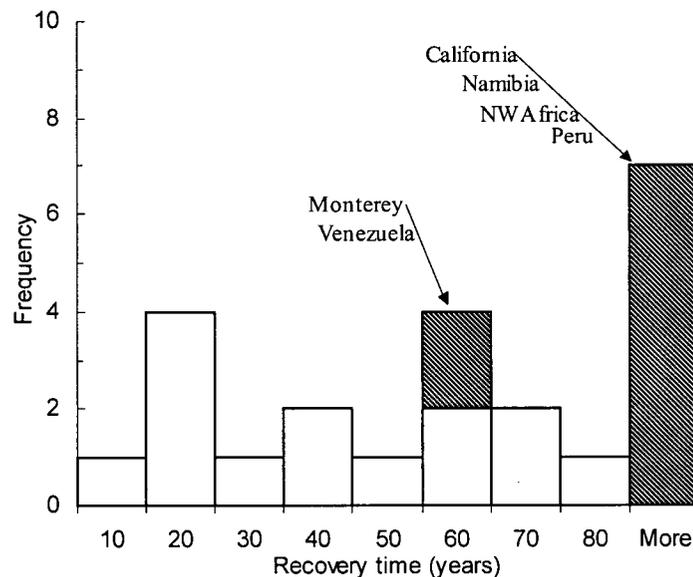


Figure 2.13. Recovery time of the 23 models perturbed by pulse fishing at the mid-trophic level, wasp-waist populations. The recovery time of the models of upwelling ecosystems is highlighted.

System recovery time of the remaining 15 models that recovered the baseline equilibrium biomasses was correlated against the different ecosystem attributes (Table 2.3). Only Finn's indices of cycling and path length are statistically correlated to recovery time ($r = -0.76$ and -0.67 , respectively). On the other hand, the assumption that ecosystem organization is a more important aspect of system stability (Ulanowicz, 1986) was not confirmed: none of the attributes of trophic web organization (Relative ascendancy and Internal flow Overhead) was correlated with recovery time. Community complexity and energetics attributes also showed low correlation, as may perhaps have been expected (Begon et al., 1990; Hansen and Jorgensen, 1990). May (1972) concluded that a simple relationship between stability and complexity may not be obtained, and in some cases, complex systems may fluctuate more than less complex ones. Here, we refute the hypothesis that stability and complexity (expressed in terms of connectance, web structure (SOI) and trophic groups richness) are correlated in the 15 models compared.

Table 2.3: Correlation among the ecosystem attributes defined in the text. Numbers in bold indicate significance at the 5% level (d.f. = 13). Recovery time (Rec. time) is the measure of stability utilized in the analysis. CI: connectance index; SOI: system omnivory index; Npools: total number of system components; FCI: Finn's cycling index; Ascnd: ascendancy; IOvh: system internal flow overhead; R/B: respiration/biomass ratio; Pp/B: primary production/biomass ratio; B/T: biomass/throughput ratio; B/P: biomass/production ratio; SThr: total system throughput.

Attribute	Complexity			Homeostasis				Energetics				
	CI	SOI	Npools	FCI	Path	Ascnd	IOvh	R/B	Pp/B	B/T	B/P	SThr
<u>Rec. time</u>	-0.10	-0.15	0.12	-0.76	-0.67	0.09	-0.32	-0.10	0.33	-0.13	-0.14	-0.28
CI	-	0.28	-0.57	0.13	-0.09	-0.47	0.53	-0.25	-0.23	-0.13	-0.06	-0.28
SOI	-	-	0.29	0.23	0.48	-0.35	0.24	0.33	0.25	-0.45	-0.40	0.77
Npools	-	-	-	-0.14	-0.02	0.22	-0.51	-0.19	-0.05	-0.37	-0.16	-0.01
FCI	-	-	-	-	0.80	0.27	-0.04	-0.26	-0.34	0.20	0.24	0.49
Ascnd	-	-	-	-	-	-	-0.83	-0.46	-0.36	0.44	0.50	-0.04
IOvh	-	-	-	-	-	-	-	0.29	0.38	-0.23	-0.32	0.27
R/B	-	-	-	-	-	-	-	-	0.63	-0.86	-0.83	-0.04
Pp/B	-	-	-	-	-	-	-	-	-	-0.55	-0.65	0.16
B/T	-	-	-	-	-	-	-	-	-	-	0.94	0.06
B/P	-	-	-	-	-	-	-	-	-	-	-	-0.07

Finn's cycling index showed a consistent negative relation with system recovery time (Fig. 2.14). Systems with a low percentage of energy recycled, simple recycling structures and short average path length (e.g. the upwelling systems off Venezuela and Monterey Bay) exhibit characteristically slow recovery time. On the other hand, systems where recycling is important, such as coastal lagoons and fjords (e.g. Schlei Fjord and Etang de Thau models), appeared more stable. To test the hypothesis that stability changes with recycling in a single system, we simulated the effect of an increase in the importance of detritus cycling in the Venezuela shelf model. The steps were as follows: first we gradually increased the diet components of detritus for heterotrophic benthos from 0 to 45% (thereby increasing the FCI from 0 to 2.8%); then we

increased the diet component of detritus for zooplankton from 0 to 95% (the FCI thereby increased from 2.8 to 24.5%). Simulations were run for each level of recycling, leading to the results shown in Fig. 2.15. A negative relationship clearly emerges between the amount of detritus cycled and the recovery time of the model. Model stability does not appear very sensitive to increasing recycling up to a certain threshold from which small changes in recycling lead to substantial reductions in recovery time.

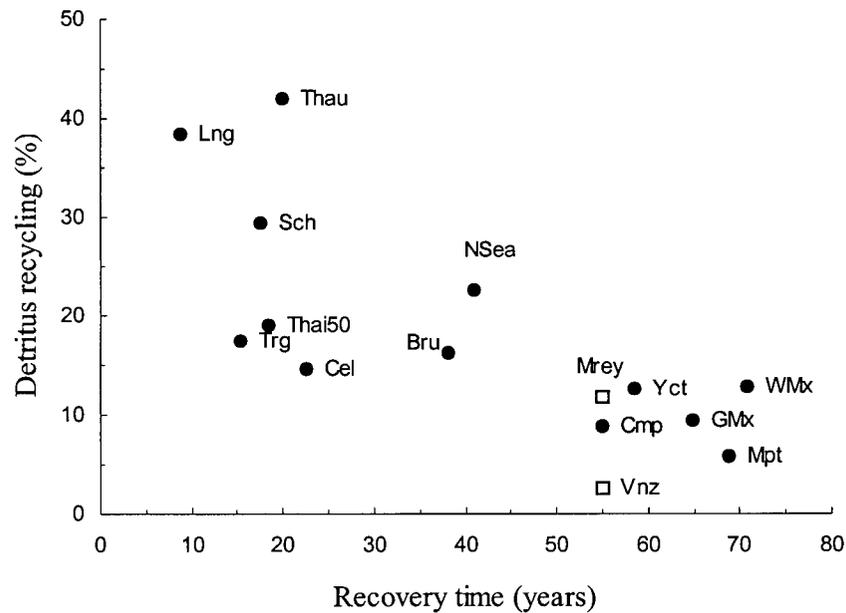


Figure 2.14. Relation between Finn's index of detritus recycling and system recovery time ($r=-0.76$; $p=0.001$; $d.f.=13$). See Table 1 for models descriptions. Empty squares indicate the recovery time of the models of upwelling systems (Monterey and Venezuela).

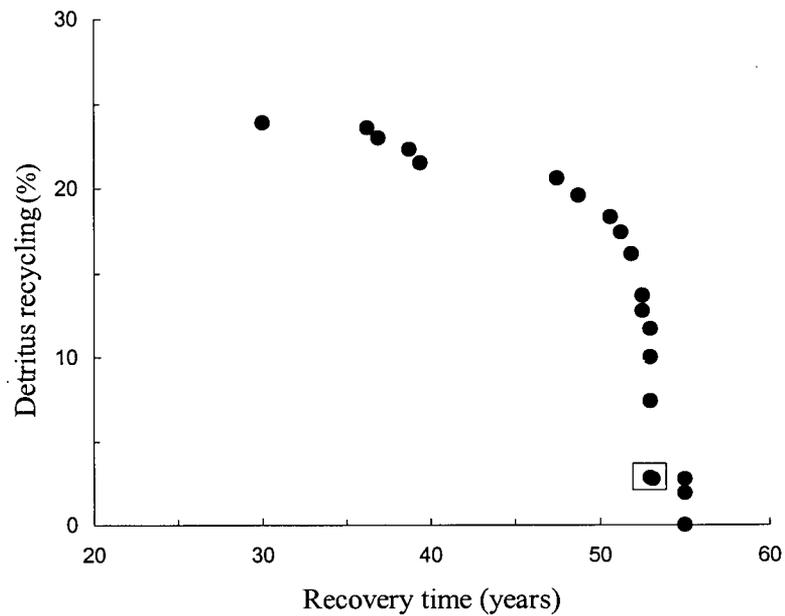


Figure 2.15. Effect of increasing detritus cycling on the stability of the Venezuela shelf model (see text for procedure). The square corresponds to the system recovery time (t_3 on Fig.1) for the baseline Finn cycling index value (2.7%).

A view of the role of recycling different from the presented here was proposed by R. E. Ulanowicz and co-workers who argued that it is perturbed systems which tend to do more recycling (Ulanowicz, 1984; Ulanowicz and Wuff, 1991; Baird et al., 1991); from this view, they concluded that recycling is a measure of stress. Indeed, Ulanowicz and Wuff (1991) suggested that in ecosystem development, the number and length of recycling routes is a more important attribute than the amount of recycling, since in some ecosystems recycling occur over short benthic cycles and do not involve loops through various trophic levels. Hence, the amount of energy and nutrients recycled may result in overevaluating the importance of recycling to the overall community. However, in the present study, recycling and path length were significantly correlated ($r = 0.80$) (Table 2.3), pointing to the substantial complexity and importance of the recycling routes for the marine ecosystem models analyzed.

We believe that Ulanowicz et al. interpretation of the role of detritus recycling as a result (and a measure) of stress to be due to they having selected a priori ascendancy as a strong and positive correlate of maturity, then evaluating all other system properties relative to ascendancy. This approach is problematic because ascendancy (or at least that of its two component meant to express the 'information content' of an ecosystem) is in fact negatively correlated with maturity

(Christensen, 1995a). On the other hand, relative overheads, a measure of stability derived from Ulanowicz's theory does show a strong relationship with Finn's index (Christensen and Pauly, 1993b). Thus we conclude that recycling does indeed have an important role in the maintenance of ecosystem stability. Basically, the higher the recycling the more quickly will the effects of perturbations be eliminated from the system (O'Neill, 1976; DeAngelis, 1980).

Traditional views of ecosystem development consider that succession culminates in a stabilized ecosystem in which biomass and symbiotic functions between organisms are maintained per unit of available energy (Odum, 1969). Odum interpreted the strategy of succession as the one of increase control and or homeostasis with the physical environment in the sense of achieving maximum protection from its perturbations. The net result of community development would be symbiosis, nutrient conservation, stability, a decrease in entropy, and an increase in information. According to Odum, biotic control of grazing, population density and nutrient cycling provide the chief positive feedback mechanisms that contribute to stability in mature systems by preventing overshoots and destructive oscillations. Our results are in agreement with the above theory to the extent it shows that systems with higher capacity to recycle detritus are systems with a higher ability to recover from perturbations. Taking, therefore, stability and recycling as directly related attributes during ecosystem development the results of this analysis provide support to Odum's theory and to previous comparative studies of marine food webs (Christensen and Pauly, 1993b; Christensen, 1995a).

Very often ecosystems develop what Odum called pulse stability, where a more or less regular physical perturbation can maintain an ecosystem at some intermediate point in the development sequence toward maturity. Connell (1978) showed that in fact intermediate levels of disturbances are essential for the maintenance of certain ecosystem characteristics, such as species diversity, even in highly mature systems. Evidence gained in ecological studies, mainly of terrestrial ecosystems, has shown that change during ecosystem development is not continuous and gradual, but it is episodic with slow accumulation of biomass and nutrients punctuated by sudden releases and reorganization (Holling et al., 1995). According to Holling, the structure of biological communities is therefore controlled through the balance of destabilizing and stabilizing forces. While destabilizing forces are important in maintaining diversity, resilience and opportunity, stabilizing forces, such as nutrient recycling, are important in maintaining productivity and biogeochemical cycles.

The role of destabilizing forces may be particularly important in pelagic marine ecosystems. In the sea, short-term physical variability is damped out by the very large heat capacity of the ocean. In turn, this large thermal capacity and the long period exchange rates between deep and near-surface waters lead to relatively large-amplitude changes at the long term scales (Steele, 1985). As a result, less robust internal ecosystem processes are needed to handle the smaller amplitude variability at short periods. The possible absence of such mechanisms, combined with increase variance with period, can mean that pelagic marine populations or ecosystems have to continually adapt to physical variability in the short as well as the long term (Holling et al., 1995). The absence of well structured recycling routes, the low recycling and reduced stability of upwelling ecosystems (Figures 2.13 and 2.14) can be considered a result of a longer-term adaptation of biological community to the physical variability and transitory nature of these systems. In fact, taking fisheries yield as an indicator, upwelling ecosystems can be considered the most variable oceanic systems (Stergiou, 1998). Bakun (1996) considered variability itself a key asset for the massive small pelagic wasp-waist populations inhabiting upwelling systems, which must rely on pulsing its abundance to cope with the temporal and spatial patterns presented by their prey, while simultaneously presenting patterns to their predators that overcome growth of intolerable levels of predation.

Model limitations

Notes of caution relating to the interpretation of simulations were presented by Walters et al. (1997), but will be summarized here. First, each Ecopath model may differ in terms of the time span which the data represent, the number of groups used, and the parameters which are estimated. It is difficult to determine what effect differences in data quality have on the simulations but it has been suggested that poor data may lead to models with a tendency for self-simplification (i.e., low persistence), through competition or predatory exclusion of some groups after disturbance by fishing (Walters et al., 1997). Of the 40 Ecopath models tested by Walters et al., those representing coastal and shelf marine ecosystems show a positive relationship between persistence and model quality (Pauly et al., in press; Figure 2.16; Table 2.4). In this analysis model persistence was ranked according to the maximum flow rate (mean v_{ij}) between predator-prey that led to persistence of all groups in the system after a disturbance. Model quality was

ranked according to the accuracy and quality of data used as input in the construction of an Ecopath model. Walters et al. (1997) suggested that positive relationships between persistence and quality have two interrelated consequences; first, it indicates the possibility that strong trophic interactions do occur in nature and lead to a selective process such that “what persists to be studied as an ‘equilibrium’ in the field is a very peculiar or particular set of interaction parameter values”; second, and consequently, one can only estimate these interaction values in models built from data accurately measured. These results differ from the studies of trophic interactions in aquatic ecosystems (McCarthy et al., 1995; Scheffer and de Boer, 1995) which show that the patchy distribution of organisms may lead to ratio dependence in predator-prey interactions, and consequently to relatively weak predator control (low v_{ij}) in aquatic food webs. Ultimately, the relationship between model quality and persistence indicates that results from dynamic simulations with Ecosim will depend in part on the quality of information used to construct the original Ecopath model.

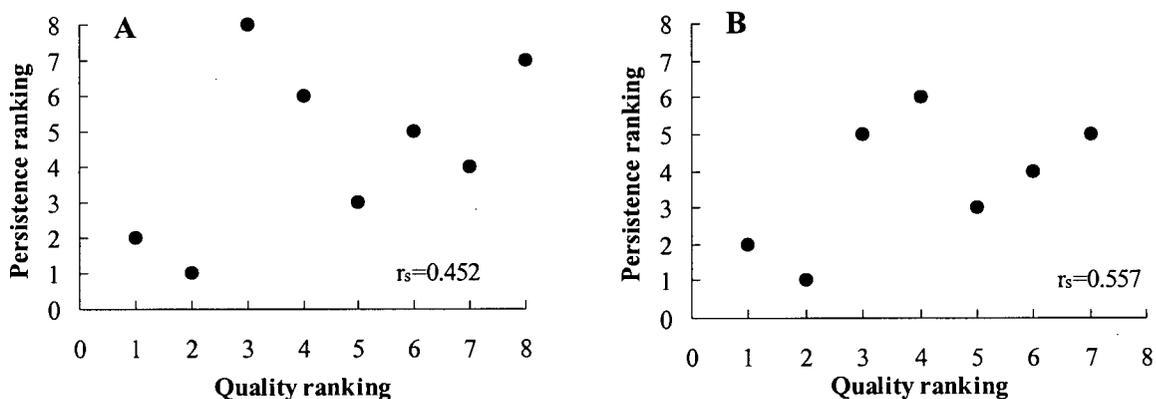


Figure 2.16. Rank correlation between model persistence and quality, for Ecopath models of (A) coastal ($r=0.452$) and (B) shelf ($r=0.557$) ecosystems.

Other limitations of the approach relate to its inherent simplifying assumptions, which ignores spatial processes, does not allow for numeric responses, as opposed to biomass predictions only, and does not take into account environmental variability, a factor frequently ignored in complex food web models (Hunter and Price, 1992). Some of these limitations, which may as well apply for many single species models, were recently addressed by incorporating into Ecosim a delay-differential model structure that is capable of tracking both numbers of individuals and biomasses of juvenile and adult stages of key species in the ecosystem (Walters et al., *in press a*), and an interface that allow for the representation of spatial processes (Walters et al., *in press b*). Walters et al. (1997) also warned about the risk of using Ecosim to extrapolate to circumstances

far from the equilibrium for which Ecopath data are available. However, if we only project a short time horizon and consider only short term dynamics, long term effects are easily missed. Despite the reservations expressed about long term simulation periods, they still can be useful in predicting the directions of biomass change, and serve as a warning to keep in mind potential delayed responses, a point that should be emphasized especially when considering complex and unstable ecosystems.

Table 2.4. Trophic models used in the regression between quality rank and persistence rank.

Shelf systems	Quality rank	Max v_{ij} persistence
Brunei Darussalam	5	20
gulf of Thailand, 10-50 m	4	5
Kuala Terenganu, Malaysia	6	11
Northern Venezuela Shelf	2	40
North Sea	1	35
Northern Gulf of Mexico	7	8
Yucatan shelf	3	8
<hr/>		
Coastal systems		
Campeche Bank, Mexico	8	6
Celestun lagoon, Mexico	5	40
Etang de Thau, France	3	4
Lingayen Gulf, Philippines	7	10
Maputo Bay, Mozambique	1	43
Schlei Fjord, Germany	2	46
Shallow areas, South China Sea	4	7
Southwestern Gulf of Mexico (coast)	6	8

Management implications

The comparative analysis of the ecosystem impacts of harvesting small pelagic fish using multi-species trophic models showed that: i) small pelagic fish play a central role in upwelling ecosystems; changes in their abundance can have considerable consequences to species both at the top and the bottom of the food web; ii) observed patterns of species replacement at the pelagic niche can be explained by the effect of fisheries and trophic interactions alone, being more evident when the system is dominated by predatory control, i.e., top-down; iii) upwelling ecosystems have characteristics of unstable systems, lacking biological mechanisms (e.g. nutrient recycling) to damp the impact of external forces created by fishing and environmental factors; and iv) quantitative prediction of the ecosystem effects of fisheries using mass-balance ecosystem models is very sensitive to the type of dominant trophic control assumptions, and may be problematic for situations of poor data quality. However, these models are capable of output

robust qualitative responses which may guide the screening of fisheries policies under ecosystem principles. In this regard, results of the present work can have direct implications to the management of small pelagic fish with ecosystem goals. It indicates that as 'wasp-waist' species in upwelling ecosystems, small pelagic forage fish will sustain much more conservative exploitation rates than what has been historically applied in the cases of stock collapse. Also, fisheries for small pelagics have a potential disrupting effect on ecosystem dynamics and may cause shifts in the species composition at the mid-trophic level. Ultimately, the characteristics of unstable systems will mean that variability is a key asset for the resilience of upwelling ecosystems, and management should in turn be prepared to cope with the unexpected changes resulting from both fishing and environmental effects.

2.4. Summary

This chapter analyzes the ecosystem impacts of harvesting small pelagic fish in upwelling systems comparing the results of simulations carried with trophic models. Results include the predicted responses of the system to fishing, in terms of changes in the biomass of small pelagic fish and other ecosystem components; the recovery time of marine ecosystems when disturbed at the mid-trophic level, wasp-waist populations; and the characteristics of stability of upwelling systems. These results are used to draw conclusions on the effect of fisheries and trophic cascades on species shift at the pelagic niche, and on the applications and limitations of multi-species trophic models in the design of ecosystem principles and precautionary measures for small pelagic fisheries.

Chapter 3. Fishing down food webs and the carrying capacity of marine ecosystems in southern Brazil²

3.1. Introduction

Recent assessments of the worldwide status of marine capture fisheries revealed alarming signs of human dominance and impact on the oceans, such as overfishing of important stocks, by-catch and discard of non-target species, and the fishing down of marine food webs (Botsford et al., 1997; Pauly et al., 1998). In line with some of these global trends, marine capture fisheries of Brazil are in a state of crisis caused by the scarcity of resources, over-capitalization of fisheries activities and the lack of sound fisheries management policies. The crisis in Brazilian fisheries occurs concurrent with major efforts to assess the potential production of fishery resources in the Exclusive Economic Zone, triggered by the country's ratification to the United Nations Convention on the Law of the Seas. Early assessments of the fisheries resources along the coast carried during the 1970s (Hempel, 1971; Neiva & Moura, 1977) pointed at a potential total catches over 1 million tons/year, when in fact, since the mid-1980s landings have stabilized around 700 thousand tons/year while many of the traditional fish stocks have become either fully exploited or overexploited (Dias-Neto, 1991a; 1991b; IBAMA, 1994a; 1994b; 1994c; Reis et al., 1994; Cergole, 1995; Matsuura, 1995; Haimovici et al., 1997). The current situation raises concerns on the limits of marine ecosystems carrying capacity i.e., whether the level of exploitation can be sustained without impairing the productivity and integrity of these ecosystems.

Brazil has an extensive coast line that extends from 5°N to 34°S, including regions of tropical and subtropical climate. Matsuura (1995) divided the Brazilian coast in five regions with distinct environmental characteristics and types of fishing activities (Fig. 3.1). In the north biological production is high as a result of the continental runoff from the Amazon river (Teixeira and Tundisi, 1967). The wide continental shelf and the rich benthic community favored the development of trawling activities in this region, mostly for shrimps and large catfishes. The northeast and east regions present oligotrophic conditions due to the influence of tropical waters from the Brazil Current. Rocky bottoms and a mostly narrow continental shelf induced the development of hook-and-line and longline fisheries for rockfishes, sharks and tunas. In the

southeast, primary production is mainly driven by seasonal upwelling of nutrient-rich, cold subtropical waters pumped by alongshore winds and by cyclonic vortexes originated from the Brazil Current (Bakun and Parrish, 1990; Matsuura, 1995). The southern part of the Brazilian coast is under the influence of the Subtropical Convergence between the southward and northward flowing Brazil and Malvinas currents. The confluence of water masses and the high volume of continental runoff provide physical and chemical conditions for high biological production on the shelf (Seeliger et al., 1997). Trawling is the main type of fishing activity in the southeastern and southern regions, although the presence of highly abundant pelagic stocks, mainly sardine, in the southeast has also lead to the development of an important purse seine fishery as early as 1950.

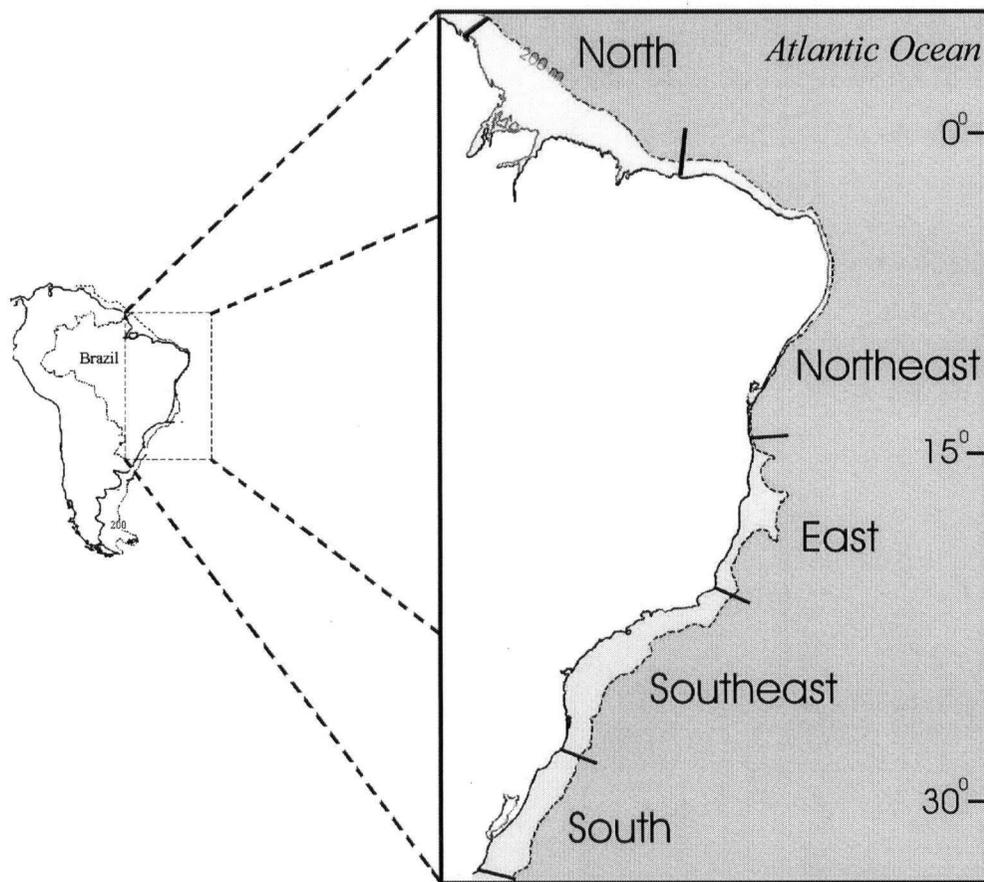


Figure 3.1. Shelf regions of Brazil. The southeastern shelf is considered from Cabo de São Tomé to Cabo de Santa Marta Grande, and the southern shelf from Cabo de Santa Marta Grande to Chui.

The regions also differ in the type of fisheries production. While catches in the north, northeast and east regions are mainly artisanal (Diegues, 1995), in the southern regions it is the industrial fisheries that provide most of the fisheries production, accounting for approximately half of the

total Brazilian catches (IBAMA/IBGE, 1995). Historically, it was in the south and southeast that industrial fisheries were mostly developed through a series of government incentives, and it is where fisheries are best documented.

This chapter presents a comparative analysis of fisheries in the southeastern and southern regions of Brazil which aims to assess the carrying capacity of the marine shelf ecosystems for harvestable species. Carrying capacity has been defined as the maximum size of a population or activity that could be indefinitely sustained without degrading the ecosystem's future productivity or suitability for that use (Odum, 1997). In the oceans, carrying capacity is usually referred to as the upper limit of biomass of organisms that can be supported by a set of primary production and food web structure (Christensen and Pauly, 1998). Fisheries yield is directly related to the carrying capacity of marine ecosystems, since there is a maximum sustainable rate of fish production associated to the total fish biomass at the carrying capacity. Also, overfishing can directly affect the carrying capacity of marine ecosystems by altering the structure of food webs and changing their potential productivity. In this chapter I analyze the carrying capacity of marine ecosystems in three ways. Firstly by computing the total flux of energy from primary producers available to different trophic levels in the food web, and the total primary production required to sustain fisheries catches (Pauly and Christensen, 1995). The ratio of these two quantities provides a straightforward measure of the "appropriated carrying capacity" (*sensu* Rees, 1996) of ecosystems, i.e. the amount of the available energy in a ecosystem already appropriated by fisheries catches. Secondly, I do a diagnosis of fisheries for the 'fishing down the food web' phenomenon using trophic level estimates and national and regional catch statistics. Finally, I analyze how fisheries are likely to alter the species composition in ecosystems structured by trophic relationships. I explore this effect by simulating a 'fishing-down-the-food-web' scenario in the southern shelf region, where traditional demersal fish stocks are overexploited and the prospects for increasing yield relies on exploiting abundant small pelagic forage fish.

3.2. Methods

The method used here to quantify the appropriated carrying capacity follows the approach developed by Pauly and Christensen (1995) for the analysis of primary production required to sustain world fisheries. Primary production required by fisheries (PPR) is estimated based on the

trophic level of the species caught, the energy transfer efficiency between trophic levels, and on the primary productivity of the two shelf regions (Table 3.1). Primary production estimates for the southeast and south were obtained from Brandini (1990) and Odebrecht and Garcia (1997), respectively. Species trophic levels (Table 3.2) were computed according to Odum and Heald (1975) using available information on diet composition, and from trophic models. In this analysis primary producers have trophic level 1, and each higher order consumers has trophic level 1 + the weighted average trophic level of its preys. Rocha et al. (1998) constructed a simplified trophic model of the Ubatuba region in the southeastern shelf that is here used to estimate the mean trophic transfer efficiency for the region. Transfer efficiency for the southern shelf is calculated from the trophic model described below. PPR estimates are based on a conversion factor of 0.06 g Carbon = 1 g wet weight of catches (Walsh, 1981) and on the mean transfer efficiency per trophic level, that is

$$PPR = catches \alpha^{(TL-1)}$$

where $\alpha = TE^{-1}$, and TE is the mean trophic efficiency measured as the proportion of the energy transferred between consecutive trophic levels (TL). PPR is commonly expressed as a percentage of the total primary production (%PP).

Table 3.1. Area, primary productivity and total primary production of southern and southeastern shelf regions of Brazil. Shelf areas were measured to the 200 m depth line using planimetry.

Region	Area $m^2 \cdot 10^{10}$	PP $gC \cdot m^{-2} \cdot year^{-1}$	Total PP $gC \cdot year^{-1} \cdot 10^{12}$
<i>Southeast</i>	17.14	100	17.14
<i>South</i>	11.40	160	18.25

Catch statistics obtained from Haimovici et al. (1997), Haimovici (1998) and from the Instituto de Pesca de Santos, São Paulo, were used in the analysis of PPR for the two shelf regions. FAO catch statistics of reported Brazilian catches were used to compute the mean trophic level of landings in Brazil from 1950 to 1994.

Table 3.2. Trophic level of the main species landed in Brazil. Trophic level estimates are from model in figure 3.2, from diet composition studies (references in table footnote), and/or from other published trophic models (Christensen and Pauly, 1993).

Group	Species	Trophic Level
Shrimps	<i>Farfantepenaeus spp;</i>	2.3
	<i>Xiphopenaeus kroyeri</i>	2.3
Lobsters	<i>Panulirus argus;</i>	2.6
	<i>Panulirus spp</i>	2.6
Small and mid-size pelagics	<i>Sardinella brasiliensis</i> ^a	2.8
	Engraulididae	3.0
	<i>Scomber japonicus</i>	3.1
	<i>Scomberomorus spp</i>	3.3
Common squids	<i>Loligo spp</i>	3.4
Miscellaneous marine fishes ^b	Osteichthyes	3.5
	<i>Micropogonias furnieri</i> ^{c,d}	3.4-3.5
	<i>Umbrina canosai</i> ^e	3.2
	<i>Cynoscion spp</i> ^{c,f}	3.9-4.0
	<i>Macrodon ancylodon</i> ^g	4.3
	<i>Trichiurus lepturus</i> ^h	4.3
	<i>Balistes capriscus</i> ⁱ	3.4
	<i>Pomatomus saltatrix</i> ^j	4.2
	<i>Pinguipes spp</i> ⁱ	3.8
	Ariidae ^k	3.8
Mugilidae ^l	3.8	
Sharks, rays, skates	Elasmobranchs ^l	3.4 -3.8
Groupers	<i>Epinephelus spp</i>	3.7
	<i>Mycteroperca spp</i>	3.7
Snappers	Lutjanidae	3.8
	<i>Ocyurus chrysurus</i>	3.8
Common dolphinfish	<i>Coryphaena hippurus</i>	3.9
Skipjack tuna	<i>Katsuwonus pelamis</i> ^m	3.9
Large pelagic fish ^{n,o,p}	<i>Thunnus spp</i>	3.9
	<i>Xiphias gladius</i>	3.9
	Other Scombroidei	3.9

a. Goitein, 1983, Gasalla & Oliveira, 1997; b. Vazzoler et. al. (in press); c. Gasalla, 1995; d. Vazzoler, 1975; e. Haimovici et al., 1989; f. Vieira, 1990; g. Juras and Yamaguti, 1985; h. Martins and Haimovici, 1997; i. Froese and Pauly, 1998; j. Haimovici and Krug, 1992; k. Araujo, 1984; l. Soares et al., 1992; m. Vilela, 1990; n. Zavalla-Camin, 1982; o. Vaske, 1992; p. Vyalov & Ovchinnikov, 1980.

The ecosystem effects of 'fishing down the food web' for anchovy in the Southern shelf was explored with a simplified mass-balance model (ECOPATH, Christensen and Pauly, 1992) of the trophic interactions in the pelagic ecosystem (Tables 3.3 and 3.4; Fig. 3.2). The model was constructed based on the pelagic species association described by Mello *et al.* (1992) for the winter and spring, and depicts anchovy as the dominant planktivorous fish species, being responsible for most of the transfer of energy from lower trophic levels to higher order consumers (Figure 3.2). The system is defined by the coordinates 32°S - 43°30'S and 51°W - 54°W, with a total area of 28,661 Km².

Table 3.3. Parameters of the trophic model of the pelagic ecosystem off southern Brazil. Underlined values, trophic levels (TL), and omnivory index (OI) were estimated by the model. An omnivory index equals zero indicates the predator feeds on a single trophic level. Cutlassfish, *Trichiurus lepturus*; Hake, *Merluccius hubbsi*, Weakfish, *Cynoscion guatucupa*; Mackerel, *Scomber japonicus*; Jack mackerel, *Trachurus lathami*; Anchovy, *Engraulis anchoita*.

Species/Group	TL	OI	B <i>tons•Km⁻²</i>	P/B <i>year⁻¹</i>	Q/B <i>year⁻¹</i>	EE	Yield <i>tons•Km⁻²• year⁻¹</i>
Cutlassfish	4.25	0.259	0.240 ^a	0.410 ^c	2.050 ^d	<u>0.852</u>	0.015 ^b
Hake	4.11	0.126	<u>0.085</u>	0.355 ^c	1.750 ^d	0.950	0.004 ^b
Sharks	3.94	1.172	<u>0.342</u>	0.400 ^c	4.000 ^e	0.950	0.130 ^b
Other pelagics	4.02	1.080	<u>0.748</u>	0.570 ^e	5.300 ^e	0.950	0.405 ^f
Weakfish	3.59	0.302	2.000 ^g	0.480 ^c	2.340 ^d	<u>0.935</u>	0.306 ^b
Mackerel	3.11	0.000	<u>1.329</u>	0.340 ^e	2.710 ^d	0.950	0.033 ^f
Jack Mackerel	3.11	0.000	0.300 ^h	0.350 ^h	3.000 ^d	<u>0.958</u>	0.054 ^f
Anchovy	3.00	0.111	13.710 ⁱ	1.290 ^j	5.155 ^d	<u>0.240</u>	—
Squids	3.32	0.185	0.200 ^k	1.500 ^e	3.230 ^e	<u>0.894</u>	—
Marine shrimps	2.00	0.000	<u>0.298</u>	3.930 ^l	19.130 ^e	0.950	0.040 ^f
Zooplankton	2.11	0.111	8.000 ^m	64.920 ^m	324.600	<u>0.619</u>	—
Phytoplankton	1.00	0.000	16.700 ⁿ	100.000 ⁿ	—	<u>0.965</u>	—
Detritus	1.00	0.179	150.000 ^o	—	—	<u>1.148</u>	—

a. Martins and Haimovici (1997); b. Haimovici (1998); c. based on Peterson and Wroblewski (1984); d. based on Palomares and Pauly (1989); e. based on other trophic models (Christensen and Pauly, 1993); f. Haimovici et al. (1997); g. IBAMA (1993a); h. Saccardo (1980); i. Lima and Castello (1995); j. Freire (unpubl.); k. Haimovici (1997); l. D'Incao (1991); m. Resgalla Jr. (unpubl.); n. Odebrecht and Garcia (1997); o. according to Pauly et al. (1993).

Table 3.4. Diet matrix of the model of the pelagic ecosystem off southern Brazil. Values represent the proportion of the diet of a predator (column) made of a given prey (row). Some of the groups (mainly sharks, weakfish, and other pelagics) have several feeding habitats such as the outer shelf and benthic habitats. For these groups an *Import* was included as a "prey" in the diet composition.

Prey \ Predator	1	2	3	4	5	6	7	8	9	10	11
1. Cutlassfish ^a	0.140	—	—	—	—	—	—	—	—	—	—
2. Hake ^b	0.020	0.100	—	—	—	—	—	—	—	—	—
3. Sharks ^c	—	—	—	—	—	—	—	—	—	—	—
4. Other pelagics ^d	—	—	—	—	—	—	—	—	—	—	—
5. Weakfish ^{d,e}	0.120	—	0.050	0.050	0.050	—	—	—	0.050	—	—
6. Mackerel ^d	—	—	—	0.100	—	—	—	—	—	—	—
7. Jack Mackerel ^d	0.030	0.030	0.020	—	—	—	—	—	—	—	—
8. Anchovy ^f	0.570	0.800	0.330	0.300	0.450	—	—	—	0.150	—	—
9. Squids ^g	0.050	0.030	0.030	0.050	—	—	—	—	—	—	—
10. Mar. shrimps ^h	0.010	—	0.070	—	0.200	0.010	—	—	—	—	—
11. Zooplankton	0.010	—	—	0.050	0.200	0.990	1.000	0.900	0.800	—	0.100
12. Phytoplankton	—	—	—	—	—	—	—	0.050	—	0.200	0.550
13. Detritus	—	—	—	—	—	—	—	0.050	—	0.800	0.350
Import	0.050	0.040	0.500	0.450	0.100	—	—	—	—	—	—

a. Martins (1992); b. Haimovici et al. (1993); c. Castello et al. (1997); d. Castello (1997); e. Vieira (1990); f. Schwingel and Castello (1995); g. Haimovici (1997); h. based on other trophic models (Christensen and Pauly, 1993).

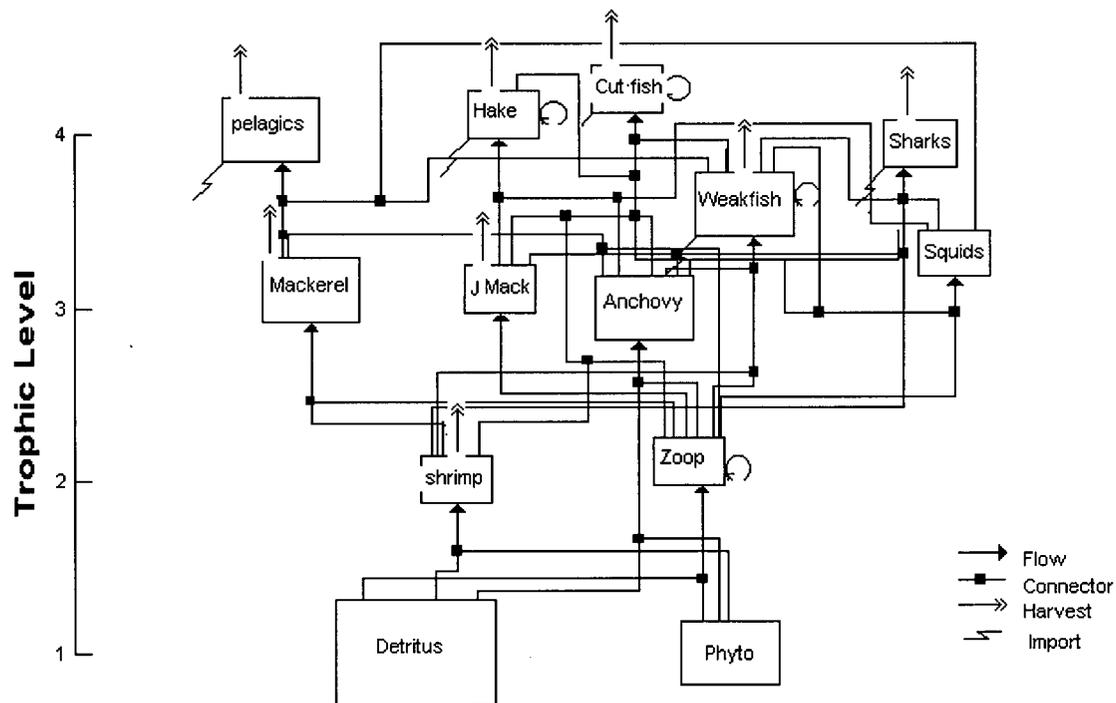


Figure 3.2. Flowchart of trophic relationships in the pelagic association off southern Brazil. It describes the flows between groups (boxes), the biomass of each group (area of boxes proportional to the log of biomass), and the respective trophic levels. Only the consumption flows are shown. For full parameter descriptions see tables 3 and 4.

'Fishing down the food web' was simulated by increasing fishing mortality (F) for anchovy from 0 to 1 year^{-1} , while maintaining F constant for other exploited groups. As some of the high trophic level species (e.g. sharks, weakfish and pelagics) are already fully exploited or overexploited (Haimovici et al., 1997), I considered fishing for anchovy as the most likely continuation of the 'fishing down the food web' effect in this system. Ecosim (Walters et al., 1997) was used to calculate the predicted changes in equilibrium biomasses of species/group and the total catch from the system over the range of F values for anchovy. The model provides biomass predictions of each group in the system as affected directly by fishing and predation, changes in food availability, and indirectly by fishing or predation on other groups in the system (Walters *et al.*, 1997). Simulations were run under two contrasting trophic control hypothesis, bottom-up and top-down, as described in Chapter 2.

3.3. Results

PPR and Trophic Levels

PPR estimates by shelf region and species landed are shown in tables 3.5, 3.6 and 3.7. Fisheries in southern Brazil already use a large proportion of the productive capacity of the shelf ecosystems. In the south, primary production required to sustain catches has changed little from the 1970s to the 1990s, being in the order of 25% of the total primary production. Little change is also observed in the mean trophic level of fisheries in the south which have been targeting mostly high trophic level species (Table 3.5). An increase in catches of tunas and sharks was observed in the southern shelf in the early 1990s accompanying the depletion of important demersal fish stocks, such as *Umbrina canosai*, *Macrodon ancylodon* and catfish species, *Netuma* spp (Table 3.5). However, this alternation of species in the catches did not result in major changes in the PPR and in the mean trophic level of landings between the two periods. Landings in the Southeast are on the other hand dominated by low trophic level species, sardine and marine shrimps being the most important stocks in terms of catch volume (Table 3.6). With the collapse of the Brazilian sardine during the late 1980s and early 1990s, and the increase in tuna and sharks catches, there was an increase in the mean trophic level of fisheries from 2.81 to 2.93. Despite the fact that catches were considerably lower in the latter period, the change in relative importance of the species landed resulted in an increase in PPR from 25.8 to 33.4 % of the total shelf primary production. Although substantially higher fishing yields are obtained in the southeast than in the south, the footprint of fisheries is relatively the same between the two regions as a result of differences in the mean trophic level of landings and the mean trophic efficiency (Table 3.7).

Table 3.5. Trophic level, mean catch and PPR estimates for the southern shelf.

Species	1975 - 1979			1990 - 1994	
	Trophic Level	Catches tons	PPR gC • 10 ¹⁰	Catches tons	PPR gC • 10 ¹⁰
<i>Micropogonias furnieri</i>	3.5	14,308	42.0	14,709	43.2
<i>Umbrina canosai</i>	3.2	16,900	25.7	9,629	14.7
<i>Cynoscion guatacupa</i>	3.9	6,439	65.2	8,785	88.9
<i>Macrodon ancylodon</i>	4.3	7,941	180.4	3,966	90.1
Miscellaneous teleosteans ^a	3.5	4,052	15.9	4,143	13.9
<i>Netuma</i> spp	3.8	3,983	30.5	615	4.7
<i>Trichiurus lepturus</i>	4.3	75	1.8	441	10.8
Demersal sharks ^b	3.8	2,584	17.0	5,931	39.1
<i>Rhinobatus horkelli</i>	3.4	1,010	2.9	460	1.3
Rays and skates	3.6	116	0.5	746	3.1
Marine shrimps	2.3	—	—	1,148	0.2
Small and mid-size pelagics ^c	3.2	1,549	1.4	3,848	5.1
<i>Pomatomus saltatrix</i>	4.2	4,290	88.1	3,521	7.2
<i>Mugil</i> spp	3.8	2,081	14.4	1,524	10.6
<i>Katsuwonus pelamis</i>	3.9	—	—	8,088	70.4
Pelagic sharks	3.7	182	0.9	547	2.9

a. *Pogonias cromis*; *Merluccius hubbsi*; *Paralichthys* spp., *Pagrus pagrus*; *Prionotus punctatus*; *Urophycis brasiliensis* and *Poliprion americanus*. b. mostly *Galeorhinus galeus*; *Mustelus schmitti* and *Squatina* spp. c. *Brevoortia pectinata*; *Scomber japonicus* and *Trachurus lathami*.

Table 3.6. Trophic level, mean catch and PPR estimates for the southeastern shelf.

Species	1977 - 1980			1990 - 1995	
	Trophic Level	Catches (tons)	PPR gC • 10 ¹⁰	Catches (tons)	PPR gC • 10 ¹⁰
<i>Micropogonias furnieri</i>	3.4	7,126	62.6	4,541	39.9
<i>Macrodon ancylodon</i>	3.7	2,053	35.9	1,870	32.7
<i>Cynoscion jamaicensis</i>	4.0	1,921	90.4	2,245	105.6
<i>Balistes capriscus</i>	3.4	—	—	2,144	19.4
<i>Sardinella brasiliensis</i>	2.8	146,520	189.4	54,414	70.3
Rays and skates	3.4	—	—	504	4.6
Marine shrimps	2.3	17,371	5.0	13,997	4.0
Sharks	3.8	517	12.6	2,144	52.2
<i>Katsuwonus pelamis</i>	3.9	1,380	46.7	7,197	243.6

Table 3.7. Summary statistics of the mean catch, mean trophic level (TL), mean transfer efficiency (TE), the primary production required by fisheries catches (PPR), and the percentage of the total primary production appropriated by fisheries (% PP) in the southern and southeastern shelves.

Region	Catch (tons•year ⁻¹)	TL	TE %	PPR gC•year ⁻¹ •10 ¹⁰	%PP
Southern					
1975-1979	65,510	3.63	8	487	26.7
1990-1994	68,101	3.64		471	25.8
Southeastern					
1977-1980	176,888	2.81	5	443	25.8
1990-1995	89,055	2.93		572	33.4

The increasing trend in the mean trophic level of catches observed in the southeastern shelf is also observed in the FAO fisheries statistics for Brazil (Fig. 3.3). Fisheries in Brazil had a

relatively constant mean trophic level of the species landed from 1950 to the early 1980s, but show a recent increase in mean trophic level caused by the combined effect of the collapse of small and mid-size pelagics (mostly sardine), and the increasing landings of large pelagic fishes (tunas and sharks) with the development of offshore fisheries. Another factor that contributes to the increase in the mean trophic level of landings is the steady increase in teleost catches. Teleosts are characterized by high trophic levels (from 3.2 to 4.3, Table 3.2), and represent the most important group in total Brazilian fisheries landings. However, the proper evaluation of the contribution of the group to the average trophic level will require higher resolution in the species catch composition statistics, which currently aggregate a large part of teleosts species into Osteichthys (Table 3.2).

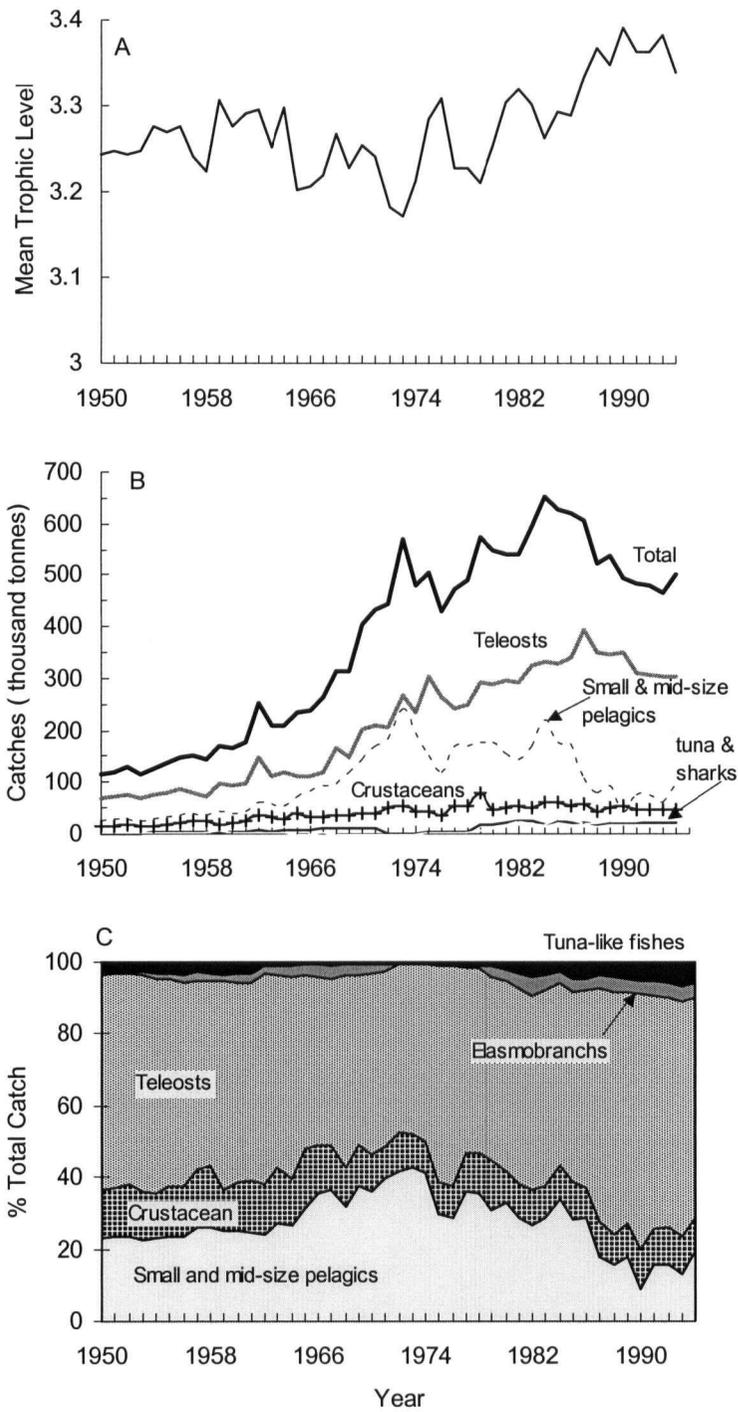


Figure 3.3. Mean trophic level (A), and species composition (B and C) of total Brazilian landings. Source FAO.

Fishing Down the Food Web

A strategy very often proposed to increase catches in exploited ecosystem is to fish down the food web for highly abundant, small pelagic planktivorous fishes after larger species are depleted. Simulation results of a fishing down food web scenario for anchovy in the southern shelf are shown in figures 3.4 and 3.5. Figures 3.4 represents the predicted equilibrium yield and biomass of anchovy, and the percentage change in biomass of all other groups in the system under “top-down” and “bottom-up” control of trophic interactions. The model predicts considerably smaller yields and optimal fishing mortality rates for anchovy under top-down control ($F_{msy, \text{top-down}} \sim 0.1 \text{ year}^{-1}$; $F_{msy, \text{bottom-up}} \sim 0.3 \text{ year}^{-1}$). Both hypotheses generate a similar pattern of decrease in biomass of higher trophic level species, increase in biomass of mid-trophic level groups and increase in zooplankton biomass with increasing F for anchovy. Predictions of biomass changes at the mid-trophic level are more pronounced under top-down control, where the release in predation mortality due to the depressed biomass of top predators leads to a sharp increase of jack mackerel abundance.

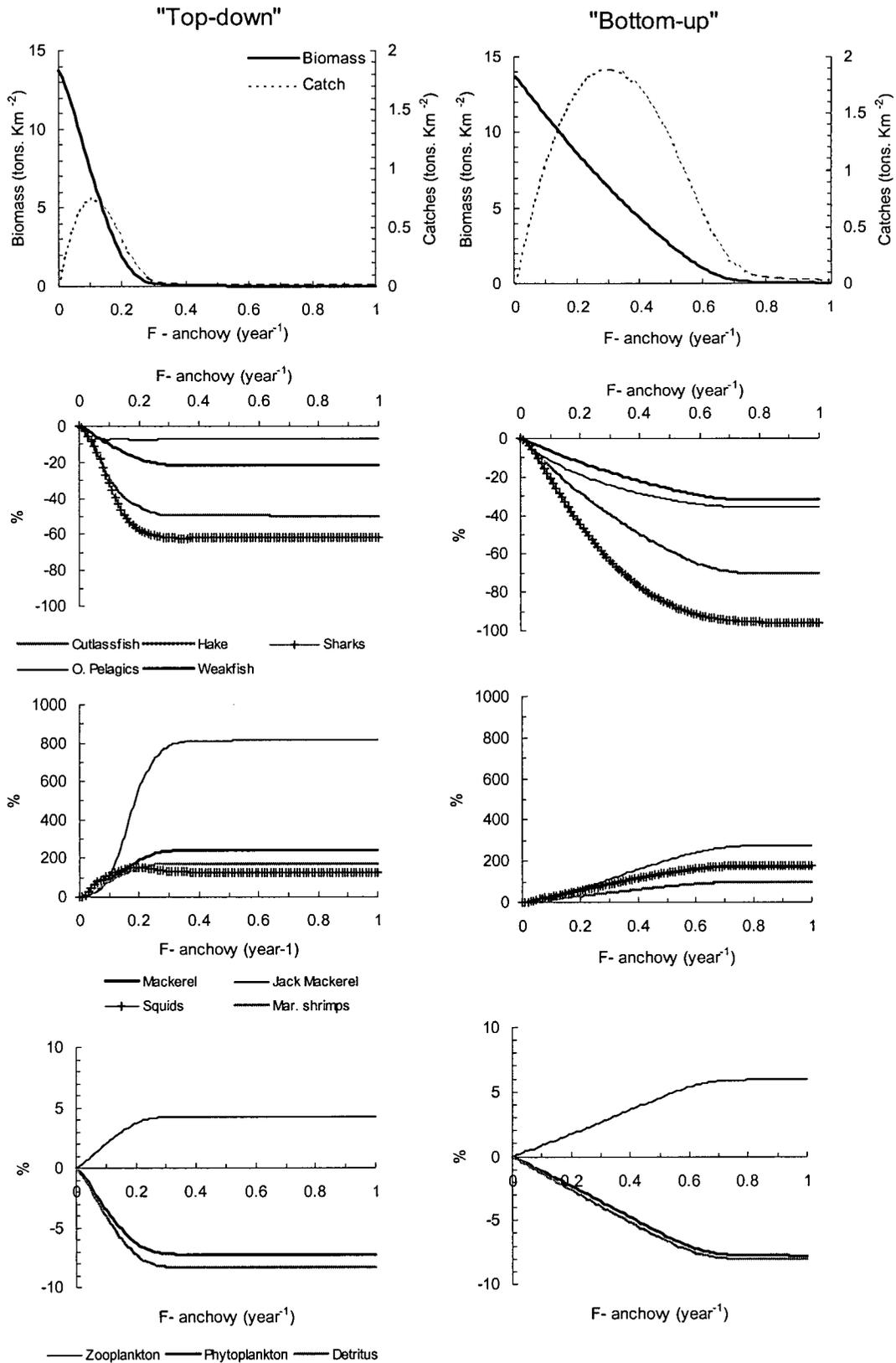


Figure 3.4. Equilibrium simulation of increasing fishing mortality for anchovy. Upper panel represents the predicted equilibrium yield and absolute biomass of anchovy. Lower panels show the predicted relative change in biomass of all other groups in the system.

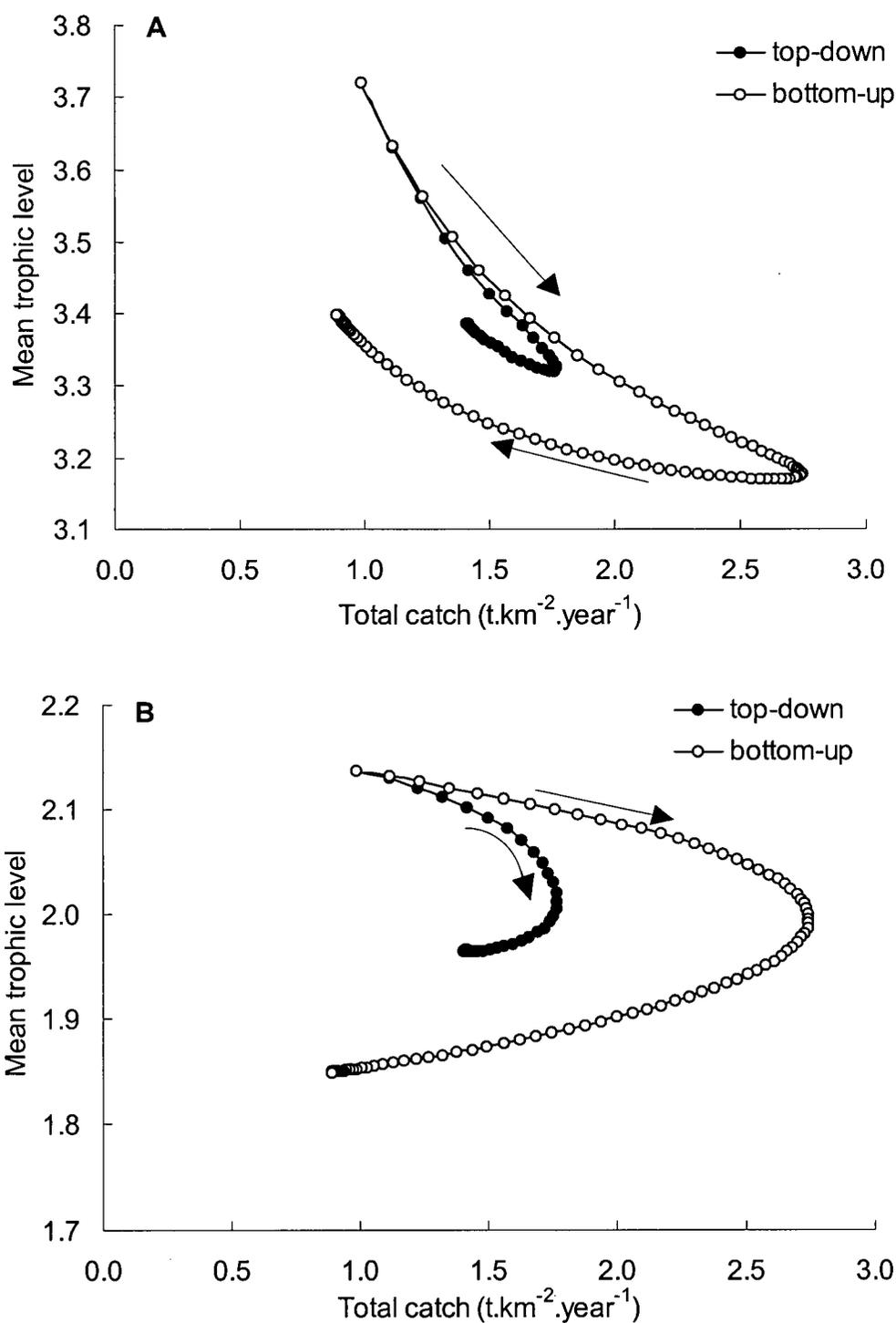


Figure 3.5. Relationship between (A) total catch from the system and the mean trophic level of catches; and (B) total catch and the mean trophic level of the system (detritus excluded) with increasing fishing mortality for anchovy. The arrows indicate the direction of increase in F , and the dots correspond to 0.01 increments in fishing mortality (from 0 to 1 year⁻¹).

Figure 3.5a shows the changes in the total production (catches from all groups) at trophic level with increasing equilibrium fishing mortality for anchovy. Fishing down the food web has the

effect of increasing yield up to a threshold fishing mortality rate for anchovy (F_{msy}) beyond which fisheries production becomes gradually impaired by overfishing and by divergence or complete interruption of major energy pathways to the higher trophic levels. With the overfishing of anchovy, total catches decrease and the mean trophic level of catches increases (less catch of low trophic level species). The backward bending curve between the mean trophic level of catches and total catch suggests that production at trophic level becomes considerably smaller when anchovy is overfished, i.e. the system is unable to capitalize the energy previously available for fisheries and other organisms at the higher trophic levels. The depressed abundance and productivity of top-predators in turn impedes the complete recovery of the mean trophic level of catches, which becomes composed mainly by mid-trophic level groups also targeted by fisheries. Parallel changes occur in the mean trophic level of the system (Fig. 3.5.b). The mean trophic level of the system is smaller than that of fisheries catches (due to the contribution of zooplankton and phytoplankton), and show a progressive decrease with the increase in anchovy exploitation. With “bottom-up” control, total system production at the end of the simulation is smaller than that originally obtained before fishing down the food web. These generic effects are attenuated under “top-down” control when the model predicts that total catch may remain high after anchovy depletion as a result of the sharp increase in abundance of other mid-trophic level species (e.g. jack mackerel, Figure 3.4) also targeted by fisheries.

3.4. Discussion

The primary production required to sustain marine capture fisheries in southern Brazil is estimated to vary between 25 and 33% of the total shelf primary production. Results indicate a level of fisheries impact in this portion of the Brazilian coast comparable to the most intensively exploited temperate shelf ecosystems of the world (Pauly and Christensen, 1995). Our estimates may be conservative considering that discards were not included in the calculations, and that part of the catches may remain unreported in official fisheries statistics (Gasalla and Tomás, 1998). Haimovici et al. (1997), for instance, suggested that discards may represent ca. 25% of total annual catches in the southern shelf. Including discards in our estimates for this region, with the same mean trophic level of the species landed, would increase the expected PPR for the early 1990s from 471 to $666 \times 10^{10} \text{ gC} \cdot \text{year}^{-1}$ and from 25.8 to 36.5% of the total primary production.

The high PPR values in the southern shelf corroborate to the belief that most commercially important estuarine, coastal, and shelf stocks are either fully or overexploited in the region, and landings are expected to decrease with current fishing pressure (Haimovici et al., 1997). The prospect of increasing catches in the region has to come from two non-exclusive strategies: i) by better utilizing or recovering stocks which are currently overfished, such as most demersal stocks (Table 3.5), and/or ii) by “fishing down the food web” for alternative resources not yet utilized, mostly anchovy and jack mackerel (Haimovici et al., 1997).

Fishing down the food web has been shown to increase catches up to some threshold fishing intensity, beyond which fisheries production may become impaired by shifts in major energy pathways in the system (Figure 3.5). Can this type of fisheries-induced change in the ecosystem happen? Fishing down the food web is not an observed phenomenon in Brazil. Instead, fisheries have been targeting high trophic level species, with the exception of sardine in the Southeast, and show a recent increasing trend due to the development of offshore fisheries for high trophic level species such as tunas and pelagic sharks. This increasing trend of mean trophic level of fisheries landings was also obtained by Pauly et al. (1998) for the Southwest Atlantic, and attributed to the development of new fisheries, which, according to the authors tend to mask the fishing down the food web phenomenon. In Brazil, both national (FAO) and regional data indicates that although fisheries expanded into areas/stocks not previously exploited there is no underlying downward trend in the mean trophic level of catches.

Regional experience with intensive fishing for a forage species in southeastern Brazil has apparently shifted a system that once supported a large fishery for sardine into one occupied by an abundant population of anchovy, *Engraulis anchoita*, that is not commercially harvested (Castello et al., 1991). Nonetheless, the extent to which the collapse of sardine fishery and the switch to an anchovy dominated system was due to human or natural factors is still inconclusive (Rossi-Wongtschowski et al., 1996). Many marine ecosystems have shown major ‘regime shifts’ or changes in species compositions and production rates apparently triggered by environmental factors but intensified by the effect of fisheries (Steele, 1996). Among the best documented examples are the sardine/anchovy switches in coastal upwelling systems (Lluch-Belda et al., 1989), the gadoid outbursts in the North Sea (Cushing, 1980; Daan, 1980), and the decline of marine mammals and outburst of pollock in the Bering Sea (Trites et al., 1999). Also, recent global assessment of the trophic level of marine fisheries (Pauly et al., 1998) provide evidence of

the fishing-down-food-web phenomenon and of associated fisheries-induced changes in the food webs similar to that predicted in Figure 3.5.

Model simulations allowed the exploration of the effects of trophic control assumptions on predicting the changes in the food web accompanying the exploitation of anchovy. Under top-down control the system responded with a marked increase in the biomass of a competitor species due to cascade effects up and down the food web. This pattern was less marked under bottom-up control, where competition for food resources limits interactions. These results, also obtained for other systems (see Chapter 2), again differs from the early emphasis placed on food competition as the driving force of species replacement (Cushing, 1980; Daan, 1980), but reinforces the potential role of predation mechanisms and trophic cascade effects in shaping the dynamics of mid-trophic level, forage species. As observed in other trophic models, the predicted F_{msy} for anchovy is very sensitive to the assumed type of control of trophic interactions, being twice as high under bottom-up assumptions. Considering the evidence that F_{msy} for small pelagics is in the order of 0.6 M (Patterson, 1992), model predictions indicate that top-down control can be relatively important in marine pelagic food webs.

Results from this study indicate that fisheries in southern Brazil already appropriate a large proportion of the marine shelf ecosystems carrying capacity. In line with recent stock assessment reports, it is suggested that the prospect of increasing catches and rebuilding stocks must rely on better management of the stocks currently overfished, fishing for offshore resources currently moderately exploited, and/or fishing down the food web for abundant short-lived, planktivorous fishes. It is showed, however, that in an intensively exploited ecosystem the proposal for increasing fisheries production by harvesting at lower levels in the food web has the potential risk of aggravating the depletion of high trophic level species besides altering the structure of the ecosystem, and thus needs to be approached with caution. The adoption of precautionary measures and ecosystem principles in fisheries policy decisions has been, at least theoretically, unanimous in fisheries literature and government agendas worldwide (see FAO Code of Conduct for Responsible Fisheries (FAO, 1995); Oceans Act Canada; GESPE, 1997). One such principles states that “regulation of the use of living resources must be based on understanding the structure and dynamics of the ecosystem of which the resource is a part and must take into account the ecological [...] influences that directly and indirectly affect resource use” (Mangel et al., 1996). If ecosystem principles and precautionary measures are to be

effectively implemented, managers and decision makers have to take the possibility of such ecosystem impacts of fishing down the food web for granted when designing policies for the exploitation of marine resources.

3.5. Summary

The carrying capacity of marine shelf ecosystems in southern Brasil for harvestable species is analyzed by (1) quantifying the amount of available primary production appropriated by fisheries catches, (2) evaluating the trend in the mean trophic level of fisheries, and (3) simulating the ecosystem effects of “fishing down the food web” in an intensively exploited shelf region. Fisheries allocate between 25 an 33% of total primary production in the southern shelf regions of Brazil. Overall, fisheries landings do not display a trend of decreasing trophic level with time, due to the collapse of the sardine fishery and the recent increasing of offshore fishing for higher trophic level species, mainly tunas and sharks. However, the simulations show that fishing down the food web through fisheries that target small pelagic planktivorous fishes, while at first increasing catches in intensively exploited regions, has the potential of actually decreasing yields, by interrupting major energy pathways to exploited, high-trophic level species. This generic effect, corroborated by global assessments of fisheries-induced changes in marine ecosystems, provides support for the design of precautionary measures for future fishing policies.

Chapter 4. The sardine fishery in the Southeastern Brazilian Bight

4.1. Introduction

This chapter reviews the status of fisheries assessment of the Brazilian sardine, and characterizes the sources of uncertainties on ecosystem, population and harvest processes of relevance for current management practice.

Sardine, *Sardinella brasiliensis*, inhabits the coastal bight (Southeastern Brazilian Bight) that extends from Cabo Frio in the north to Cabo de Santa Marta Grande in the south, encompassing the coastal waters of four states, Rio de Janeiro (RJ), São Paulo (SP), Paraná (PR) and Santa Catarina (SC) (Figure 4.1). The main oceanographic characteristic of the region is the seasonal presence of cold, nutrient-rich South Atlantic Central Water (SACW) on the inner shelf, i.e. 10 to 50 m deep (Pires-Vanin and Matsuura, 1993). Being on the western side of the ocean, the large scale boundary current (Brazil Current) flows poleward. Large scale, alongshore wind stress is in the same direction, particularly during austral spring and summer, which favors the upwelling of the SACW into the coastal region. The two major centers of wind induced coastal upwelling are in Cabo Frio and Cabo de Santa Marta Grande (Figure 4.1). Bakun and Parrish (1990) found the spawning strategy of the Brazilian sardine to be like that of the California sardine in the Southern California Bight: sardine spawning occurs mainly during spring and summer, in the enriched environment formed downstream of the upwelling center of Cabo Frio (Bakun and Parrish, 1990). In this period, retention and concentration mechanisms are favored by the coastal configuration which shelters the inshore regions from the strong alongshore winds and, as a result, turbulent mixing is decreased to a minimum within the bight, as is the offshore Ekman transport. An enclosed gyral circulation tends to form inside the Bight interior, which further prevents the advection of eggs and larvae to offshore regions.

The intensity of the upwelling decreases in autumn and it is absent in winter when the water column is more homogeneous. Vertical mixing during this season is controlled by the frequency and intensity of cold fronts which put nutrients back in suspension to be utilized by phytoplankton. Cyclonic vortexes are also observed in the region, originating from the meandering of the Brazil current on the shelf break (Pires-Vanim and Matsuura, 1993). Their

presence is associated with localized (5 to 10 nm) subsurface upwelling of SACW into the euphotic zone and enhanced primary production. Two oceanographic processes are therefore responsible for controlling the productivity of Southeastern Brazilian shelf ecosystem: the penetration of the SACW and the formation of frontal vortices. The first has seasonal frequency but show marked interannual variation in intensity. The vortices, on the other hand, were registered in 3 out of 7 years of observations and seem to lack periodicity.

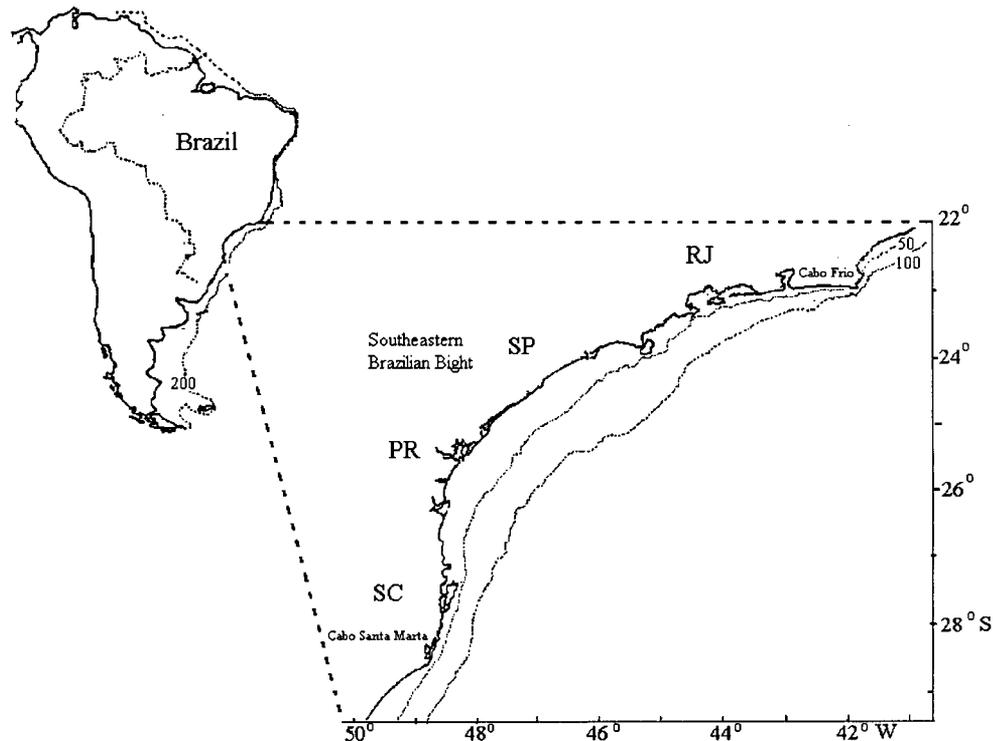


Figure 4.1. Detail of the Southeastern Brazilian Bight, which encompasses the distribution area of sardine, *Sardinella brasiliensis*, and the fishing area of the purse seine fleet. Sardine distribution area includes the coastal region of four states, Rio de Janeiro (RJ), São Paulo (SP), Paraná (PR) and Santa Catarina (SC). Depth in meters.

The seasonal penetration of the SACW in the coastal region has a direct influence on the variability of primary production and on the quantitative and qualitative composition of the pelagic and benthic community (Pires-Vanin et al., 1993). Oceanographic conditions prevalent during summer create conditions for localized new primary production by diatoms. However, nano and picoplankton are characteristically more abundant due to general oligotrophic conditions encountered in the bight. Salps are particularly abundant during summer. Salps consume considerable amounts of phytoplankton and are apparently not important in the diet of higher order consumers (fishes). Their presence and dominance in the pelagic ecosystem during the summer thus represent an alternative trophic flow to the classic phyto-zoo-fish structure normally present in these systems. Pires Vanin et al (1993) also emphasize the role of salps in

exporting organic matter (in the form of fecal pellets) to the benthic community. In the pelagic system the most abundant fish species besides sardine are the anchovy, *Engraulis anchoita*, and the jack mackerel, *Trachurus lathami*.

In the benthos, the organic matter exported from the pelagic and other adjacent systems is processed by a diverse community of bacteria and benthic organisms. Assessment of species diversity in the region indicated the presence of 195 megafauna and 424 macrofauna species in the benthos, and more than 180 demersal fish species (Rocha et al., 1998) which show remarkable variation in dominance as a result of seasonal variability of food sources (Pires-Vanin et al., 1993). Pires Vanin et al. (1993) divide the benthic community into 6 trophic groups, with occurrence and abundance varying seasonally. The groups are suspension feeders, surface detritivores, sub-surface detritivores, carnivorous generalists, carnivorous specialists and omnivorous. In summer the organic matter settled from the pelagic system is mainly utilized by omnivorous suspension feeders and surface detritivores. In winter, turbulent mixing of the bottom associated with the frequent passage of cold fronts is responsible for disrupting the suspension feeders and surface detritivore fauna, and for benefiting the sub-surface detritivores and carnivores.

The demersal fish community has 4 main trophic groups: pelagic feeding fishes (eating mostly fishes and crustaceans); and benthic feeding fishes, which are divided among the species that eat mostly bottom surface invertebrates, sub-surface invertebrates and demersal fishes. The majority of species utilize the surface invertebrates as the main food source. However, during the summer there is an increase in importance of fish species that utilize the pelagic system as major trophic pathway.

The presence of demersal fish stocks and the relatively smooth, sandy-muddy bottom favored the early development of trawling activities in the Southeastern Brazilian Bight. The main demersal stocks exploited in the region are the white croaker *Micropogonias furnieri*, king weakfish *Macrodon ancylodon*, weakfish *Cynoscion jamaicensis*, triggerfish *Balistes capricus* and the marine shrimps *Xiphopenaeus kroyeri*, *Farfantepenaeus brasiliensis* and *F. paulensis*. The presence of large pelagic stocks, mainly sardine, has also influenced the development of an important purse seine fishery as early as 1950. New offshore fisheries for tunas, sharks and rockfishes were developed during the last two decades following the depletion of many

traditional stocks. Tunas and sharks are mainly caught with longlines and pole-and-line, while bottom longlines are employed in the rockfish fisheries (Gasalla and Tomás, 1998).

Sardine fishery development

Until the beginning of the century sardine catches were mainly used for subsistence of coastal communities. This artisanal fishery still exists in most states, catching sardines in bays and estuaries along the coast, using cast nets and seine nets. More recently, a fishery based on small purse seiners targeting juvenile sardines in inshore areas has developed to supply live-bait for bonito pole-and-line fishing boats. However, today, most of the sardine catches come from the industrial fishery based on purse seiners.

The first purse seiners appeared ca. 1910 and gradually diverged from the artisanal and small scale sector (Diegues, 1995), particularly during the 1930's with the introduction of power engines. The first vessels were constructed by Portuguese, Spanish and Italian immigrants using traditional models from their homeland. The nets were originally made of cotton, demanding a great amount of effort for maintenance, but this was substituted by nylon during the 1960s (Diegues, 1995). The present day industrial fishery utilizes rectangular purse seine nets 700 to 900 meters long, 50 to 60 m high and a mesh size of 12 mm (Valentini and Cardoso, 1991). Purse seiners usually fish in areas up to 60 m deep, although sardines may occur in areas up to 100 m deep. The fishery was originally mainly carried out at night, during darker periods of the lunar cycle, approximately 18 days per month. Fishing time was then still determined by a visual search; shoals migrating to the surface waters during dusk excite the phosphorescence of diatoms and allow visualization experienced fishers. Catch volume and handling time made the fishing operation considerably slow (up to 6 hours to complete a set) and determined that landings took place in ports close to the catching areas. In fact that also determined a positive relationship between the areas of sardine concentration and the landing volume in ports along the coast (Valentini and Cardoso, 1991).

During the late 1960's government tax incentives (Código de Pesca, Lei 221, 1967) attracted a considerable amount of resources to the fishing sector which expanded the number of industries for catching and processing fish products for export. Government incentives lasted from 1967 to

1978, and resulted in unprecedented changes in the fishery. Sardine then became the main Brazilian fishery resource in terms of volume, with total annual catches increasing from ca. 38 thousand tons in 1964 to a historical peak of 228 thousands tons in 1973 (Fig. 4.2). The average landings during 1983-1987 period were 124 thousand tons.year⁻¹ and accounted for 31.8 % of the total fish catches in the region and for about 25 % of the national marine catches (IBAMA, 1995).

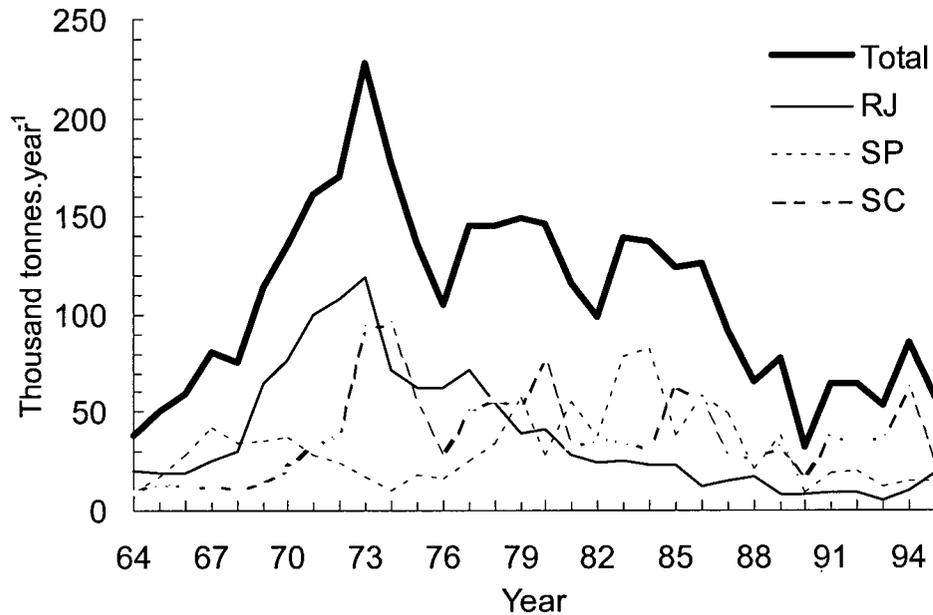


Figure 4.2. Sardine landings by the three main state fleets in Rio de Janeiro (RJ), São Paulo (SP), and Santa Catarina (SC).

Another program of government incentives aimed at the modernization of the fleet lasted from 1983 to 1985. It resulted in an increase in fleet capacity (tonnage) of approximately 300% compared to the 1970's, a doubling of the number of fishing vessels, and the introduction of technological innovations (e.g. sonar and power block) that considerably increased the fishing power of purse seiners (Valentini and Cardoso, 1991). The fishery then experienced a marked decrease in catches, mainly from 1987 to 1990, which culminated with the collapse of the stock and a crisis in the commercial/industrial sector (IBAMA, 1995). With the decline of the stock and the low catches in 1990, the canning industry started relying on imported sardines and some fishing vessels shifted their target to other less productive stocks, mainly Mugillidae, jack mackerel (*Trachurus luttami*), mackerel (*Scomber japonicus*) and bonito (*Katswonus pelamis*). Since the collapse of the fishery there is no indication of stock recovery (R. Habiaga, pers.

comm), although catches in the southern distribution range of the stock have been increasing during recent years (Fig. 4.2). Today, economic recovery is also hampered by the higher price of sardine compared to imported fish, which in turn increases the internal pressure for more government subsidies to the fishing and processing sectors.

The collapse of the fishery was attributed to diverse causes (Valentini and Cardoso, 1991; Castello, 1992, Matsuura et al., 1992), here divided between proximate and ultimate causes following Clark and Munro (1997). Among the proximate causes of collapse are i) the excessive fishing effort exerted by almost 500 boats (licensed and illegal), ii) intense fishing on juvenile fish (length less than 17 cm) all over the area of occurrence of the stock, and iii) alterations in the oceanographic system which resulted in higher mortality of larvae in 1986, decrease in recruitment in 1987, and low stock biomass in 1988. Short-term economic interests, government incentives driven by the same interests, and the lack of compliance with regulations all may have acted together as ultimate causes of collapse.

Overview of Management Context

The management of marine fisheries in Brazil is executed mostly by the federal government, which is responsible for assessing the status of the stocks and for setting and enforcing regulations on the use of marine resources in the Exclusive Economic Zone. Governmental institutional arrangements for regulating fisheries activities has been changing over the years. Until 1989 fisheries were under the agenda of a federal sub-secretary for fisheries development (SUDEPE). From 1989 to 1997, fisheries became one of the agendas of a federal Institute for the Environment and Renewable Resources (IBAMA), subsidiary of the Ministry of Environment. IBAMA was created by the fusion of four federal agencies responsible for issues on environmental protection (SEMA), forestry (IBDF), fisheries (SUDEPE) and rubber production (SUDHEVEA). Recent institutional changes have modified the governmental involvement with fisheries management. The recently established Department of Fisheries and Aquaculture (DFA), a subsidiary of the Ministry of Agriculture, is now responsible for defining the policies and programs to foster the development of fisheries and aquaculture activities in freshwater and marine areas. The specific attributions of DFA in relation to fisheries management are:

- to promote the implementation and assessment of policies and projects that support the development of artisanal, industrial and recreational fisheries;
- to develop studies, procedures and rules for the proper exploitation of fisheries resources;
- to identify and indicate the need for new scientific knowledge necessary for the development of fisheries and aquaculture;
- to define and implement programs that incentive regional and de-centralized forms of management, based on principles of institutional interaction, community participation and cooperation.

In this new arrangement, IBAMA is responsible for the implementation or enforcement of the policies defined by the Department of Fisheries and Aquaculture. Policy execution is ideally carried out in cooperation with regional and municipal agencies of fisheries.

Fisheries assessment research also went through distinct phases over the years (Castello and Haimovici, 1991). The first strategy for assessing fish stocks was implemented in the late 1950's with the establishment of a national system of fisheries statistics and assessment of industrial fishing fleets. A next stage, initiated during the 1970's, aimed at the surveying and assessment of the productive potential of fish stocks along the coast (Neiva and Moura, 1977). During the 1980's a system of expert consultation 'Grupo Permanente de Estudo' (GPE) was established for each of the main fisheries resources, i.e., shrimps, demersal fishes, sardine, lobsters, snappers and tunas. The objective of the GPEs was to provide recommendations for both management and research based on the analysis of biological, technological and socio-economic information on these major resources. However, management recommendations produced in the GPEs were very often ignored or not effectively implemented due to the lack of political decisions, usually restrained by conflicting interests, and lack of enforcement.

Overall, fisheries assessment and management have degraded considerably during the last years as revealed by the status of overexploitation of many resources, the lack of updated information on stocks and fisheries caused by the interruption of statistical sampling programs, and the lack of resources for research and enforcement (Instituto de Pesca, 1993). Since the Earth Summit in 1992, an inter-institutional Fishing Sector Executive Group (GESPE) was created to implement a National Fishing and Fish Farming Policy plan aimed at fostering a better integration among institutions (public and private) for the reorganization of fisheries management in Brazil (GESPE, 1997). The follow up of this plan is still uncertain and beyond the scope of this thesis.

The plan recognizes as ultimate goal of fisheries management to ordinate and foster the sustainable use of fisheries resources, which is defined as the maintenance of the equilibrium of ecosystems and preservation of the species under exploitation; economic profitability of fishing activities; generation of jobs and a fair work compensation (GESPE, 1997).

The current regulatory mechanisms adopted in Brazil to manage fisheries activities include (Castello, 1992): limits on mesh size; limits on size of fish landed; limits on fishing effort by license control; temporal fishing closures; control of the type of gear allowed; and catch limits. The fishery for sardine is mostly regulated by temporal fishing closures and limit on the size of fish caught. Policies adopted from 1976 to 1990 included: i) a three months fishing closure during the spawning period (December to February); ii) minimum size in the catch of 17 cm (size of first maturation), with a tolerance of 15% of catch weight below the minimum size; and iii) limit of the number of fishing licenses. In 1991, with the evidence of stock collapse, policies were reformulated to include another fishing closure during the recruitment period (June to August), to restrict the amount of illegal size fish in the catch to 5% of total weight, and more rigid control of licensing of fishing boats. The recruitment closure was revoked in 1995 given the relative recuperation in the total catch volume to ca. 80 thousand tons in 1994.

Overcapitalization created by repeated government incentives, and the lack of long term planning and enforcement, resulted in an overgrown fishery with a fleet capable of catching more sardines than the most optimistic assessments of stock production. Debate on the legal size of fish caught, and the length of fishing closures permeates the discussions on the current fishing regulatory mechanisms. At the same time evidence of changes in oceanographic conditions in the bight, and associated variations in larval survival and recruitment success, suggest a volatile fishery prone to periodic "boom and bust" cycles. Further, the marked increase in anchovy biomass during the decline of sardine stock awakens concerns on the impact of sardine fishery on the ecosystem of the Southeastern Brazilian Bight, and on the ability of the stock to recover given a possible shift in the ecosystem (Castello et al., 1991). In this scenario, fisheries management requires ecological information to predict the effects of fishing on the short and long term ecological sustainability of the system. Ecological information would, in principle, provide the basis for discussing the following management questions:

- I. in the long term, what type of regulatory mechanism would be more appropriate for managing the fishery, and what is the expected outcome (catches, chances of collapse, etc.) under different levels of exploitation?
- II. in the short term, what type of strategies would be required to foster the rehabilitation of the stock?

The fishery is also the target of scientific questions which aim to understand the causes of recruitment fluctuations and ecosystem changes, such as:

- I. are fluctuations in sardine catches related to global-scale climate changes (Rossi-Wongtschowski et al., 1996)?
- II. what are the biological-oceanographic factors responsible for the success or failure in sardine spawning and recruitment (Saccardo and Rossi-Wongtschowski, 1991; IBAMA, 1995)
- III. can the apparent shift between sardine and anchovy result from fishing-induced changes in the ecosystem (Castello et al., 1991)?

Scientific recommendations produced by the GPE/Sardine during the early 90's (IBAMA, 1991; 1992; 1993b; 1994d) pointed to a list of ecological research activities to be explicitly undertaken in order to acquire new knowledge for managing the fishery.

Research priorities included:

- to obtain independent estimates of stock size using either acoustic surveys or egg production methods;
- to continue the collection of fisheries data and biological sampling of the catches along the coast;
- to update the information on licenses and boats currently fishing;
- to monitor oceanographic conditions through surveys and remote sensing;
- to analyze temporal oceanographic anomalies off the coast.

Research priorities are mainly aimed at increasing the descriptive knowledge about the status of the stock and fishery and improving the understanding of the oceanography of the Southeastern Brazilian Bight. Few attempts have been made to design research programs to improve the functional knowledge of processes affecting the fishery, and to evaluate how the understanding

of these processes would improve the management practice for sardine. Among the processes scientists are uncertain about, those controlling biological production and those directly influencing harvest control deserve a closer attention in order to improve the quality of harvest decisions.

Studies on *Sardinella brasiliensis* carried since 1950 provided substantial information on the reproductive biology of the species, early life history, estimation of population parameters and stock assessment (Saccardo and Rossi-Wongtschowski, 1991; IBAMA, 1995). But monitoring of stock biomass during the last decades has been quite erratic. The lack of updated information on the stock and the confounding effect of environmental signs and overfishing complicates the understanding of critical processes for management. This chapter reviews the status of sardine stock assessment and characterize the sources of uncertainties on ecosystem, population and harvesting processes of relevance for current management practice.

4.2. Methods

The analysis is divided in three sections. The first describes the structure and dynamics of the Southeastern shelf ecosystem and analyzes the changes that followed the collapse of the sardine fishery. The second section analyzes the observed changes in the sardine population with data on stock and recruitment. Finally, the third section analyzes how the catchability coefficient has changed with time and stock size, and what the likely consequences are for harvest control.

Ecosystem structure and dynamics

The Southeastern Brazilian Bight encompasses an area of distinct environmental characteristics and types of activities, and defines an appropriate unit for ecosystem management purposes (Matsuura, 1995). In this section, the analysis of the structure and dynamics of the Southeastern Brazilian shelf ecosystem is based on a trophic mass-balance model adapted from Rocha et al. (1998). Rocha et al. (1998) constructed a trophic model (Ecopath) of the Ubatuba shelf ecosystem, in the Southeastern Brazilian Bight, which describes the structure of the system at summer conditions during the late 1980s. The model was built with ten functional groups representing organisms with a similar role in the food web, plus detritus (Box 4.1). This model

was adapted as follows to reflect annual conditions in the Bight, to represent in detail the main harvested species in the system and, as modified, has 22 boxes.

- 1) Primary production, biomasses, P/B ratios and catches of all groups in the system were adjusted to a one year period. Annual primary productivity in the Southeastern Bight was obtained from Brandini (1990). Biomass of plankton and benthic organisms were adjusted according to their seasonal abundance described in Pires-Vanin (1993). Catches of fish and shellfish groups were adjusted to one year according to data from the Instituto de Pesca, Santos (see table 3.6, Chapter 3).

- 2) The box *Small pelagic fish* in Rocha et al. (1998) was split among *Sardine*, *Anchovy*, and *Other forage fish*. The latter represents small and middle-sized pelagic species such as *Opisthonema oglinum*, *Harengula clupeiola*, *Brevoortia spp*, *Trachurus spp*, and *Chloroscombrus chrysurys*. Biomass and P/B data for sardine was obtained from VPA (section 2) and from Cergole (1995). Sardine was split between adult and juvenile pools to explore the effect of harvest on recruitment rates in the dynamic simulations (parameter details on Table 4.1). Anchovy biomass is from direct acoustic assessments (Castello et al., 1991), and production estimate is from the southernmost stock and anchovy in Brazil (K. Freire, unpublished). Sardine and anchovy diets were obtained from Goiten (1983) and Schwingel (1996), respectively. Biomass of *Other forage fish* was considered the difference between the biomass of *Small pelagic fish* in Rocha et al. (1998), and the sum of *Sardine* and *Anchovy* biomasses.

- 3) The box *Benthic feeding fish* in Rocha et al. (1998) was split among individual demersal stocks of white croaker, *Micropogonias furnieri*, king weakfish, *Macrodon ancylodon*, triggerfish, *Balistes capriscus*, Rays/Skates, and other *Benthic feeding fish*. Parameters P/B and Q/B for the demersal stocks were obtained from data on growth and mortality in *FishBase* (Froese and Pauly, 1998). Diets were obtained from Juras and Yamaguti (1985), Gasalla (1995), Soares et al. (1992) and *FishBase*. Triggerfish was split between adult and juvenile pools to represent differences in feeding habits and distribution of the species during its life cycle; while adults are mostly demersal and benthic feeders, juveniles are pelagic zooplanktivores (Zavala-Camin and Lemos, 1997; FishBase, 1998). Parameters P/B and Q/B for juvenile triggerfish were assumed similar to the fast growing species in the model (i.e. small forage fish). Ecotrophic efficiencies were considered 0.9 for all individual pools for which

biomass data was not available. This assumption, which implies that 90% of the production is either consumed or exported (harvested) from the system, can be expected for groups that have abundant consumers or are fully exploited. Biomass of the box *Benthic feeding fish* was considered the difference between the sum of estimated biomasses of all demersal pools, and the biomass of the original *Benthic feeding fish* group in Rocha et al. (1998).

4) The box *Pelagic feeding fish* in Rocha et al. (1998) was split between weakfish, *Cynoscion spp.*, and other Pelagic feeding fish. To represent the trophic ontogeny reported for weakfish stocks (Haimovici, 1997), the group was split between *Adult* and *Juvenile weakfish*. Parameters (P/B and Q/B) for Adult weakfish were calculated from growth and mortality data in *FishBase* (Froese and Pauly, 1998). Juvenile weakfish P/B and Q/B rates were considered the same estimated for small forage fish. Diets for adult and juvenile weakfish were obtained from Gasalla (1996) and Haimovici (1997), respectively. Ecotrophic efficiencies of both groups were assumed 0.9. Biomass of the box *Pelagic feeding fish* was considered the difference between the sum of estimated biomasses of Adult and Juvenile weakfish, and the biomass of the original pelagic feeding fish group in Rocha et al. (1998).

5) A box representing bonito, *Katsuwonus pelamis*, was added to the model. Bonito diet is from Vilela (1990), biomass estimates from Jablonski and Matsuura (1985), and parameters Q/B and P/B derived from growth and mortality estimates for the species in FishBase (1998).

6) The box *Omnivorous benthos* in Rocha et al. (1998) was split between marine shrimps and other Omnivorous benthos. Marine shrimps include stocks of *Farfantepenaeus brasiliensis*, *F. paulensis*, and *Xiphopenaeus kroyeri*. Parameters P/B and Q/B of Penaeid shrimps were obtained from growth and mortality estimates on D’Incao (1991). Ecotrophic Efficiency was considered 0.9. Biomass of the box *Omnivorous benthos* was considered the difference between the estimated biomass of *Marine shrimps*, and the biomass of the original *Omnivorous benthos* group in Rocha et al. (1998).

7) Finally, harvest information was aggregated in three fishing fleet types according to Gasalla and Tomas (1998): *Purse seiners*, catching mostly sardine; *Bottom trawl*, catching weakfish, Rays/Skates, white croaker, king weakfish and triggerfish; *Shrimp trawl*, catching marine shrimps; and *Pole-and-line* catching bonito.

Box 4.1. Ecopath models of the southeastern Brazil shelf ecosystem.

Trophic groups identified by Rocha et al. (1998) for the model of the Ubatuba shelf ecosystem, southeastern Brazil.	Trophic groups in the model of the southeastern Brazil shelf ecosystem adapted from Rocha et al. (1998).
<ol style="list-style-type: none"> 1. Phytoplankton: composed by phytoflagellates and diatoms 2. Zooplankton: small calanoid copepods 3. Salps: mainly <i>Thalia democratica</i> 4. Bacterioplankton: dominated by free bacteria feeding on detritus 5. Omnivorous benthos: Penaeid shrimps, chitons and echinoids 6. Carnivorous benthos: Crabs, asteroids, polychaetes and some gastropods 7. Detritivorous benthos: Polychaetes, gastropods, bivalves, ophiuroids, cumaceans, amphipods and tunicates 8. Benthic feeding fish: Sciaenidae, Rajidae, Serranidae, Triglidae, Batrachoididae, Haemulidae, Paralichthyidae, Gerreidae, Bothidae, Lophiidae, Rhinobatidae, Sparidae and Mullidae. 9. Pelagic feeding fish: <i>Cynoscion guatucupa</i>, <i>C. jamaicensis</i> and <i>Merluccius hubsii</i> 10. Small pelagic fish: Sardine, <i>Sardinella brasiliensis</i>, and Anchovy, <i>Engraulis anchoita</i> 11. Detritus. 	<ol style="list-style-type: none"> 1. Phytoplankton 2. Zooplankton 3. Salps 4. Omnivorous benthos 5. Marine shrimps 6. Carnivorous benthos 7. Detritivorous benthos 8. Other Benthic feeding fish 9. King weakfish 10. Croaker 11. Rays/Skates 12. Triggerfish 13. Juvenile triggerfish 14. Other forage fish 15. Anchovy 16. Adult sardine 17. Juvenile sardine 18. Other pelagic feeding fish 19. Adult weakfish 20. Juvenile weakfish 21. Bonito 22. Detritus

Parameter adjustments had to be made in order to balance the model, i.e., to make estimates of biomass and fluxes among groups consistent with biological and ecological constraints. In particular, two groups showed Ecotrophic Efficiencies (EE) larger than 1 after the first iteration: *Benthos Detritivores*, and the *Detritus* box. To balance the model biomass of *Benthos Detritivores* was increased by 50%. The final biomass (30 tonnes.Km⁻²) is lower than the value of 40.3 tonnes.Km⁻² used in the summer model (Rocha et al., 1998), and it is consistent with the lower abundance of benthos detritivores observed in the other seasons (Pires-Vanin, 1993). The major problem in making the rate of detritus accumulation balance detritus consumption in the system was due to the large consumption rates of bacteria. Christensen and Pauly (1996) warned of the difficulties in representing flows associated with bacteria in Ecopath, which tend to completely overshadow the other flows in the system. One option suggested by the authors, and adopted here, was to exclude bacteria from the model since in the present analysis no special emphasis needed to be given to the microbial food web (i.e., the microbial food web is considered as an adjacent ecosystem (Christensen and Pauly, 1996)). The importance of bacteria in the diet of organisms in the system was then transferred to detritus. Finally, to make the Ecotrophic Efficiency of *Detritus* less than 1, the importance of detritus in the diet of *Marine*

shrimps, *Benthos omnivores* and *Benthos detritivores* was lowered and compensated by a proportional increase in the importance of other prey in the diet of these groups. Also, the gross efficiency of *Benthos detritivores* was also increased from 0.09 to 0.11.

Model and catch data were used to reevaluate the total flux of energy, originated from primary producers, available to different trophic levels in the food web, and the total primary production required to sustain fisheries catches in two time periods: from 1977 to 1980, before the overfishing of sardine and other demersal stocks; and from 1990 to 1995, after the sardine stock collapse.

The trophic model was also used to examine hypotheses about the dynamic responses of the system to changes in fishing rates. For this purpose, simulations were carried with Ecosim (Walters et al., 1997) following methodology described in detail in chapter 2. Recent improvements in Ecosim (Walters et al., in press) allow for a more realistic representation of linkages between split pool pairs (juvenile and adult stages), through flow of biomass and numbers of individuals, using a delay difference model for each split pool case in Ecopath. Parameterization of the delay difference model is carried by the user entering information on growth, age and weight at transition from juvenile to adult stage (see table 4.1 for some examples). Ecosystem linkages such as changes in predation and consumption rates by juvenile and adult pools can therefore be captured in a age-structured population dynamics model embedded in the trophic model.

Table 4.1. Parameters of the split pools in Ecopath used by the delay difference model in Ecosim. K is the von Bertalanffy growth parameter (year^{-1}), w_k is the weight (g) at the age t_k (years) fish graduate to the adult pool. Parameters for sardine were obtained from Cergole (1995). Parameter values for weakfish and triggerfish are from FishBase (1998).

Split pool	K	w_k	t_k
Weakfish	0.3	100	2.0
Triggerfish	0.5	128	1.0
Sardine	0.5	44	1.5

The model also allows for explicit representation of hypotheses about changes in growth rates, foraging time and time at risk to predation with increasing (decreasing) feeding opportunity. These assumptions are critical to the form of implied 'stock-recruitment' relationship generated for each split species by the model. Much of the dynamics of trophic interactions in a aquatic system has been shown to depend on how time spent feeding varies with foraging opportunities

in limited spatial refuges from predation (Walters and Juanes, 1993; Walters and Korman, 1999); foraging time by an individual fish must balance growth and predation risk in order to increase the chances of survival. That is particularly true during the early life stages most vulnerable to predation. The Ecosim interface allows for the input of constraints on time spent feeding by any group in the system by asking the user to enter the maximum relative increase in time spent foraging when food intake is low (F^{\max}). Time spent foraging influence both the rate of effective search (a_{ij}) and the time spent vulnerable to predation (v_{ij}) from equation 3, Chapter 2 (see details also in Walters et al., in press). In summary, setting high F^{\max} allow for ample change in time foraging so as to compensate any decrease in food availability and consumption (relative to the baseline consumption estimated by Ecopath). Low F^{\max} constrains the rates of effective search and represents the hypothesis that individuals already spend most of their time foraging (Walters et al., in press).

Spawning Stock and Recruitment

In this section, data from sardine stock assessment is used to describe changes in stock biomass and recruitment. Cergole (1995) used a Virtual Population Analysis (VPA) to reconstruct the population abundance of sardine from catch at age data obtained from 1977 to 1990 (Table 4.2). In this part of the analysis direct biomass estimates from acoustic surveys and egg abundance data are used to 'tune' the VPA previously done by Cergole (1995). Model tuning aims to obtain biomass and natural mortality estimates that are consistent with independent indexes of stock abundance.

Table 4.2. Catch (millions of fish) at age data used in the reconstruction of sardine population abundance with VPA (source Cergole, 1995). B_t stands for survey biomass estimates (tons). Eggs represent sardine egg density (mean number of eggs $\cdot m^{-2}$), considered as an index of spawning stock biomass.

Age	1977	1978	1979	1980	1981	1982	1983	1984	1985	1986	1987	1988	1989	1990
0	1128	1	3376	13478	4213	8738	313	568	1	6	21	0	0	0
0.5	1833	2852	6038	3478	4215	7055	5809	820	846	23	407	0	0	0
1	402118	164566	354700	976780	424802	492432	294253	208697	186006	293338	316145	155400	331937	120548
1.5	559070	599465	491212	1021383	744115	869070	1208221	679130	773750	702224	585065	325813	289694	146473
2	829722	977036	1059383	655215	711816	457199	793925	670381	611004	867987	535453	498911	756411	204722
2.5	585457	600130	506812	566758	306476	300217	487702	583035	551344	513391	385174	260897	214554	157672
3	65150	101541	79080	26277	32075	17411	19126	101428	135006	233370	108346	49292	54542	14530
3.5	18502	20322	8699	839	1691	468	3217	24377	12053	4994	4351	416	928	1336
B_t	388000													77000
Eggs	11	25	10	10	295									3

To simplify the calculations it was assumed that the fishery takes place in a relatively short period of time during which the population is subjected only to fishing mortality. The basic reconstruction equation for any cohort in a discrete fishery is (Hilborn and Walters, 1992):

$$N_{a,t} = \frac{N_{a+1,t+1}}{s} + C_{a,t}$$

where $N_{a,t}$ accounts for the number of fish of age a alive at time t , s is the annual survival rate ($= e^{-M}$), M is the natural mortality rate, and $C_{a,t}$ is the observed catch of age a fish at time t . It was also assumed that no fish are left alive after age 3.5. Fishing mortality is expressed in terms of age-time specific exploitation rates $u_{a,t} = \frac{C_{a,t}}{N_{a,t}}$, which represent the fraction of individuals captured during the fishery. To initialize the backward recursion calculations, terminal exploitation rates were assigned for the last age in all years according to the procedure in Box 4.2.

Box 4.2. Virtual Population Analysis procedure for reconstruct sardine biomass at age (Walters and Punt, 1994).

1. set $u_{a,T}$ (the exploitation rate for the fully vulnerable ages in the last year T of data) equal uT ;
2. calculate the fully vulnerable harvest rate (u_t) in each year (1 to $T-1$) as the average exploitation rate of the ages 2 and 3 (considered fully vulnerable to the fishery);
3. set $N_{3.5,t} = C_{3.5,t}/u_t$ for all $t < T$;
4. for ages not completely vulnerable in the last year T , calculate $N_{a,T} = C_{a,T}/(v_{a,T}u_T)$, where $v_{a,T}$ are the terminal relative vulnerabilities. Relative vulnerabilities at age for the last year of data were estimated as the average vulnerabilities calculated for early years in the assessment.

Finally, the probability distribution for each possible terminal exploitation rate (uT) and natural mortality rate (M) were obtained by tuning the VPA with biomass acoustic assessments and indexes of egg density, considered proportional to the spawning stock biomass (Table 4.2). Sardine biomass in 1977 (388,000 tons) was considered the average estimation of acoustic surveys carried out between 1974 and 1980 (Johannesson, 1975; Rijavec and Amaral, 1977; Saccardo, 1983). The 1988 biomass (77,000 tons) refers to the upper limit of the acoustic estimation obtained by Castello et al. (1991). Monitoring of sardine spawning in the Southeastern Brazilian Bight (Matsuura, 1995) provided measures of spawning intensity (eggs.m⁻²), that were used as relative indexes of spawning stock biomass.

Bayes posterior probability distributions were assigned to each parameter combination:

$$p(u_{Ti}, M_j / D) = \frac{L(D / u_{Ti}, M_j) P(u_{Ti}, M_j)}{\sum_i \sum_j L(D / u_{Ti}, M_j) P(u_{Ti}, M_j)}$$

where $p(u_{Ti}, M_j / D)$ is the posterior probability of terminal fishing mortality and natural mortality rates given the abundance time series data (D), $L(D / u_{Ti}, M_j)$ is the likelihood of the data given that parameter combination is true, and $P(u_{Ti}, M_j)$ is the prior probability of the parameters. Uniform prior probability distribution were assigned to u_T ($U(0,1)$) and M ($U(0.95,1.36)$). Pauly's (1980) empirical equation was used to compute the range of natural mortality values expected for the Brazilian sardine, based on growth parameters and water temperature values suggested by Cergole (1995), and on a correction factor of 0.8 suggested by Pauly (1980) for schooling fishes.

The likelihood for the relative spawning stock biomass index (y_t) with log-normal error ($y_t = q SSB_t e^{\epsilon}$) was calculated according to Walters and Ludwig (1994) and Walters and Punt (1994)

$$L(y_t / u_T, M) = SS^{-\frac{(n-1)}{2}}$$

where $SS = \sum_t (Z_t - \bar{Z})^2$, $Z_t = \log\left(\frac{y_t}{SSB_t}\right)$ and SSB_t is the spawning stock biomass in year t from VPA. Sardine biomass assessments from acoustic surveys were considered direct measurements of absolute biomass of adult fish (age 1+) with normal error. The likelihood for survey biomass (B_t) was calculated as

$$L(B_t / u_T, M) = e^{-\frac{(\hat{B}_t - B_t)^2}{2\sigma^2}}$$

where \hat{B}_t is the adult stock biomass from VPA and σ^2 is the variance of the observation uncertainty. The total likelihood of parameters u_T and M was obtained by combining the two likelihood functions, that is

$$L(D / u_T, M) = L(y / u_T, M) \cdot L(B / u_T, M)$$

Stock distribution, effort dynamics and catchability change

The reconstructed time series of population abundance also provides information useful for the analysis of biases on fishery-dependent index of abundance (cpue), and for the evaluation of stock catchability changes with time, temperature, stock size and distribution. Stock catchability (q) was computed based on the relationship between fishing effort (f) and the effective fishing mortality rate (F) from VPA, i.e. $F=q \cdot f$. Effort data was obtained from log-book information from 1977 to 1983 in the three main state fleets (Rio de Janeiro, São Paulo and Santa Catarina).

Information on fleet characteristics, effort allocation and stock distribution were used to analyze the observed changes in stock catchability. Effort allocation data was used to test the hypothesis that purse seiners allocate effort spatially according to an Ideal Free Distribution (Hilborn, 1985; Gillis et al., 1993). The Ideal Free Distribution predicts that the foraging benefits in an area will be proportional to the availability of resources divided by the number of foragers in the same area. If an individual is free to move so as to maximize its own benefits, the result is an equilibrium effort distribution where foragers (vessels) in different areas have the same profit rate (cpue). The test for the Ideal Free Distribution is therefore used as an indicator of the efficiency of purse seiners in allocating effort spatially across the stock distribution area. Following Gillis et al. (1993), we tested for the equalization of cpue among fishing areas in the southern part of Bight (Fig. 4.3) using effort allocation data from the Santa Catarina purse seine fleet. The proportion of the total sardine catch in each area within each month is regressed against the proportion of the total effort in the same area during the same month. If effort is allocated so that cpue is equalized among areas, then

$$\frac{C_i}{f_i} = \frac{\sum_i C_i}{\sum_i f_i} = cpue$$

where C_i and f_i are the catch and effort in area i , and cpue is the value equalized among all areas in the month considered. In this analysis cpue is expressed as tons of fish catch per time searching. By rearranging the equation above, we have

$$\frac{f_i}{\sum_i f_i} = \frac{C_i}{\sum_i C_i}$$

which is a linear regression with intercept 0 and slope 1. If the Ideal Free Distribution applies to the data, all points should fall along a line of slope 1, regardless of the monthly cpue value.

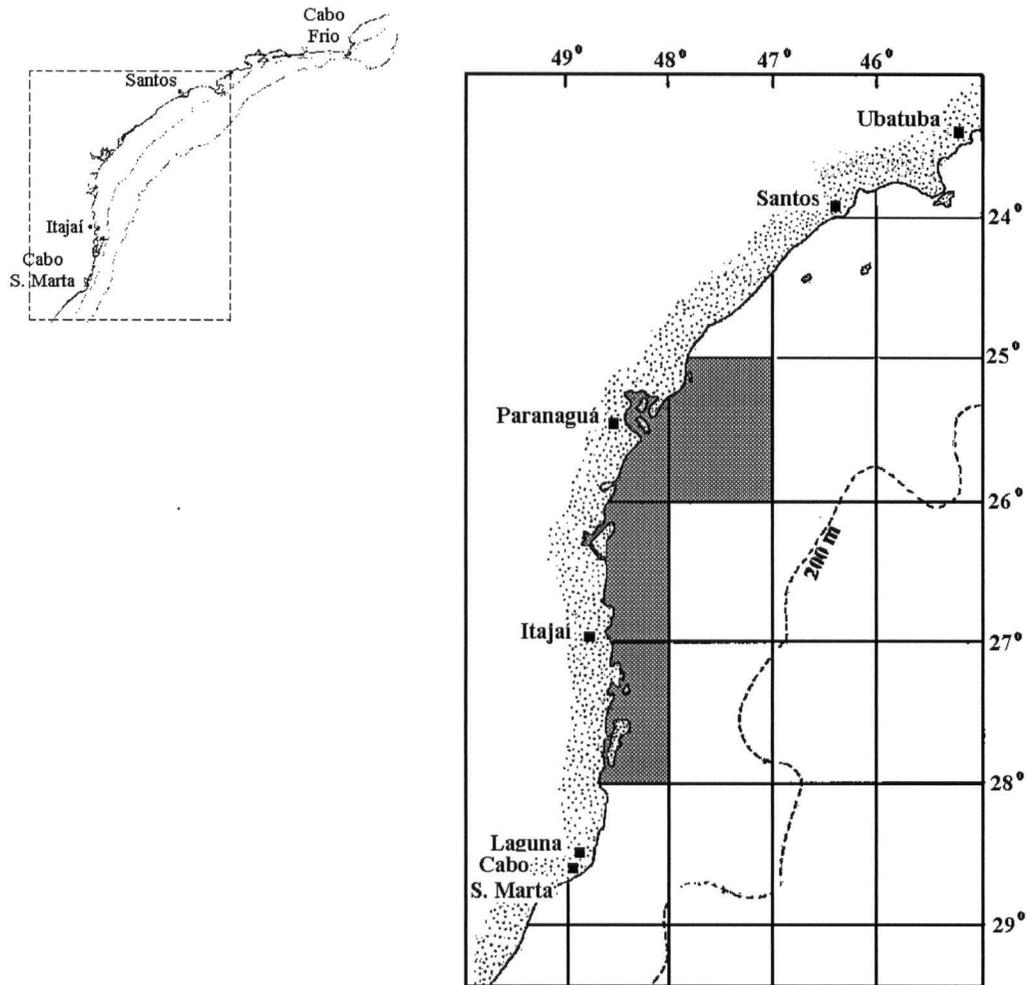


Figure 4.3. Fishing areas (shaded) of the Santa Catarina fleet used in the analysis of effort allocation.

4.3. Results and Discussion

Ecosystem structure and dynamics

Figure 4.4 shows the flow diagram representing the major components and trophic flows in the Southeastern shelf ecosystem. Model parameters are shown in tables 4.3 and 4.4. The model depicts phytoplankton and detritus at trophic level 1, as primary producers, planktonic and benthic consumers at trophic level 2, small pelagics, juvenile stages of weakfish and triggerfish, and benthos carnivores at intermediate trophic levels, and all demersal and pelagic feeding fish groups at the top of the food web.

Table 4.3. Parameters of the Ecopath trophic model of the Southeastern shelf ecosystem. Underlined values, trophic levels and omnivory index were estimated by the model.

Species/Group	Trophic level	Omnivory index	Biomass tons• Km ²	P/B year ⁻¹	Q/B year ⁻¹	EE	Catches tons• Km ² • year ⁻¹
Phytoplankton	1.0	0.000	24.00	70.00	-	<u>0.93</u>	—
Detritus	1.0	0.190	10.00	-	-	<u>0.90</u>	—
Salps	2.0	0.000	20.00	5.40	18.00	<u>0.00</u>	—
Zooplankton	2.1	0.053	4.12	60.00	288.00	<u>0.84</u>	—
Benthos omniv.	2.1	0.003	13.14	0.40	2.84	<u>0.55</u>	—
Marine shrimps	2.1	0.003	<u>0.31</u>	3.93	18.00	0.95	0.081
Benthos detrit.	2.3	0.169	30.00	3.00	27.27	<u>0.88</u>	—
Anchovy	2.8	0.233	2.33	1.29	11.20	<u>0.16</u>	—
Benthos carniv.	2.9	0.374	35.00	0.96	3.28	<u>0.30</u>	—
Sardine	2.9	0.177	0.63	1.92	11.20	<u>0.47</u>	0.317
Juvenile sardine	2.8	0.177	0.27	7.00	23.33	<u>0.25</u>	—
Other forage fish	2.9	0.177	5.00	1.29	11.20	<u>0.07</u>	—
Juv. Weakfish	3.1	0.001	<u>0.12</u>	2.00	10.00	0.90	—
Juv. Triggerfish	3.2	0.019	<u>0.02</u>	2.00	10.00	0.90	—
Croaker	3.4	0.246	<u>0.32</u>	0.40	3.88	0.90	0.027
Rays/Skates	3.5	0.162	<u>0.01</u>	0.40	4.00	0.90	0.003
Triggerfish	3.5	0.098	<u>0.10</u>	0.90	6.13	0.90	0.013
Other Bent. fish	3.5	0.163	0.29	0.92	5.20	<u>0.52</u>	—
Other Pel. fish	3.7	0.114	0.34	0.48	5.60	<u>0.85</u>	—
Bonito	3.7	0.053	0.41	0.98	4.51	<u>0.10</u>	0.040
King Weakfish	3.8	0.445	<u>0.12</u>	0.90	6.16	0.90	0.011
Adult Weakfish	3.9	0.102	<u>0.02</u>	0.90	6.70	0.90	0.013

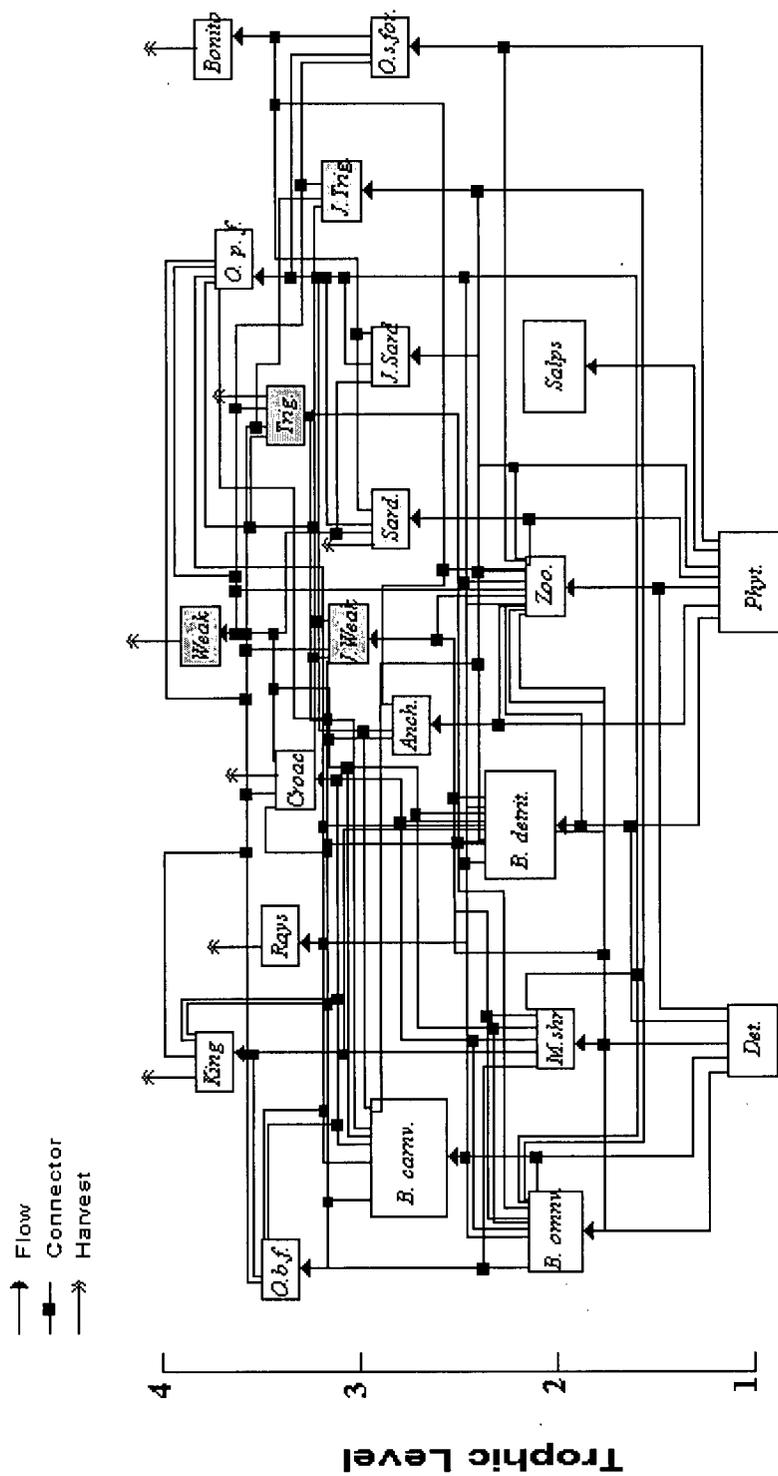


Figure 4.4. Trophic flows diagram of the Southeastern Brazilian shelf ecosystem. Only consumption and harvest flows are shown. Box area is proportional to the biomass. Groups defined as Phytoplankton (Phyt.); Detritus (Det.); Salps; Benthos omnivores (B. omniv.); Zooplankton (Zoo); Benthos detritivores (B. detrit.); Anchovy (Anch.); Benthos carnivorous (B. carnv.); Sardine (Sard.); Juvenile Sardine (J. Sard.); Other forage fish (O. s. for.); Juvenile weakfish (J. Weak); Triggerfish (Trig.); Juvenile Triggerfish (J. Trig.); White croaker (Croac.); Rays/Skates (Rays); Other benthic feeding fish (O. b. f.); King weakfish (King); Adult weakfish (Weak); Bonito; and Other pelagic feeding fish (O. p. f.). The shaded boxes depict split pool groups that are linked by stock-recruitment relationships during simulations. (Model adapted from Rocha et al., 1998).

Table 4.4. Diet matrix of the trophic model of the Southeastern shelf ecosystem. Values represent the proportion of the diet of a predator (column) made of a given prey (row). Dots are preys with less than 1% importance to a given predator.

Prey \ Predator	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	
1. Phytoplankton	1.00	0.85				0.10	0.30	0.20		0.20											
2. Detritus		0.10	0.99	0.99	0.73			0.38													
3. Salps																					
4. Zooplankton		0.05	•	•	0.12	0.70	0.20	0.80	0.80	0.80	0.90	0.90	0.15	0.15	0.10	0.10	0.02	0.10			0.02
5. Benthos omniv.							0.02		0.05	0.05	0.02	0.02	0.15	0.10	0.10	0.10	0.06				0.01
6. Marine shrimps									0.10						0.05	0.1					0.25
7. Benthos detrit.			•	•	0.05		0.32		0.05	0.05	0.04	0.17	0.50	0.40	0.40	0.50	0.05	0.23	0.30		0.25
8. Anchovy																					0.26
9. Benthos carniv.							0.08				0.04	0.28	0.28	0.28	0.40	0.28	0.01	0.03	0.05		0.01
10. Sardine																					0.07
11. Juv. sardine																					0.20
12. Other forage fish																					0.26
13. Juv. weakfish													0.02	•		0.01	0.05				0.10
14. Juv. triggerfish														0.01							0.02
15. Croaker														•		0.01					0.10
16. Rays/Skates																					•
17. Triggerfish																					0.02
18. Other benth. fish													0.02	0.04							0.10
19. Other pel. fish													0.02	0.02							0.10
20. Bonito																					0.10
21. King weakfish													0.02	•							0.05
22. Adult weakfish																					0.01

Three peculiar features of the ecosystem are represented in the model. First the partition of the system between pelagic and benthic food chains at lower trophic levels (1 to 3) representing energy pathways originated from phytoplankton and from detritus. Benthic and pelagic food chains are mainly linked at the top of the food web by predators, such as weakfish, that optimize foraging benefits by feeding from both systems, and by the juvenile stages of demersal species that are active pelagic planktonic feeders (e.g. weakfish and triggerfish). Second, the model depicts the partition of the mid-trophic level pelagic niche among *Sardine*, *Anchovy*, *Other forage fish*, and juveniles of top predator groups. Finally, the model represents the relatively high abundance of Salps noticed by Pires-Vanin et al. (1993) as major primary consumers that are apparently not utilized by higher order consumers in the system.

Table 4.5 compares several ecosystem attributes obtained with network analysis in Ecopath. Comparisons are made with the original model of Rocha et al. (1998) and with 9 other trophic models of upwelling ecosystems listed on Chapter 2. Inter-ecosystem comparisons are particularly relevant for global attributes, considered common to all upwelling systems (Jarre-Teichman and Christensen, 1998). These are ecosystem characteristics relative to ascendancy, recycling, path length, trophic transfer efficiency, and also fishery related attributes, such as the mean trophic level of catches. For instance, the Southeastern shelf ecosystem share common characteristics with other upwelling systems, such as the low recycling of nutrients, low relative ascendancy, low trophic transfer efficiency, and fisheries that target mostly low trophic level species. Local characteristics, such as the primary production and total catches, are more difficult to compare since almost all upwelling systems for which models were available represent very productive eastern boundary current ecosystems. Differences between the modified model of the Southeastern shelf ecosystem and the original model of Rocha et al. are mainly related to the size, activity and utilization of the system. The modified annual model reflects a smaller system (lower primary production and system throughput) with higher catches of lower trophic level groups. Also, recycling was relatively higher in Rocha's model and may possibly result from the authors including bacteria as one explicit group in the model. The models otherwise have similar attributes within the range of values expected for upwelling systems.

Table 4.5. Ecosystem attributes used in the comparison of trophic models of upwelling ecosystems. Upwelling models refer to the trophic models described in Chapter 2.

Attributes	Rocha et al.1998	Modified model	Upwelling models	
			Average	Range
Global characteristics				
Ascendency	37.80	27.50	32.97	16.20-40.60
System Omnivory	0.10	0.14	0.16	0.11-0.32
Connectance Index	0.30	0.24	0.26	0.23-0.32
Finn's Cycling Index	14.51	7.33	8.11	1.58-13.60
Mean Path Length	3.54	3.16	2.78	2.45-3.01
Mean Transfer Efficiency	4.45	5.10	5.00	3.60-7.40
Fisheries Mean Trophic level	3.01	2.86	2.85	2.22-3.28
Local characteristics				
Total system throughput	6,373	5,314	24,256	8,058-59,677
Net Primary Production	1,802	1,680	7,836	3,290-22,059
Total Catches	0.10	0.60	19.99	0.95-91.67

Ecopath calculates the transfer efficiencies between the successive discrete trophic levels in an ecosystem as the ratio between the sum of the exports plus the flow that is transferred from one trophic level to the next, and the throughput on the trophic level. The transfer efficiencies between trophic levels II and V (herbivores and third level carnivores) are shown in table 4.6. A pattern emerges where lower trophic levels, specially herbivores/detritivores, have a higher transfer efficiency than groups at higher trophic levels. This pattern was also observed in other models of marine food webs (Christensen and Pauly, 1993) and it is consistent with higher respiration losses expected for long lived and more active groups at the top of the food chain. The mean trophic transfer efficiency of all flows in the system is 5.1 %, which is below the mean transfer efficiency of 10% estimated by Pauly and Christensen (1995) across different types of marine ecosystems, but in line with their estimates for upwelling systems. Upwelling ecosystems are considered relatively inefficient in transferring energy up the food web. Their energetic inefficiency seems to be related to the characteristics of primary productivity and food web organization. The high and variable new primary production characteristic of upwelling systems yields a higher export of carbon compared to more stable and less productive systems, where most of the primary production is regenerated (Berger et al., 1989). The variability of upwelling systems involves a continuous change in conditions that result in simpler food webs that lack fully co-adapted autotrophs, heterotrophs, and decomposers. Thus sporadic and seasonal nutrient injection stimulates rapid growth of phytoplankton which will bloom not being grazed sufficiently to prevent exponential increase; a large part of this unutilized primary production will end up being exported from the euphotic zone towards the seafloor. Part of the detritus exported from the pelagic system is recycled back into the food web by the activity of

benthos detritivores and omnivores. It is estimated that in the Southeastern shelf about 34% of the flows originates from detritus, although recycling (including detritus recycling) represents only 7.33% of the total system throughput.

Table 4.6. Transfer efficiencies between trophic levels calculated using the trophic aggregation routine in ECOPATH.

Source	Trophic level			
	II	III	IV	V
<i>Producers</i>	11.5	3.9	2.4	4.6
<i>Detritus</i>	6.7	2.4	3.5	4.1
<i>All flows</i>	9.9	3.6	2.6	4.5

Estimates of the total primary production required to sustain catches (PPR) during the 1970s and 1990s are shown in table 4.7. PPR estimates for the 1970s were obtained by changing the catches in the trophic model with the values observed from 1977 to 1980 (as in Chapter 3). Notably low PPR values (~4%) are estimated for fisheries in the Southeastern shelf in both time periods, compared to values between 25 and 33% estimated in Chapter 3 using a different method. Ecopath calculates the PPR of catches of a given group by first identifying all the paths in the trophic network that lead primary production (or detritus) to the harvested group. For each path, the catches are then raised to the primary production equivalents using the product of the catch, the gross growth efficiency of each path element (=production/consumption), and the proportion the next element of the path contributes to the diet of a given path element (Christensen and Pauly, 1996). At each consecutive step down the path, the calculated flow is divided by the ecotrophic efficiency of the path element (so that the resultant PPR reflects the fact that not all biological production is utilized at consecutive trophic levels). Ecopath thus offers a more rigorous method to calculate PPRs, compared to the approach used in Chapter 3 where the mean trophic efficiency between trophic levels is used to raise catch values to the primary production equivalents. Assuming an average trophic efficiency of 5% causes, for instance, an overestimation of the PPR of low trophic level species (that make up the bulk of the catches) for which transfer efficiencies are substantially higher (Table 4.6).

The relatively low footprint of fisheries in the region is on the other hand expected from the low trophic level of catches, and may be conservative considering that discards were not included in the calculations, pelagic sharks were not included in the model, and that part of the catches may remain unreported in official fisheries statistics (Gasalla and Tomas, 1998).

Changes in the catch composition between the two periods are related to a modest increase in catches of triggerfish and rays/skates, decrease in catches of croaker, sardine and marine shrimps, and an increase in landings of bonito, *Katswonus pelamis*, which resulted in an increase in the mean trophic level of fisheries from 2.81 to 2.86.

Table 4.7. Trophic level, mean catch and PPR estimates for the main species landed in southeastern Brazil.

Species	1977 - 1980			1990 - 1995	
	Trophic Level	Catches tons	PPR tons•Km ² •year ⁻¹	Catches tons	PPR tons•Km ² •year ⁻¹
Bonito	3.73	1,380	4.35	7,197	23.09
White croaker	3.32	7,126	24.43	4,541	15.95
King weakfish	3.74	2,053	18.10	1,870	18.42
Weakfish	3.80	1,921	13.26	2,245	16.68
Triggerfish	3.37	—	—	2,144	3.70
Sardine	2.84	146,520	20.79	54,414	7.72
Rays and skates	3.41	—	—	504	2.59
Marine shrimps	2.00	17,371	0.47	13,997	0.38
Total Catch and PPR		174,991	61.70	86,912	68.38
%PP			3.67		4.07
Fisheries Mean TL		2.81		2.86	

In terms of ecosystem change between the two time periods a question remains on whether the energy previously available at lower trophic levels in the form of sardine biomass was lost due to stock overfishing, was reallocated to other species in the ecosystem (e.g. anchovy, triggerfish), or simply reflect a decrease in the productivity of the system. And also whether this new system configuration is in a stability domain that would impede the recovery of the sardine stock. Simply put, can the current system configuration support a larger biomass of sardine?

The understanding of how ecosystems are structured and how they change in response to human impact has at its core the understanding of the dynamics of ecosystems succession and resilience. Holling (1986, 1992, 1995) suggested four primary phases in an ecosystem succession cycle which synthesize common features observed in both terrestrial and aquatic systems (Fig. 4.5). The phases are: *exploitation*, in which rapid colonization of recently disturbed areas by opportunist species (r-strategy) occur and lead to a growth in the size of the system (stored capital); *conservation*, in which the system slowly accumulates and stores energy and material, and develop a more complex structure (increase in connectedness) until a climax is attained. Characteristics of this phase is the highly efficient processes of energy utilization and conservation, and the presence of K-strategy species; *release*, in which the tightly bound

accumulation of biomass and nutrients becomes increasingly fragile (overconnected) until it is suddenly released by physical or biological disturbances and unexpected events such as forest fires, storms, insect pests, intense pulses of grazing, etc.; and *reorganization*, in which processes of nutrient mobilization minimize losses and reorganize nutrients to become available for the next phase of exploitation. The model depicts two aspects of stability. First the ability and speed with which systems recover from perturbations which, according to the inter-ecosystem comparison carried in Chapter 2, is mostly influenced by mechanisms of nutrient recycling in the food web. The second aspect, that of the resilience of ecosystems, is represented by an arrow in the top left corner of the model which suggests that changes into another ecosystem structure following perturbation is most likely to occur during the release and reorganization phases.

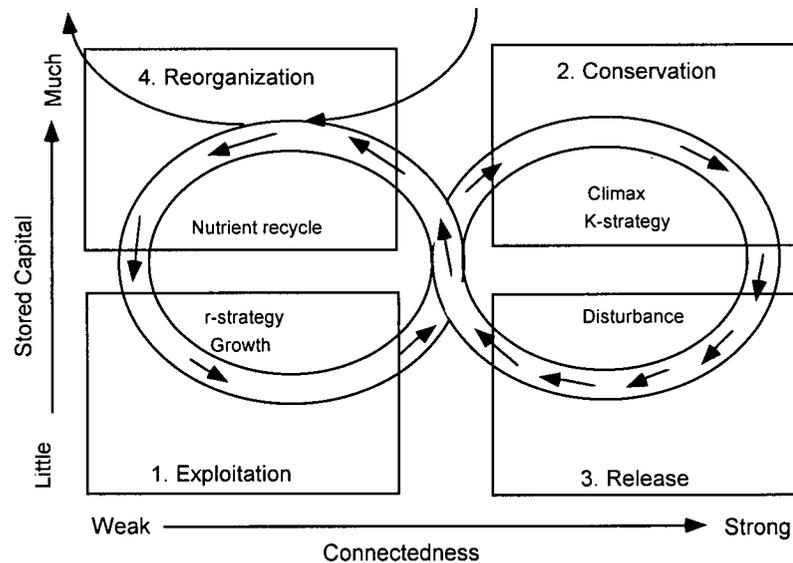


Figure 4.5. Holling's four phase model of ecosystem dynamics. During the cycle of exploitation, conservation, release and reorganization, biological time flows unevenly. It is slow from the exploitation to the conservation phase, then very rapid to the release (when the overconnected system triggers sudden changes by agents such as fire, disease, etc.), rapidly to reorganization and back to the exploitation phase. Resilience and recovery are determined by the fast release and reorganization sequence, whereas stability and productivity are determined by the slow exploitation and conservation sequence. The arrow in the top left corner of the model suggests the phase where change into another ecosystem structure following perturbation is most likely to occur (source Holling, 1995).

The four phases model considers that the dynamics of ecosystems is organized across scales in time and space around the operation of a small number of nested cycles of exploitation, conservation, release and reorganization, each driven by a few dominant variables (plants, animals and abiotic processes) (Holling, 1992). Examples of regional resource management (Gunderson et al. 1995) also suggest that institutions and societies achieve periodic advances in understanding and learning through similar cycles of growth, production (greatest efficiency), release (crisis) and renewal that shape the spatial and temporal dynamics of ecosystems.

Holling's four phases model thus provides a framework that is useful for understanding both the dynamics of ecosystems (its structure and change) and the functioning of institutions bound to resilience.

The study of the structure and dynamics of the Southeastern Brazilian shelf ecosystem (Pires-Vanin, 1993) indicates that this system is conditioned by cyclical physical events that control seasonal changes in the trophic structure and in the patterns of energy flow in the biological communities. The seasonal upwelling cycle is in fact nested in a hierarchy of cycles of different speeds, or time scales, as suggested in table 4.8. At faster speeds there are bacteria and phytoplankton organisms, which have characteristically higher turnover rates. Individual phytoplankton live for a few days and succession of populations in a patch or bloom can change significantly in the same time scale. Physical processes such as pulses of favorable wind stress, storms, small scale vortexes of low residence time, and transient upwelling events caused by internal waves and fronts can all influence biological succession at this scale. Aidar et al. (1993) showed that phytoplankton biomass in the Southeastern bight is usually limited by the lack of nutrients, specially nitrogen, and it is mostly dominated by species of the nano-plankton which are better adapted, with a higher surface-volume ratio, to explore the general oligotrophic conditions. Once the system is disturbed by the intrusion of nutrient rich South Atlantic Central Water (SACW), species of the nano-plankton are substituted by other larger phytoplankton species better adapted to the new conditions. Physical processes operate at faster speeds to control small-scale water turbulence and influence the rate of encounter between planktonic predators and their prey (Mann and Lazier, 1991). Zooplankton and benthic invertebrates occupy an intermediate level in the time-scale hierarchy between phytoplankton and fishes. The structure of benthic communities in the southeastern shelf is mainly influenced by the seasonal cycles of upwelling which favor distinct types of organisms during summer and winter (Pires-Vanin, 1993).

Table 4.8. Time-scale hierarchy of physical and biological variables controlling the dynamics of the Southeastern shelf ecosystem.

Speed of change	Variables	Time scale	Equivalent physical force
Fast	Bacteria	Hours - Days	Turbulent mixing, tides, breeze, storms, vortexes
	Phytoplankton		
Intermediate	Zooplankton	Days - Months	Seasonal cycles of upwelling
	Benthic organisms		
Slow	Mid-trophic level fish	Years - Decades	Cycles in upwelling intensity and El Niño (ENSO)
	Higher trophic level fish		
	Marine mammals		
	Management institutions		
	Programs of economic incentives		
Very slow	Scientific understanding	Decades -Centuries	Global warming
	Large Marine Ecosystems		
	Human myths of nature		

Most fish species fit into the category of slower variables, with turnover rates in the order of years and cycles in production in the order of years and decades. Cycles in marine fish populations bear close correspondence to the long term climatic-oceanographic regimes of the oceans. Characteristic of the sea is the “red noise” type of variability spectrum, in which the variance of physical processes increases significantly with the time scale from hours to decades (Steele, 1985). This inherent dynamics of the oceans is thought to influence marine fish populations in two ways: first, the damped short and medium time scale variability create conditions that favor reproductive strategies such as high fecundity and absence of parental care, that rely on a relatively predictable combination of enrichment, concentration and dispersal mechanisms at these scales. Second, the absence of mechanisms to cope with the short-term variability may make marine fish populations susceptible and adaptable to variability at longer time scales. Examples of fish populations that show decadal oscillations in abundance are found in almost every marine system. Bakun (1996), for instance, compiled examples of synchronous oscillations in several fish populations geographically isolated from each other, but apparently driven by a common environmental property. These low-frequency population cycles varied among species, but were generally characterized by a period of rapid population growth in the decade from the mid-1970s to the mid-1980s followed by stock declines after the mid-1980s (Fig. 4.6). According to Bakun the Brazilian sardine followed the pattern of “crashing” after the mid-1980s.

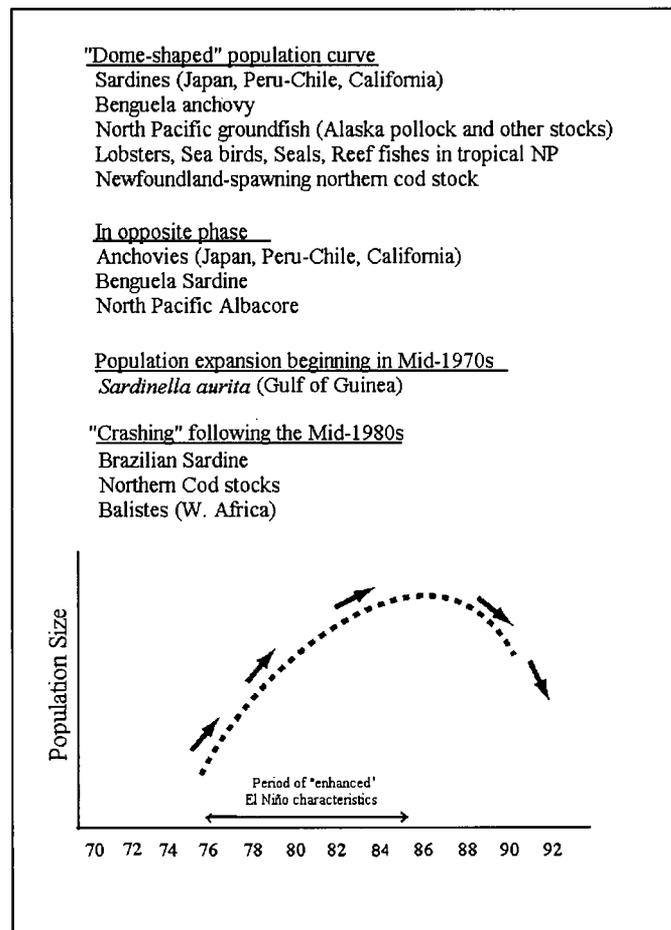


Figure 4.6. Pattern of variation observed in many marine fish populations according to the "Dome-shaped" hypothesis (source Bakun, 1996).

Management institutions, such as fishing policies, programs of economic incentives to fisheries development, and the scientific understanding of ecological phenomena, also present characteristics of slow change, as has been the case with the development of the sardine fishery in Brazil. At even slower speeds there are the changes in the configuration of Large Marine Ecosystems, both in terms of structure (number of species, trophic organization) and functioning (processes controlling production, recycling, etc.). That correspond to the speed of long term events such as those accompanying global warming effects. For instance, it is suspected that an increase in greenhouse effect would enhance the land-oceanic temperature contrast and intensify the upwelling along continental margins (Bakun, 1992). This phenomenon has been already reported for several regions of the world using multi-decade data on the intensity of upwelling-producing wind stress (Bakun, 1992), although its likely effects on small pelagic fish populations and marine ecosystems is still debatable. At the human dimension, that is also the scale at which myths about nature endure, as stated by Light et al. (1995) in the case of water management in

the Everglades: “[t]he myth of “quest for control” has persevered through the past century and is characterized by a rational decision maker model that assumes that institutions can solve resource problems based on “objective knowledge” and the exploitation of technology in the name of progress”.

Accompanying the increase in the time scale up the food web there is also an increase in area occupied by an individual species during its life cycle. For instance, certain fish species swim hundreds of kilometers during their life span, while most phytoplankton and zooplankton organisms have a distribution range confined to patches of a few kilometers. The combination of time and space hierarchies in the processes controlling biological variability result in a generic pattern in which larger organisms smooth out the effects of fluctuations in the smaller prey populations (Mann and Lazier, 1991).

Connections do exist between processes at different scales . A critical feature of such hierarchies is that larger, slower levels usually maintain constraints within which faster levels operate, in other words, slower variables control faster ones (Holling, 1992). Holling (1995) also suggests that at certain conditions slower and larger levels in ecosystems may become briefly vulnerable to small events and fast processes. In forest systems, for example, fast variables can dominate slow ones particularly at climax stages when the system is so overconnected that it lacks the resilience necessary to cope with forest fires or insect outbreaks (Holling, 1995). Also, during the phase of reorganization, when the system is underconnected and with weak regulation, there are opportunities for the establishment of a diversity of pioneer species which can result in completely different final ecosystem configurations (Holling, 1995). Therefore, sometimes fast variables can control slower ones. The analog of this process in the sea can be represented by the concept of Lasker windows. The success of a year class of a fish population depends on a diverse array of events that influence the survival of an individual fish from the egg stage to the recruitment size. Lasker (1975, 1980) and collaborators suggested that recruitment would be largely determined during a critical period in the early life history when the first feeding larvae have to find food of appropriate concentration and quality to avoid starvation. The formation of fine-scale patches of highly concentrated food particles depends on the existence of a temporal window, typically in the order of 5 days, during which turbulent mixing energy by the wind remains low so that particles can accumulate. The frequency of these calm periods of short time scale, called Lasker windows (Bakun, 1996), is thought to be responsible for most variability in

anchovy larvae survival and recruitment success in the California Current system, with potential consequences to the population size and to other species in the ecosystem.

A central question for fisheries management is whether the switches in species composition observed in heavily exploited marine ecosystems represent a natural and reversible change caused by oceanic regimes or do they reflect a loss of resilience of ecosystems and a change of state caused by excessive exploitation. Several biological-oceanographic processes may be at play to cause the observed regime shifts in marine ecosystems following disturbance by fisheries and natural events. A review of the last 18 years of publications (referenced in the Aquatic Sciences & Fisheries Abstracts, ASFA) on the causes of fluctuations in small pelagics showed that the majority of the papers (30 out of 52) associate changes to direct fishery and environmental effects. These include processes such as long term changes in temperature, wind intensity, and food enrichment mechanisms, such as the ones proposed by Bakun and co-authors, that directly affects recruitment success of fish populations. In the following section I used Ecosim to examine the effect of long term changes in food enrichment, food competition and predation on small pelagic forage fish (sardine) production. The ecosystem model was best suited to investigate possible relationships between changes in sardine recruitment rates and these ecosystem processes, specifically the interactions between sardine and anchovy. The simulation consisted of adding to the trophic model of the southeastern shelf a time forcing function that generates a 10 year cycle in primary productivity, as suggested in figure 4.6. During this time period, sardine fishing rate was maintained constant at twice the baseline fishing mortality. Figure 4.7 shows the predicted changes in the biomass of phytoplankton, sardine and anchovy, as well as in sardine recruitment. Results indicate that relatively small changes in primary production (+-50% the baseline primary productivity) can lead to larger changes in fish biomass. Sardine and anchovy are equally affected by changes in food enrichment, although sardine biomass declines faster than anchovy when food conditions worsen, due to the high fishing mortality. The combined effect of food enrichment and fishing generates a cyclic non-stationary pattern in sardine recruitment rates that culminates with the collapse of the stock.

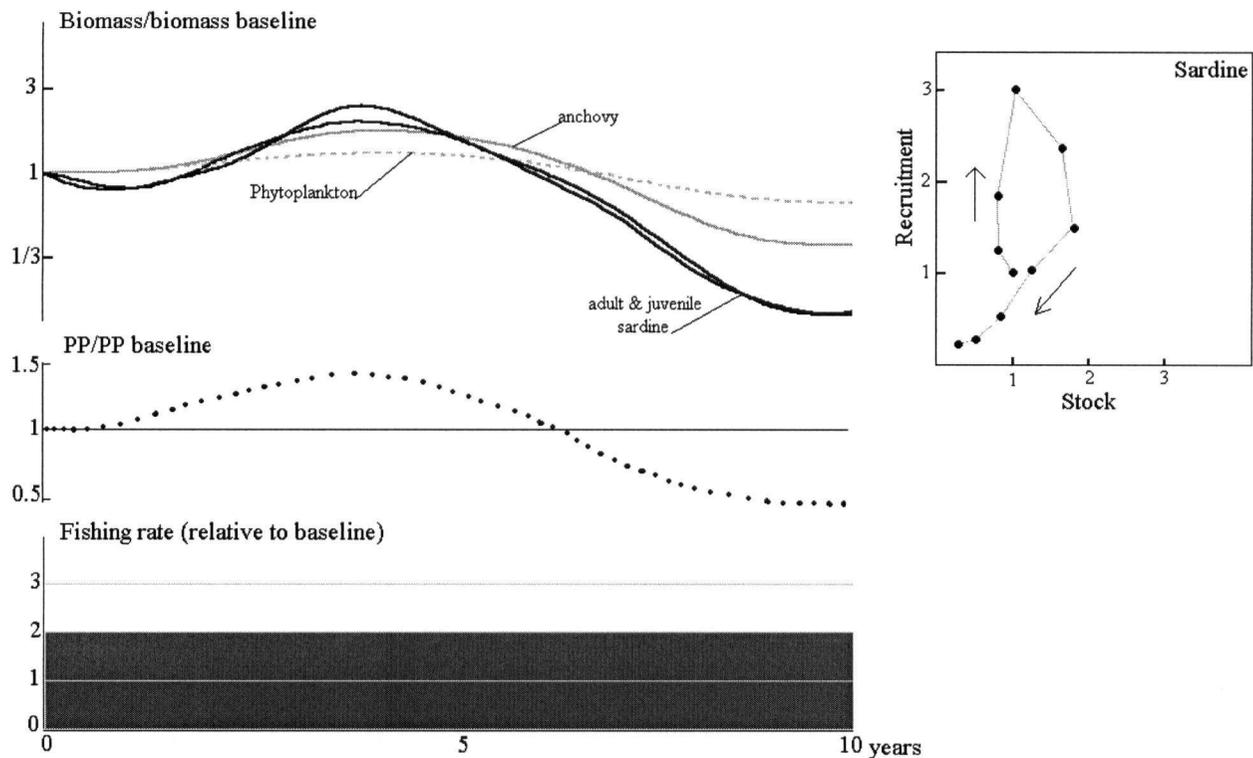


Figure 4.7. Output predicted by Ecosim with a cyclic regime in primary productivity (PP). Simulation run under a bottom-up trophic control. Not all groups in the system are represented. A fishing rate for sardine twice as high as the baseline value was applied during the simulation. The panel on the right represent the relationship between stock and recruitment for sardine obtained with the simulations on the left.

Trophic mechanisms are also used to explain apparent regime shifts in the productivity of small pelagics. The most frequently visited hypotheses are food competition, and predation of adult anchovy/sardine on the early life stages of the competing species (Santander et al. 1983; Alheit, 1986; Butler and Pickett, 1988; Butler, 1991; Valdez Szeinfeld, 1991). Cury et al. (in press) also point at behavioral causes such as the “school trap” phenomenon commonly observed in small pelagics. The “school trap” is caused by behaviour mechanisms that drives sardines, anchovies and sardinellas species to school together with other species when their relative abundance is diminishing. By doing so they subordinate their specific needs to a different set of environmental preferences, such as migration paths, habitat types, etc., not necessarily optimal for the species. Under these conditions stock productivity is expected to remain low for longer periods.

The hypothesis of species replacement by food competition has been also used to explain shifts in species composition other than sardine-anchovy. Caverivieri (1991) and Bakun (1996), for instance, suggest that the collapse of sardine, *Sardinella aurita*, in the upwelling system of the

Gulf of Guinea led to a rapid increase in the abundance of triggerfish, *Balistes capriscus*, which is a semi-pelagic species as adult and pelagic planktonic feeders as juvenile. The apparent shift in dominance may result from climatic changes (more specifically to changes in continental runoff) but it is also considered that juvenile triggerfish effectively replaced the collapsed sardine at the mid-trophic level pelagic niche. Parallel changes have been observed in the Southeastern Brazilian Bight, where an inverse relationship between *Balistes capriscus* and *Sardinella brasiliensis* is noted in catch data from 1977 to 1995 (Table 4.6; Zavalla-Camin and Lemos, 1997). The hypothesis of replacement by food competition implies two interrelated assumptions; first that the mid-trophic level pelagic niche is occupied by a dominant species, and that a competing species may “fill the environmental void” created by the depletion of the dominant one (Turner and Bencherifi, 1983); second that food is limiting production, so that even in the absence of fishery the depleted population would not recover its biomass. In many cases, the hypothesis of food competition between sardine and anchovy has been refuted by considerable differences between the diets of the two species. In the Benguella system, for instance, competition between the two species seems to be limited by differences in the size composition of the diet, where sardine usually consume smaller prey than anchovy (Louw *et al.*, 1998).

Evidence of predation of adult sardine/anchovy on eggs and larvae of the competing species would point to the existence of “trophic triangles” in the pelagic niche. In this case adults of sardine and anchovy share a common prey pool, while also feeding on the early life stages of the other. Thus reducing the biomass of one species of the pair would lead to an increase in prey availability and in the abundance of the competing species, which in turn would cause an increase in larvae and juvenile mortality due to predation. More common in marine and freshwater systems are however the “trophic triangles” among adult and juvenile stages of top predators and a third forage species that is both competitor/predator of juveniles and prey of adult stages (Walters and Kitchell, in press). A classic example is the cod-clupeid system in the Baltic sea (Rudstam *et al.*, 1994 in Bax, 1998), where adult cod actively preys on adult and juvenile herring, while adult herring has cod eggs and larvae as a major food source. Therefore the depletion of adult cod may lead to planktivorous fish dominance that may prevent cod recruitment. Walters and Kitchell (in press) suggest that this type of trophic mechanism may be responsible for compensatory recruitment changes observed in marine fish populations that have been subjected to overfishing, including many clupeid species. The authors also noted the possibility of “trophic quadrangles” in zooplanktivorous fish, where adults feed selectively on

larger zooplankton than juveniles; reductions in adult fish biomass would cause an increase in large zooplankton that feed on smaller zooplankton groups also utilized by juvenile fish.

There are two reasons to not support the hypothesis of predation relationships between sardine and anchovy in the Southeastern Brazilian shelf. First, the lack of evidence of eggs and larvae in stomach contents of both species (Goiten, 1983; Scwingel, 1996). Second, which corroborates the first, is that although sardine and anchovy inhabit the same region, spawning behavior differs between species (Matsuura et al., 1992). While sardine spawning occurs in the surface warm mixed layer during spring and summer, anchovy spawns all year round mainly beneath the thermocline, inside the cold SACW which is present in the shelf bottom layers during spring and summer. Eggs and larvae of both species are found mainly above the thermocline in the coastal regions. Therefore adults and early life stages seems to be spatially segregated during the peak spawning season. There is also no evidence of marked changes in food (zooplankton) selection with size between juvenile and adult stages of sardine (Saccardo and Rossi-Wongtschowski, 1991) which would make the case for “trophic quadrangles” at the bottom of the food web.

Dynamic simulations with Ecosim were used to evaluate the effect of changing purse seine fishing rates on sardine biomass. In the following scenario it is assumed that most sardine predation mortality occurs during the species early life stages. Adult and juvenile sardine compete for food with other small forage fish as well as with juvenile stages of some apex predators (weakfish). Simulations were run under different hypotheses on the type of trophic control in the system and on the maximum relative foraging time of apex predators. The fishing scenario consisted of imposing high fishing rates on sardine for 4 years and then having the fishery closed to let the stock rebuild (Fig. 4.8). When the system is bottom-up controlled or when the maximum foraging time of apex predators is low ($F^{\max} = 1$) sardine promptly (within 2 years) recovers its baseline biomass once the fishery is closed. Consequently, food does not apparently limit production and any decrease in fishing mortality would be expected to result in the stock recovery. However when predation is controlling production at lower trophic levels and higher relative foraging time is assigned to apex predators ($F^{\max}=2$) sardine biomass is maintained at a depressed level even after the fishery is closed; the population usually takes up to 10 years to recover its baseline biomass. Figure 4.8 represents the two types of responses obtained with Ecosim; the depensation scenario results from allowing apex predators (specially *Pelagic feeding fish*) to increase substantially its feeding time and consequently its consumption

rates to compensate for the decrease in sardine biomass; the high consumption rates in turn impede the prompt recover of the depressed population by imposing high mortality rates on juvenile fish. In the simulations increase in the biomass of competing forage fish with a decrease in sardine biomass was never observed. Results however imply that apparent regimes of low productivity in small pelagic fish could be explained as well by increasing predation mortality and consequent depensation in recruitment rates following stock collapse. Myers et al. (1995) found some evidence of depensation in 5 out of 128 marine fish populations for which time series of stock and recruitment data were available. Among them there are three clupeid fish stocks, the Spring spawning Icelandic herring, Pacific sardine and Georges Bank herring, which were severely overfished and remained commercially extinct for decades. The authors consider as possible causes of depensation multispecies effects such as nonlinear feeding responses of predators to changes in abundance of preys, as well as reduced reproductive success at low population densities (Allee effect).

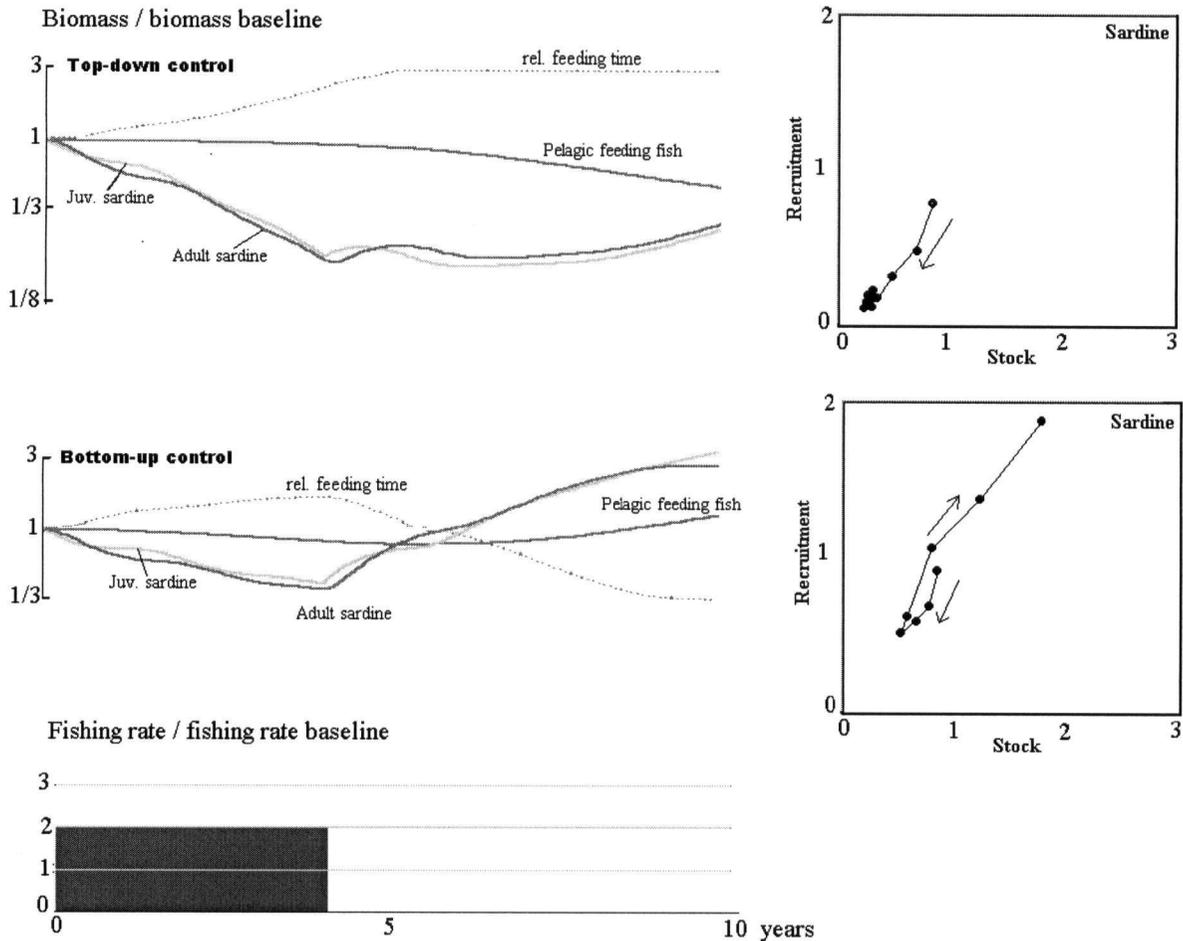


Figure 4.8. Output predicted by Ecosim with selective predation mortality on juvenile sardine. Not all groups in the system are represented. The model includes a Delay-difference representation of changes in numbers and biomass of sardine, weakfish and triggerfish. The panels on the right represent the relationship between stock and recruitment for sardine obtained with the simulations on the left; after 4 years of heavy exploitation (2 times the baseline level) the sardine purse seine fleet is shut down to let the stock recover. Dotted lines represent the change in foraging time of pelagic feeding fish.

Walters et al. (in press.a) warned about the possibility of strong depensatory effects, and multiple equilibria in community structure, when predators in the system are assigned higher limits to the time spend feeding (F^{\max}) with decreasing food availability. That creates, according to the authors, results analog to the effect of including a Type II functional response of predators to the availability of preys. Empirical and theoretical studies of predator-prey systems have tended to identify three types of functional responses (types I, II or III as in Holling 1959) relating predation mortality rate and prey density. Type I response assumes that search by predators is random, and that the number of prey eaten by a predator would be directly proportional to prey density. Conversely, types II and III assume non-linear responses of predators to prey density as a result of behaviour processes, e.g. when predators are able to aggregate to areas where prey

numbers are high, as well as for the result of handling and satiation. In both cases predation rates may in effect increase with the decrease in prey density to cause depensation in production rates at low prey population size and multiple stability states. Field and laboratory studies have been able to demonstrate the existence of the latter two types of responses in both terrestrial (Holling, 1959; 1973) and aquatic systems (Peterman, 1977; Peterman and Gato, 1978; Peterman et al., 1978). In these systems resilience seems to be conditioned by lower thresholds, e.g. in fish stock abundance, beyond which disturbance will lead to completely different system stable states.

Verifying this hypothesis in the field is however very difficult because it will require estimating how predation mortality changes with the biomass of consumers and preys under uncontrolled and variable conditions determined by other environmental factors. Alternatively, the depensation hypothesis can be checked against the reconstructed time series of sardine spawning biomass and recruitment from VPA (Table 4.9; Fig. 4.9). Several processes can influence the productivity of an exploited fish population. Hilborn and Walters (1992) argued that sum of environmental and multispecies effects on a stock are likely to be most important during the fish early life stages, when larvae and juveniles are more vulnerable to sub-optimal environmental conditions, predation and competition for food. For convenience, in a population analysis the net effect of juvenile survival (i.e., recruitment) is usually represented by a stock-recruitment relationship. The focus on stock-recruitment relationships has also a practical reason, since it directly links a control variable (stock) and a rate of future stock production (recruitment).

Table 4.9. Biomass at age estimated from VPA with M of 0.95 (natural mortality rate with the highest probability given the observed data, see figure 4.10) and terminal exploitation rate (u_T) of 1. Total stock biomass in a given year is calculated as half the sum of biomasses at age, since age data was structured in half year intervals.

Age	1977	1978	1979	1980	1981	1982	1983	1984	1985	1986	1987	1988	1989	1990
0	350528	280876	287939	218962	326795	367600	246166	323621	208524	82895	74979	75656	25583	—
0.5	317051	253275	207292	231203	327349	312687	229626	148288	129678	103097	81599	56954	19259	—
1	320029	344982	266047	228379	190202	280686	321411	346618	197596	147042	116207	137727	60058	19788
1.5	195671	186436	142018	136540	99303	166362	183081	167970	163196	124531	98701	101394	34557	17330
2	139246	153119	126492	92801	73854	57433	122941	141791	125399	123638	74488	55308	54671	13491
2.5	54688	51937	37495	36140	19475	18826	43625	5646634	57449	40620	27009	19315	13085	9931
3	8678	11338	7212	2052	2453	1258	1936	12053	11953	18696	8255	3054	3312	843
3.5	2820	2767	993	83	175	48	368	3324	1567	511	419	39	84	111
Total	360566	375290	290129	247998	192731	262306	336681	364111	278580	227519	162539	158418	82885	30747
u_t	0.40	0.38	0.51	0.59	0.60	0.38	0.41	0.38	0.44	0.55	0.56	0.41	0.94	—

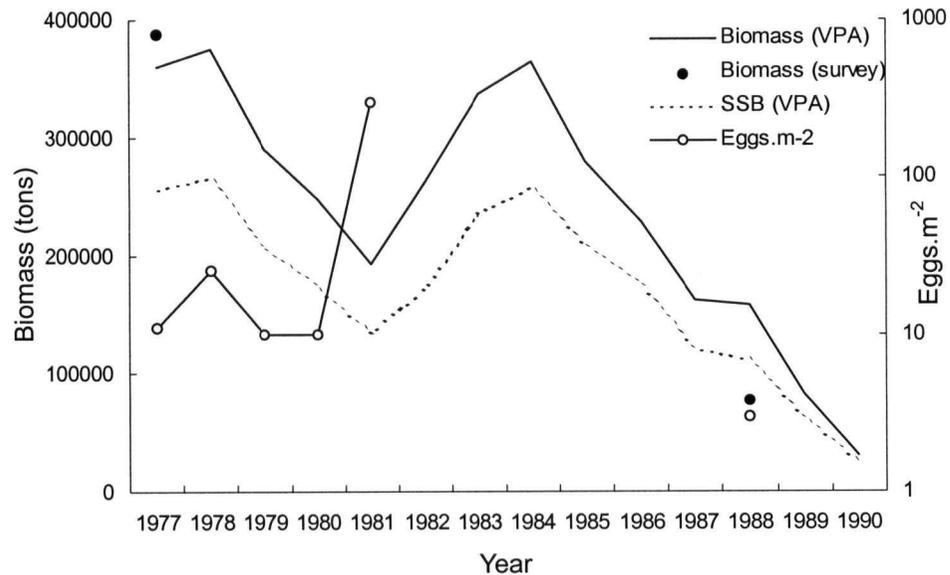


Figure 4.9. Reconstructed time-series of sardine biomass from VPA with annual natural mortality rate (M) of 0.95 year^{-1} (parameter value with maximum likelihood). Also shown in the graph are the estimated spawning stock biomass (SSB) and the observed egg densities and stock biomass from surveys.

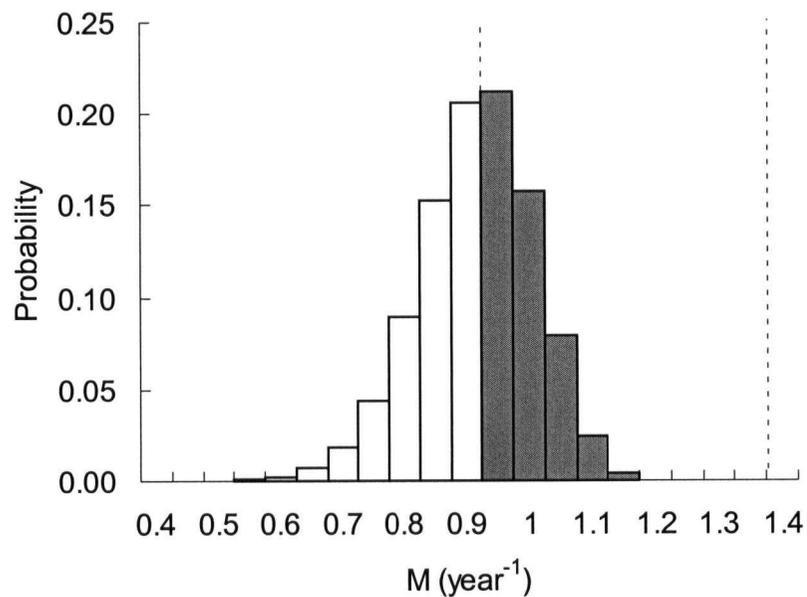


Figure 4.10. Bayes marginal posterior probability distribution of natural mortality rate (M) from VPA analysis. Shaded bars between dashed lines represent the range of M values expected for sardine using Pauly (1980) equation.

Stock and recruitment data obtained from VPA supports equally well three different hypothesis that explain the changes in sardine production observed during the 1970s and 1980s. These

hypotheses are represented below by functions relating stock size and recruitment (Figs. 4.11 and 4.12):

Hypothesis 1: *Recruitment decreased in response to a gradual decline of the spawning stock biomass due to overfishing.* In this case recruitment can be properly described as a function of stock size. Environmental processes impose an interannual recruitment variability described by a log-normal statistical distribution. This hypothesis is consistent with the decrease in recruitment that accompanied the decrease in spawning biomass from 1977 and 1990 (Fig. 4.11). In this time period it is estimated that the total stock biomass declined from ca. 350,000 tons to 80,000 tons, with an average exploitation rate of 0.5 (Table 4.8).

Hypothesis 2: *Recruitment declined in response to overfishing and is forced to stay at low levels due to depensatory mechanisms* Recruitment is modeled as a function of stock size and according to different degrees of depensation in the average stock-recruitment relationship (Fig. 4.11). Interannual recruitment variability is also assumed to have a log-normal statistical distribution. Several processes can contribute to depensation in stock production including competitive exclusion at the pelagic niche, increased predation mortality at low stock size, reduction of intraspecific diversity, or even behavioural processes such as the “school trap” phenomenon.

Hypotheses 1 and 2 are represented by a Beverton-Holt stock recruitment function modified to include depensatory effects (Myers *et al.*, 1995):

$$\text{Recruits} = \frac{aSSB^x}{1 + \frac{SSB^x}{K}} e^v$$

where parameter a is the maximum recruits per spawning stock biomass (SSB) as SSB approaches 0, the product $a \cdot K$ is the maximum number of recruits, and x controls depensation in the recruitment curve (depensation occurs when $x > 1$). All recruitment variability is described by a log-normal error (v).

Model parameterization was carried as follows. For both hypothesis, the maximum number of recruits was considered known from the historical experience, being set to $12 \cdot 10^9$, thus eliminating one unknown parameter (K). Parameter x was set to 1 to represent the hypothesis of no depensatory mortality (Hypothesis 1) and to a value of 2 to represent strong depensation

(Hypothesis 2). Model parameterization was completed by finding the maximum likelihood estimator of parameter a , i.e. the maximum recruitment rate at low spawning stock biomass. The kernel of the likelihood function with log-normal error was calculated according to Walters and Ludwig (1994). Final model parameterization is shown in table 4.10.

Table 4.10. Parameters used in the representation of density-dependent hypothesis of stock-recruitment relationships.

Parameters	Hypothesis 1: no-dependation	Hypothesis 2: depensation
a	135	867
K	0.0888	0.0138
x	1	2

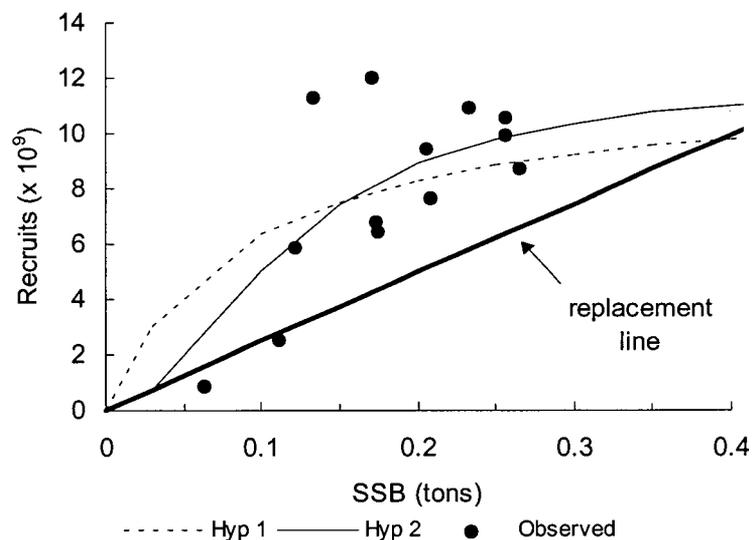


Figure 4.11. Graphic representation of the two hypothesis used to describe the relationship between spawning stock biomass and recruitment. The replacement line represent the number of recruits needed to replace the correspondent spawning stock biomass.

Hypothesis 3: *Recruitment declined as a result of overfishing and recruitment failures caused by long-term, low-frequency environmental effects, according to Bakun's "dome-shaped" regime hypothesis.* According to Bakun (1996) the Brazilian sardine showed a pattern of "crashing" following the mid-1980s which is consistent with synchronous oscillations observed in several other marine populations from the mid-1970s to the mid-1980s (see Fig. 4.6). In this case, recruitment is described by a nonstationary relationship between stock and recruitment driven by low-frequency environmental cycles (Fig. 4.12). Recruitment time series present a decadal signal superimposed on the interannual variability.

Hypothesis 3 was represented by a modification of the Beverton and Holt model according to Walters and Parma (1996):

$$\text{Recruits} = \frac{aSSB}{1 + \frac{aSSB}{K}}$$

where parameters a and K are expressed as function of density-independent and density-dependent mortality risks. Accordingly, $a = \exp^{-M_1}$ and $K = \frac{M_1}{M_2(\exp^{M_1} - 1)}$, where M_1 represents

density-independent mortality risk and M_2 density dependent mortality risk. M_1 influences both a (maximum recruits/spawner) and K (maximum recruitment) and hence was considered the parameter subjected to external environmental cycles. The model was parameterized by fixing the density-dependent mortality risk and making M_1 , the density-independent mortality risk, follows a sinusoidal trend with period of 10 years and maximum and minimum value of -3.576 and -4.576 (range = 1), i.e.

$$M_{1,t} = M_1 + \text{range} \cdot \text{Sin}\left(\frac{t \cdot \pi}{10}\right)$$

Optimal environmental conditions were assigned to the mid-1980's to make the model consistent with Bakun's "dome-shaped" regime hypothesis (Figure 4.12).

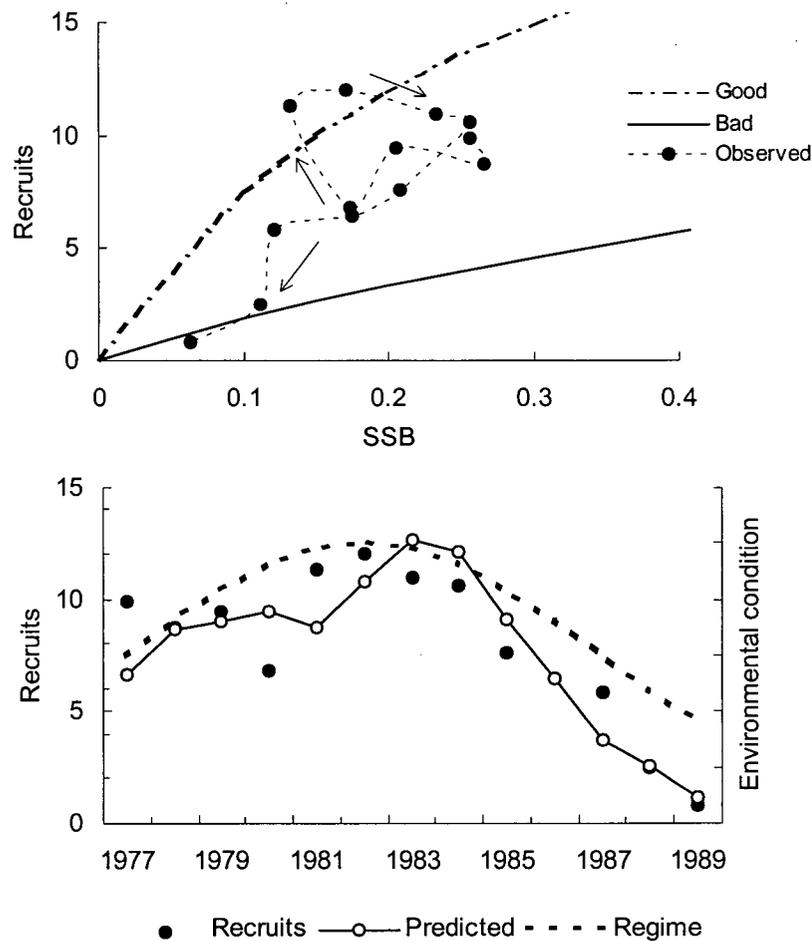


Figure 4.12. Graphic representation of the “dome-shaped” regime hypothesis (hypothesis 3). Upper panel shows the two extreme stock-recruitment relationships modeled to represent a “good” and a “bad” environmental regime. The model is used to generate a sinusoidal trend in the marine carrying capacity which results in a dome-shaped relationship of recruitment with time (lower panel).

Stock distribution, effort dynamics and catchability change

Table 4.11 lists the total effort (number of trips), corrected by the average vessel tonnage in each state, and the calculated catchability coefficient obtained from the comparison between fishing effort and the effective fishing mortality rate. Effort data was obtained from log-book systems effective from 1977 to 1983 in all three state fleets.

Table 4.11. Effort, fishing mortality and catchability of sardine stock to purse seiners off Rio de Janeiro (RJ), São Paulo (SP) and Santa Catarina (SC). Number of trips was considered a reliable effort index for this time period, considering that there were no significant changes in the number of fishing days per trip, and that trips were usually of short duration (average 1 day).

Year	RJ		SP	SC	Total Effort	F	q
	Effort ^a <i>tripsx1000</i>	tonnage ^b	Effort ^a <i>tripsx1000</i>	Effort ^a <i>tripsx1000</i>	<i>trips .tons</i>	<i>year⁻¹</i>	<i>(trips.tons. year)⁻¹</i>
1977	7.604	38.2	2.074	3.484	527.3	0.923	0.00175
1978	7.977	34.9	2.439	3.210	518.9	1.103	0.00212
1979	1.990	32.0	3.792	2.872	346.9	1.475	0.00452
1980	2.158	29.1	2.232	5.703	399.9	1.395	0.00349
1981	1.510	24.9	4.984	2.602	360.0	1.615	0.00448
1982	2.029	24.3	4.237	3.433	375.3	1.454	0.00387
1983	2.495	20.2	5.728	2.479	399.2	0.984	0.00246

a. Source: PDP - Doc. Tec., n.07; Instituto de Pesca de São Paulo - Divisão de Pesca Marítima; Relatório do Sistema de Mapa de Bordo.

b. Mean tonnage was used as a factor to compensate for changes in effort efficiency due to changes in boat size off RJ. The mean tonnage of the boats off SP and SC was assumed constant (42.5 tons) during the period (SUDEPE, 1986).

During this brief period of time the catchability coefficient did not show a clear increasing trend, as one would expect as the result of technological innovations to locate and capture fish. This is, however, consistent with the fact that the major technological innovations occurred in the sardine fishery after 1985 with government incentives to renovate the fleet (IBAMA, 1995). The catchability coefficient does show an inverse relationship with stock biomass (Fig. 4.13). Saccardo (1983) also emphasized the role of the oceanographic configuration in conditioning the catchability of the stock to purse seiners. For instance, temperatures below normal off Rio de Janeiro in 1979 and 1981 seems to have caused the displacement and concentration of sardine shoals to the south thus increasing the catchability of the stock to the operating fleet (Fig. 4.14). It is therefore possible that the correlation between stock biomass and catchability is in fact conditioned by a third variable (e.g. Sea Surface Temperature). To isolate the effect of temperature on catchability, a partial correlation analysis (Blalock, 1972) between biomass and catchability was done allowing the mean sea surface temperature in the Bight explain all it can of both variables. Partial correlation coefficients (Table 4.12) indicate that temperature has only a slightly effect on the correlation between B and q, which are strongly negatively correlated. Similar trends have been observed in other small pelagic species (MacCall, 1976; Csirke, 1989), and explained as a result of three interacting processes (MacCall, 1990; Pitcher and Parrish, 1993; Pitcher, 1995). First, schooling and shoaling, which are behavioural adaptations evolved to cope with the volatility of the pelagic environment, cause fish to maintain a roughly constant shoal size by interchange of individual fish from depleted shoals to intact ones. Second, shoals

tend to occupy preferably the areas of the sea with high habitat suitability, so that as the number of fish and shoals decrease, the area occupied by the species is also reduced (range collapse). The third factor, which is technological, involve the fact that purse seiners are very efficient in locating and capturing fish shoals, so that individual fish in an area become more catchable as stock density decreases.

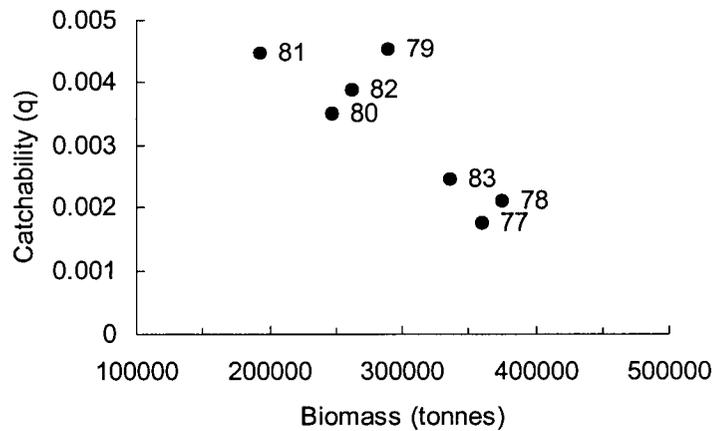


Figure 4.13. Relationship between catchability to the purse seine fleet and sardine stock biomass. Data points labeled with years.

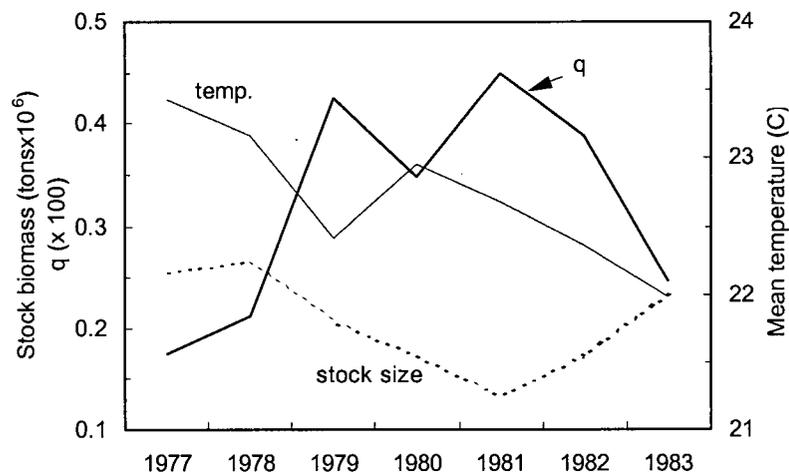


Figure 4.14. Changes in the catchability of sardine with stock size and the mean sea surface temperature in the Southeastern Brazilian Bight. Temperature was obtained from the COADS database and the average computed for the whole shelf area.

Table 4.12. Results of partial correlation analysis between catchability, stock size and sea surface temperature.

Variables	Correlation
Catchability vs. Stock biomass	-0.887
Catchability vs. Temperature	-0.459
Temperature vs. Stock biomass	0.335
Partial Correlation of Catchability and Stock biomass	-0.877

In the case of the Brazilian sardine, the decrease in stock biomass observed from the mid-1970s to the early 1990s appeared to be followed by a substantial reduction in the distribution range of the species (Fig. 4.15), which tended to concentrate in smaller areas on the southern and central parts of the bight. This decrease in spatial range is also consistent with the changes in the regional distribution of landings (Fig. 4.16) which became highly concentrated in the south after the mid-1980s. However, it is still unclear whether the collapse in distribution range was due exclusively to the interaction between environmental and behavioural mechanisms, or a result of a depletion of geographically separated stocks. The hypothesis of two separated groups of sardine in the Southeastern Bight is supported by differences in size composition, spawning locations and time (Rossi-Wongtschowski, 1977), and protein biochemical types (Vazzoler and Phan, 1976), which all indicate the existence of one group in the north, between 22° and 25° S, that spawns during spring and summer, and a second group in the south (26° to 28° S) spawning mainly in spring. On the other hand, results of egg and larvae surveys indicate that spawning has taking place in different locations throughout the years and seems to be mostly determined by oceanographic conditions (Matsuura, 1988). In this sense, the observed concentration of sardine to the south would be a result of better oceanographic conditions in the area, and the depressed total biomass, which would force shoals to occupy a fairly restricted geographical range.

The effect that the collapse in distribution range had on stock catchability is still unknown given the lack of information on fishing effort by each state fleet since the mid-1980s. Ultimately, the increase in stock catchability depends on how efficient are purse seiners in following the fish with the range collapse, that is, on how fishing effort is allocated. This question is addressed in the next sections by looking at the fleet characteristics and movement over the Bight.

Fleet characteristics

The purse seine fleet is basically divided among three states, Rio de Janeiro (RJ), São Paulo (SP) and Santa Catarina (SC).

Rio de Janeiro

In 1977 a total of 300 boats was fishing sardine in the Southeastern Brazilian Bight. Wiefels & Jablonski (1979) concluded from sampling 2/3 of this total that ca. 52 % of the boats were fishing on waters off RJ. From the sampled boats, 14.5 % had less than 15 m, 60.5 % between 15 and 22 m and 25 % between 22 and 27 m. Purse seiners targeted sardine and other pelagic species, specially mackerel *Scomber japonicus*. The importance of mackerel in the catches became more important after 1982, when the species made up to 70% of the total catches. From 1982 to 1985 the fleet was composed by an average of 167 boats constantly in activity and by 123 boats eventually in activity for less than 3 months per year. By 1985 ca. 40% of this fleet had more than 20 tons (average size 18.6 m) and 60% had less than 20 tons (average size 12.3 m). Most of the sardine catches came from the "constant" boats and from those with tonnage larger than 20 tons. Both fleet components also fished on alternative species, although this activity was more important for the smaller boats usually restricted to nearshore areas (less than 50 m). At that time there were at least 8 major landing ports along the coast. Variations in the oceanographic conditions and fish distribution determined the importance of each of the landing ports, as boats were highly mobile in the search for the most productive sites within the state waters (SUDEPE, 1986). Larger boats (tonnage larger than 20 tons) were at least 3 times more efficient in finding and capturing fish shoals than smaller boats (SUDEPE, 1986).

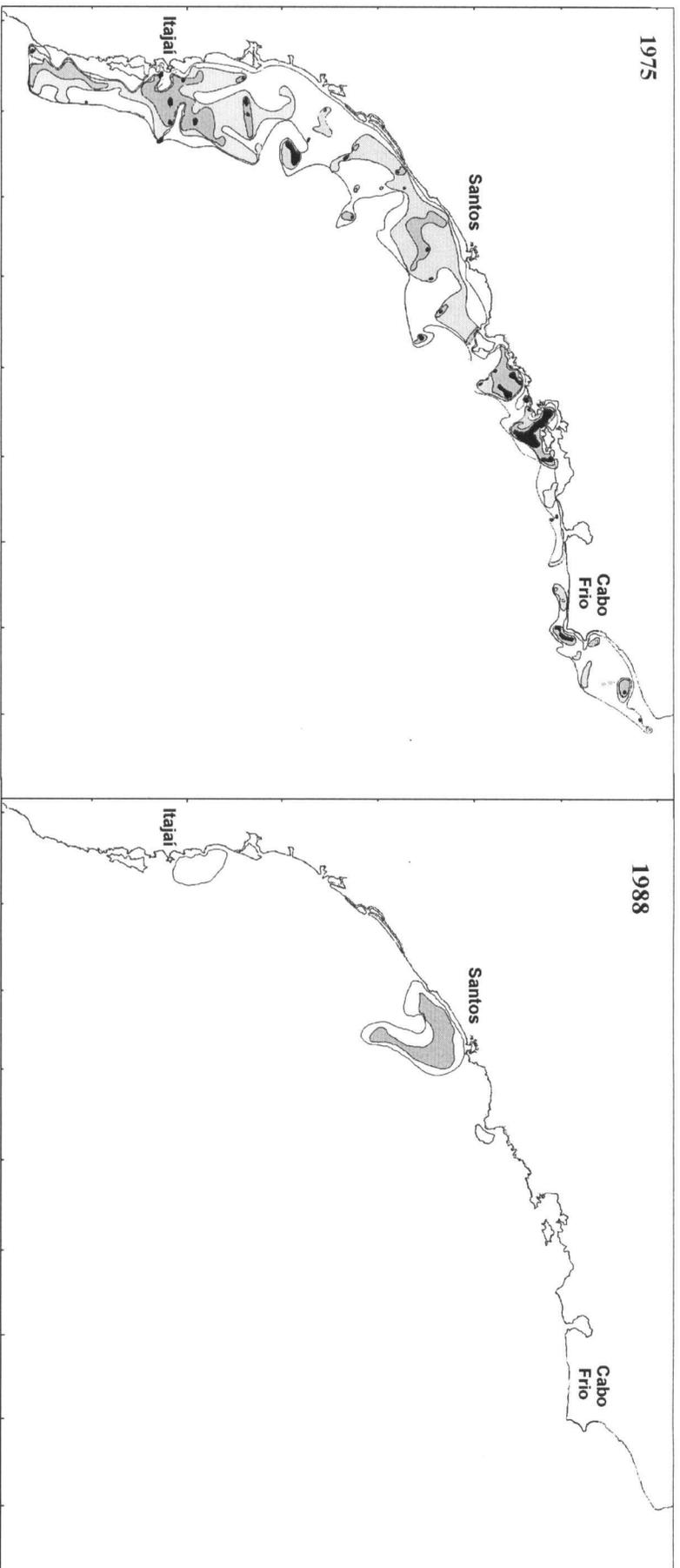


Figure 4.15. Sardine stock distribution area as estimated by acoustic surveys. Left panel: 1975 (Johannesson, 1975); Right panel: 1988 (Castello et al., 1991). Fish densities are indicated by the shades of grey.

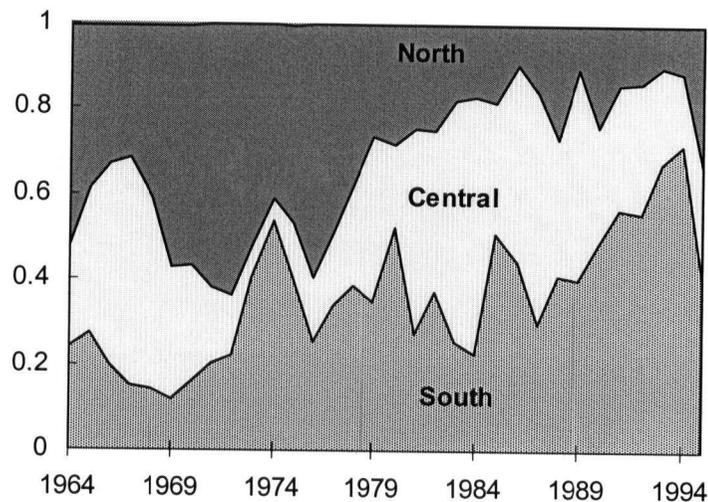


Figure 4.16. Proportion of total sardine landings by fishing area. South refers to landings in Santa Catarina, central to São Paulo, and north to Rio de Janeiro (source IBAMA, 1995).

In 1987 the number of boats with tonnage superior to 20 tons decrease to 69 (Valentini and Cardoso, 1991). This decrease was balanced by an increase in the number of smaller boats, who had sardine as one of the target species. Part of the larger boats that used to fish sardines were adapted to fish bonito, *Katswonus pelamis*. Valentini and Cardoso (1991) suggested that the number of purse seiners licensed on RJ remained relatively high even after the decrease of the sardine catches after 1981, since sardine was not anymore the mainly elected species in the fishery, but one of the alternative pelagic fishes. The first attempt to regulate the number of fishing licenses came in 1989 with the *Portaria IBAMA 1347/89*. At that time there were a total of 105 licensed boats and about 180 illegal boats fishing for sardine off RJ. Vessel numbers and characteristics did not change significantly until 1992, although a decrease in the number of active boats with the decrease in catches was observed. Of the 162 licensed boats, 131 were considered artisanal due to their small size and tonnage (< 20 tons), and the lack of technological devices. The 31 remaining boats were more equipped (sonar and power block), with tonnage between 20 and 81 tons and power between 110 and 150 HP. Even after the efforts to legalize all the purse seiners there are still boats fishing sardine without license.

São Paulo

The number of purse seiners in São Paulo increased from 55 in 1973 to 120 boats in 1988 (Valentini and Cardoso, 1991). With the collapse of the fishery in the late 1980s and early 1990s, there was a decrease in the number of boats actively fishing. In 1989, only 77 of the 113 licensed vessels were active; 47 in 1990; 35 in 1991; and almost all fleet was inactive in 1992 (IBAMA, 1991; 1992; 1993; 1994). Illegal boats were also observed in SP, making up to 34 boats in 1989 and only 6 in 1990. Overall, boat characteristics remained similar along the years, mean size of 19 meters, mean tonnage of ca. 55 tons and 260 HP power. However, some of the vessels acquired technological innovations such as sonar and power blocks after government incentives for fleet modernization during the 1980s.

Santa Catarina

Since the early 1970s the Santa Catarina's fleet was characteristically the most technologically equipped and with larger vessels among the three states. The number of boats increased from 54 to 105 between 1973 and 1988. Fleet mean characteristics were: size 21 meters, tonnage 73 tons and 262 HP of power. The SC fleet significantly increased fishing power after 1985, following the government incentives, with the introduction of sonar and power-block. Technological improvements to locate and catch fish were particularly improved in 1988. With the collapse of the stock in the late 1980s the number of active boats progressively declined. Only 74 of the 107 licensed boats were actively fishing in 1991. A total of 12 boats still remained illegal in the fishery in 1991.

Fleet movement and effort allocation

Typically, fishing operation by purse seiners is very slow, involving sometimes up to 6 hours to complete a set. Catch volume and the long handling time determine that landings take place in ports close to the catching areas, thus creating a straight relationship between areas of sardine concentration and the landing volume in different ports along the coast (Valentini and Cardoso, 1991). Therefore, data on the origin of purse seiners at different landing ports along the coast can

provide information relevant for understanding fleet movement in the fishing ground. Figure 4.17 describes, for each state fleet, the proportion of licensed vessels that landed sardine in the different states between 1989 and 1991. The first conclusion from this analysis is that fishing boats distribute differently according to their origin; boats from RJ maintain a fairly restricted fishing area, mostly concentrated in their own state waters; boats from SP appear to utilize ports from the other two states more regularly; and the SC fleet landed sardines either in SP or in SC. The second conclusion refers to changes in fleet distribution with time, where the two most mobile fleets (SP and SC) seemed to concentrate their activity (landings) to the southern part of the stock distribution during the period analyzed. In 1989 ca. 65% of the SP fleet were actively fishing in the waters of both SP and SC, while in 1991 this proportion was more than 80%. As for the SC fleet, the southernmost state, the proportion of the fleet landing exclusively in the state waters increased from 30 to ca. 65% between 1989 and 1991. This information is consistent with the observed increase in the proportion of catches from the south (Fig. 4.16), and seems to corroborate to the hypothesis that purse seiners (at least those from SP and SC) followed sardines with the collapse in distribution range to the south in this time period. Results also indicate the possibility that the collapse in the distribution range limited access to the stock to roughly one third of the fleet, that from Rio de Janeiro, which is mostly composed by smaller and less technologically equipped boats that operate almost exclusively in the northern end of the species distribution area.

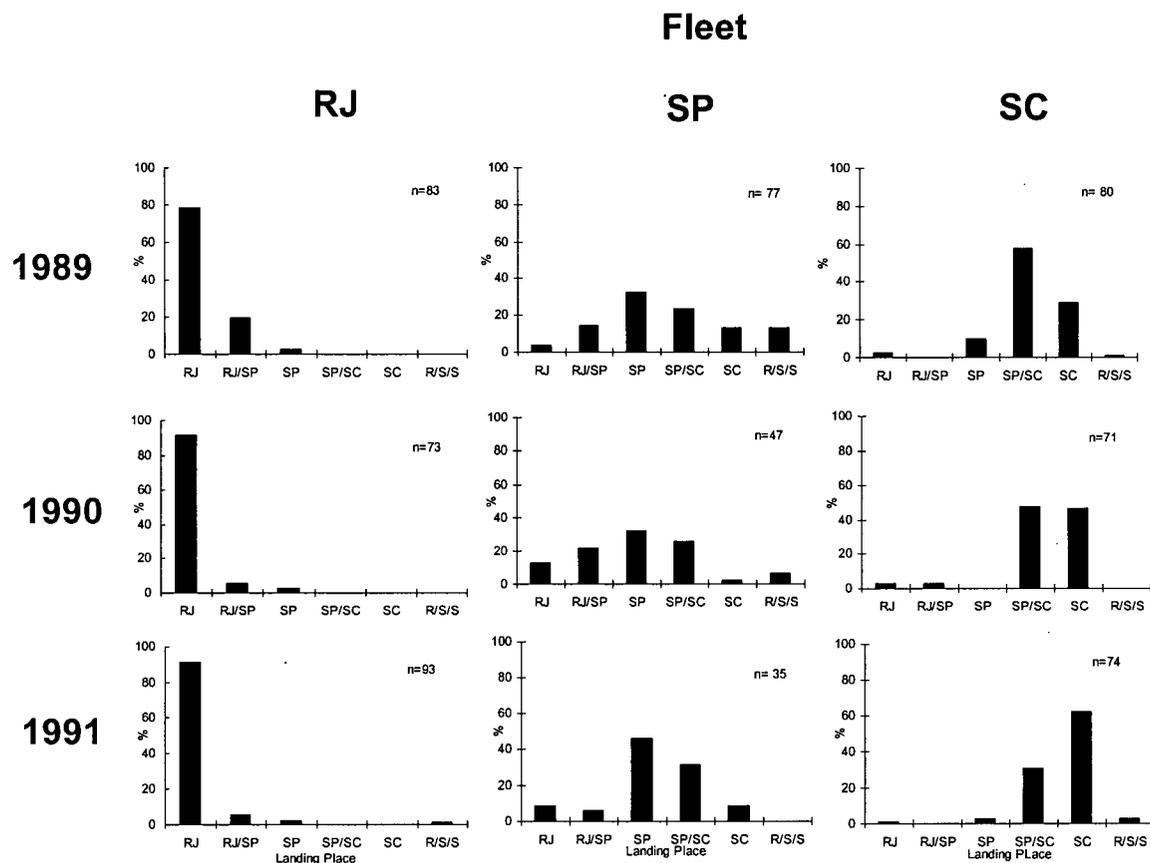


Figure 4.17. Fleet distribution by landing place. Landing places were grouped in 6 categories: restricted to Rio de Janeiro (RJ); occurring in both Rio de Janeiro and São Paulo (RJ/SP); restricted to São Paulo (SP); occurring in both São Paulo and Santa Catarina (SP/SC); restricted to Santa Catarina (SC); occurring in the three states (R/S/S).

Another likely consequence of an efficient process of search and effort allocation is that boats will move to equalize catch per unit of effort across the stock distribution area according to an Ideal Free Distribution (Hilborn, 1985; Gillis et al., 1993). Figure 4.18 shows the results of the regression of the proportion of catch in area i (c/C) on the proportion of the effort in area i (f/F) during 1990 and 1991. The ideal free distribution appears to be a good approximation to the dynamics of purse seiners off the coast of Santa Catarina, although slopes smaller than 1 were observed in the two years analyzed. That indicates higher than average return rates when proportional effort is high and smaller than average return rates when proportional effort is low. Such small deviations from the IFD line can be explained by diverse factors, including increasing information exchange between boats with increasing effort, and by patterns of exploratory behaviour adopted by skippers, which by searching areas with low cpue for better fishing opportunities may cause a decrease in average return rates in areas with low proportional effort (Gillis et al., 1993). Overall, results confirm that purse seiners are highly efficient in following

shoal distributions, and that fleet dynamics may play an important role in creating the observed increase in catchability with decrease stock size and range.

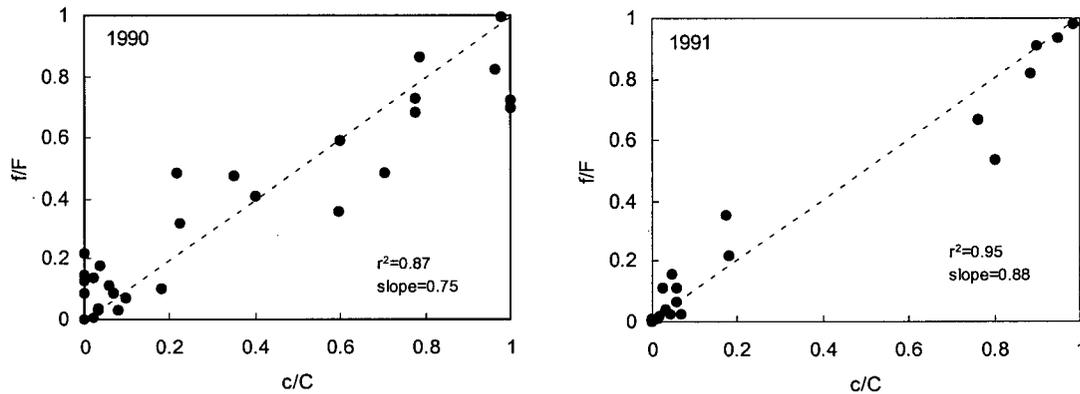


Figure 4.18. Test for the equalization of cpue among fishing areas off Santa Catarina (see map on figure 3). c/C is the proportion of the total catch in area i , and f/F is the proportion of the total effort in area i . Regression slopes are statistically different from 1 (1990: $df = 26$; $t = 3.69$; $P = 0.001$; 1991: $df = 17$; $t = 2.33$; $P = 0.032$).

The analysis of stock catchability, range collapse and effort allocation has two general consequences for sardine stock assessment. First it indicates that cpue and other fishery dependent indexes of abundance are potentially biased by the behaviour of fish and by the characteristic non-random search of fishing vessels. Second, it questions the effectiveness of harvest control by effort limitation in preventing stock overfishing, specially with the overcapacity of the fleet. Besides being affected by the increasing catchability, tactics of effort control by fishing closures are particularly inefficient when fishers reallocate effort temporally (Fig. 4.19). For instance, up to 1990 effort was controlled by one fishing closure during the spawning season. With the prospect of stock collapse in 1991, a second fishing closure was established during the recruitment months. As a consequence, effort (measured by the number of trips of the SC fleet) was simply reallocated to the other months of the year, total effort being almost the same between the two years. These results indicate that much insight can still be gained in controlling harvest by understanding fishers dynamics in allocating effort in space and time.

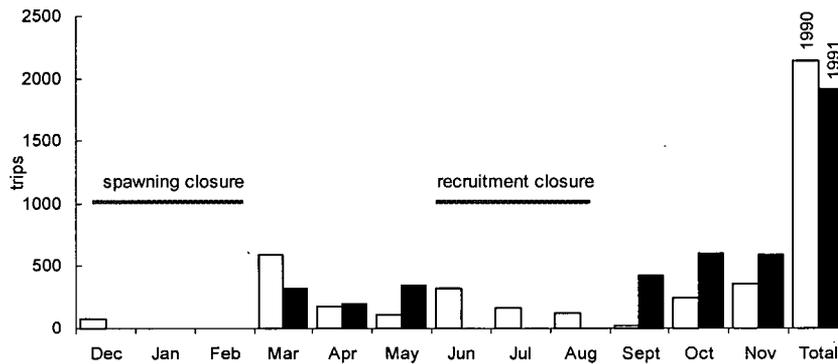


Figure 4.19. Monthly effort allocation by the Santa Catarina fleet before (1990) and after (1991) the establishment of a recruitment closure.

4.4. Summary

This chapter reviews the status of sardine stock assessment and analyze the current ecological uncertainties in the management of the fishery. The ecosystem of the Southeastern Brazilian shelf is structured around the operation of physical-biological cycles of different speeds, the most documented ones being the seasonal upwelling cycle, and the decadal regimes determined by multi-year variability in the intensity of physical forces controlling biological production. The latter is particularly important for the management of fishery resources because it operates at the time scale commensurate with the life span of most marine fish populations. Fisheries in the Southeastern shelf have been targeting mostly low trophic level species and have since the late 1970s experienced an increase in the mean trophic level of landings. The scale of fisheries impact and the effect of environmental regimes are often associated to changes in the structure of the ecosystem and to a decrease in recruitment rates of the sardine population. The combined effect of fishery and natural processes make it difficult however to characterize the productivity of the population and to predict the results of rehabilitation measures for the sardine stock. Also, given the current regulatory mechanisms, the implementation of any measure to control harvest will encounter difficulties created by the behavior of the fish and the dynamics of the fishing fleet, which seems to be responsible for changes in the stock catchability.

Chapter 5. Analysis of harvest decisions and information needs in the management of the Brazilian sardine. Comparing multi-species and single-species modeling approaches

5.1. Introduction

This chapter aims to evaluate the short and long term predictions of the impacts of harvest strategies and controls for the Brazilian sardine, and to discuss the relative values of reducing current uncertainties on ecological processes. Results are used to recommend on the types of research that would most likely provide the type of information needed to improve the quality of decisions, and on the precautionary measures that should be adopted in face of the ecological uncertainties.

One the major tasks of fisheries assessment is to estimate the tradeoffs of management choices. Also, as a scientific activity, fisheries research involves a process of learning about nature in which alternative ideas, or hypotheses, are contrasted against observations and experiences, so that a better understanding of the potential responses of systems being managed can be achieved through time. In these activities models are usually employed as tools to test our understanding of the mechanisms in the system, to provide the basis for both understanding of known patterns and prediction about situations not yet encountered, and to provide the means for evaluating the potential effects of various kinds of decisions (Hilborn and Mangel, 1997).

Fisheries assessment can be based on two types of modeling approaches: single-species and ecosystem or multi-species models. Ecosystem models are in their infancy and have been little used to date. Single-species models are based solely on the analysis of population processes such as growth, mortality and recruitment, and has been the most widely applied approach to provide advice on the consequences of fishery regulatory tactics. By definition, multi-species models consider not only the biological processes of the target population but also the ecological (e.g. predation, consumption, competition) and technological (e.g. by catch) interactions with other species in the ecosystem. Ecosystem impacts of fisheries has become an important concern in fisheries management and one of the most important issues in fisheries science. Therefore, a

central question for fisheries assessment today is on how to evaluate and communicate the impacts of alternative fishing policies on marine resources and ecosystems. Multi-species models have been proposed as tools for guiding the implementation of ecosystem principles in fisheries management, but exactly how the approach could be used, and also what should be the role of single-species approaches in this new paradigm, are still unclear. Such comparisons have not been performed explicitly before.

Following the framework outlined in chapter 1, this chapter analyzes how management decisions in the sardine fishery can be made under current ecological uncertainties, and how recommendations differ according to two modeling approaches: a single species and a multi-species model. Models are employed in this analysis to evaluate two types of decisions. The first concerns the evaluation of strategies for sardine stock recovery. The analysis aims to evaluate the short term predictions of stock recovery according to different fishing strategies. The second type of decision relates to the choice of long term fishing strategies. I discuss the value of reducing uncertainties about ecological processes, the opportunities for improving understanding of these processes, and the precautionary measures that should be adopted in face of ecological uncertainties.

5.2. Methods

Modeling approaches

The evaluation of the performance of fishing strategies was carried with two modeling approaches: a single-species delay-differential model (Deriso, 1980; Fournier and Doonan, 1987) and a multi-species trophic model (Ecosim, Walters et al., 1997).

Single-species approach

Fishing strategies were evaluated with a Delay-Differential model used as an operating model in Monte Carlo simulations. The model predicts next year's biomass (B_{t+1}) and numbers (N_{t+1}) according to the equations (Hilborn and Walters, 1992):

$$B_{t+1} = s_t [\alpha N_t + \rho B_t] + w_k R_{t+1} \quad (1)$$

$$N_{t+1} = s_t N_t + R_{t+1} \quad (2)$$

where w_k is the weight at recruitment age k (years), $s_t = \lambda(1-h_t)$ is the total survival rate, λ is the natural survival rate ($\lambda=e^{-M}$), M is the instantaneous natural mortality rate ($=0.95 \text{ year}^{-1}$), and h_t is the exploitation rate. The exploitation rate can be calculated as the ratio catch/biomass in a given year, or as a function of fishing effort, i.e., $h = 1 - e^{-qE}$, where E is effort and q the catchability parameter. Catchability was represented by an inverse function of stock abundance:

$$q = q_1 B^{-q_2} \quad (3)$$

where q_1 is a proportionality constant and q_2 is the degree to which catchability increases with declining stock size.

The delay-differential model also represents growth and recruitment processes. Growth in mean body weight at age is described by a Ford-Walford plot of the type $w_a = \alpha + \rho w_{a-1}$, where α and ρ are constants from the regression between weight w at consecutive age classes $a = k, k+1, \dots$ fully vulnerable to the fishery. Sardine parameter values for α ($= 0.025$) and ρ ($= 0.896$) were obtained by regressing data on weight at consecutive ages from Cergole (1994). Recruitment (R_{t+1}) is included in the model as functions representing different stock-recruitment hypotheses (Table 5.1).

Uncertainties are included in three processes/states: (1) the relationship between spawning stock and recruitment; (2) the relationship between stock biomass and catchability; and (3) the assessment of stock biomass at sea. Uncertainties in the relationship between stock and recruitment were represented according to the hypotheses about recruitment changes outlined in chapter 4. For decision analysis, all hypotheses were assigned equal degree of belief, i.e., they are assumed to fit the available data equally well. The hypotheses and models used in this analysis are described in table 5.1.

Table 5.1. Hypothesis, models and parameters used to predict recruitment rates in the Delay-differential model (source chapter 4).

Hypothesis	Model	Parameter values
1. Recruitment is a function of stock size	$\text{Recruits} = \frac{aSSB^x}{1 + \frac{SSB^x}{K}} e^v$	a = 135 K = 0.0888 x = 1 v = 0.4
2. Recruitment is a function of stock size with depensation at low stock sizes.	$\text{Recruits} = \frac{aSSB^x}{1 + \frac{SSB^x}{K}} e^v$	a = 867 K = 0.0138 x = 2 v = 0.4
3. Recruitment is a function of stock size and low frequency environmental regimes.	$\text{Recruits} = \frac{aSSB}{1 + \frac{aSSB}{K}} e^v$ $a = \exp^{-M_1}$ $K = \frac{M_1}{M_2(\exp^{M_1} - 1)}$	$M_{1,t} = -3.576 + 1 \cdot \text{Sin}\left(\frac{t \cdot \pi}{10}\right)$ M ₂ = 0.152 v = 0.4

Uncertainties in the relationship between stock biomass and catchability were described by marginal posterior probability distributions for parameters q_1 and q_2 (equation 3) based on catchability data from chapter 4. Probabilities were computed using Bayesian analysis,

$$P(q_1, q_2 / \text{data}) = \frac{L(\text{data} / q_1, q_2) \cdot p(q_1, q_2)}{\sum L(\text{data} / q_1, q_2) \cdot p(q_1, q_2)}$$

where the likelihood of a given parameter combination $L(\text{data}/q_1, q_2)$ is calculated assuming that catchability values present a log-normal distribution (i.e. assume only positive values), and the prior probability distribution of parameters $p(q_1, q_2)$ have an uniform distribution. The likelihood of a given parameter combination was calculated as

$$L(\text{data} / q_1, q_2) = e^{-1/2 \left(\frac{SS}{SS_0} \right)}$$

where, $SS = \sum_t (\ln q - \ln \bar{q})^2$, $SS_0 = \sum_t (\ln q - \ln \hat{q})^2$, q is the catchability coefficient calculated from VPA and observed effort data (see chapter 4), \bar{q} is the estimated catchability from q_1 and q_2 , and \hat{q} is the estimated catchability at best fitting q_1 and q_2 . Figure 5.1 shows the estimated marginal posterior probability distribution of catchability parameters.

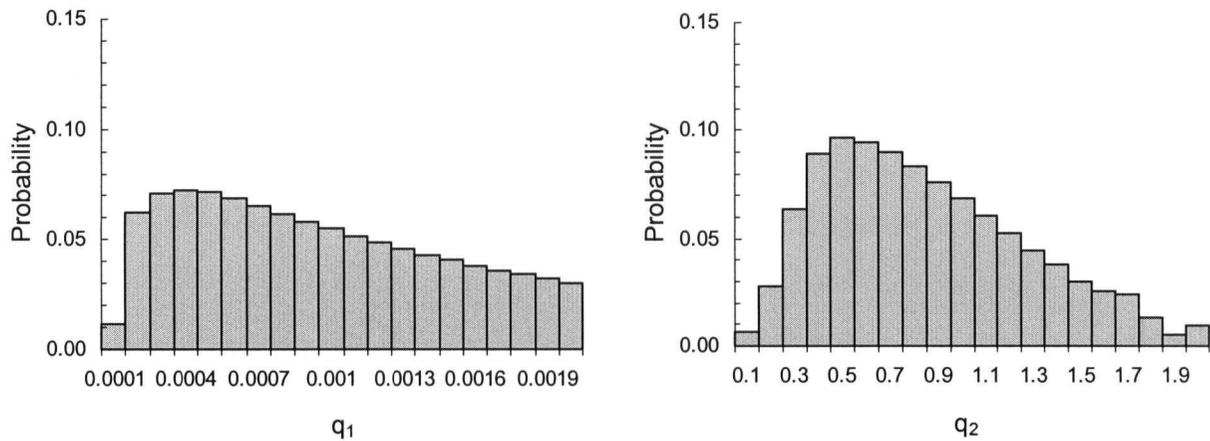


Figure 5.1. Marginal posterior probability distribution of catchability parameters q_1 and q_2 (from equation 3) for the Brazilian sardine fishery based on data from 1977 to 1983 (see chapter 4).

Finally, uncertainties in the estimation of stock biomass by direct methods (e.g., acoustic surveys, egg production, etc.) were introduced by including a normally distributed error around the true stock biomass (Frederick and Peterman, 1997), where

$$B_{est} = B_t + (B_t \cdot CV \cdot w)$$

B_{est} is the estimated stock biomass in year t , B_t is the true biomass, CV is the coefficient of variation of the biomass estimation procedure ($0 < CV < 0.5$), and w is a normally distributed variable with mean 0 and variance 1.

Monte Carlo simulations were used to evaluate the expected outcomes of fishing strategies for sardine. Three criteria are used in the evaluation of strategies: average catches, catch variability, and the probability of stock collapse. These criteria were selected because they represent three types of objectives commonly observed in fisheries management:

- Maximize yield. In effect, the increase in fisheries catches represent more fish to the industry, more economic opportunities to the capture sector and, consequently, more job offers.
- Maximize catch stability. Very often, the major interest with a management plan is to guarantee the stability or low variability of catches, and therefore maintain a constant supply of fish to the industry.
- Minimize the chances of fishery collapse. That is a fundamental objective to any fisheries management plan, considering the ecological and economic costs associated with the collapse of fisheries.

Two types of fishing strategies are evaluated:

- Catch control: the total catch allowed in a given year is defined in advance. Three types of catch control options are considered: constant allowable catch; total allowable catch defined by a constant exploitation rate; and total allowable catch defined by a minimum stock escapement.

- Effort control: that represents the *status quo* policy of fishing control in the sardine fishery, involving the definition of a limit to the total effort allowed in a given year, and a minimum size of fish in the catches. In this specific case the effort unit used was the number of trips corrected by the mean tonnage of boats, as in chapter 4. Ideally the analysis of a purse seine fishery should use as effort unit any measure of fishing time such as fishing days, time searching, etc. Nonetheless, the characteristic short duration of purse seiners trips in the sardine fishery allows for a reasonably good approximation between the number of trips and the number of fishing days.

Figure 5.2 represents the structure of the decision problem analyzed. The choice for one fishing strategy in the left hand side will depend on the objectives considered and on the uncertainties on diverse processes and states (depicted as branches diverging from the circles). For instance, the choice for an strategy of catch control is made difficult by uncertainties on population characteristics, such as virgin biomass and productivity, as well as on the size of the stock in the sea. The choice for an allowed level of effort is on the other hand influenced by the stock productivity (i.e. recruitment) and the catchability to the purse seiners. All decisions are subjected to the inherent uncertainties about the future environmental regime.

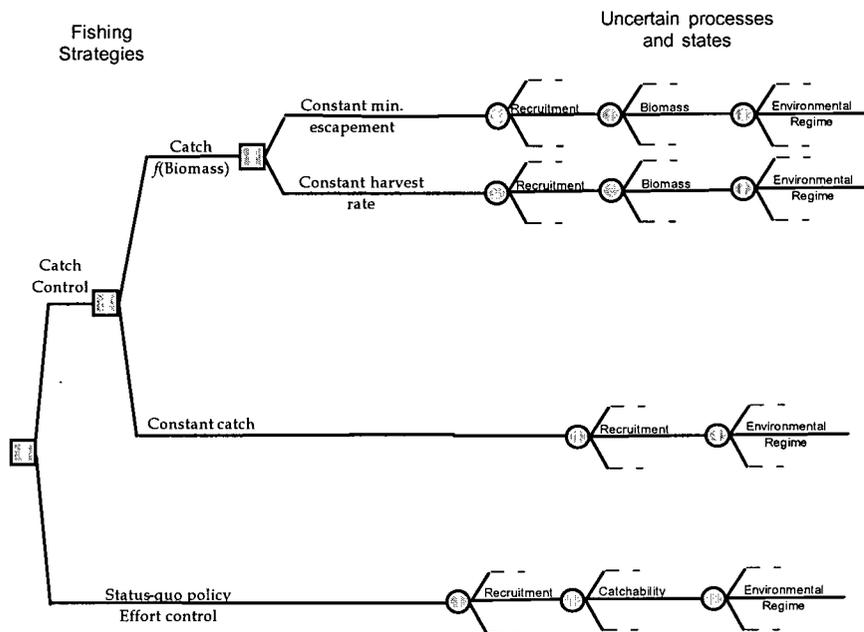


Figure 5.2. Conceptual structure of a decision analysis on the choice for fishing strategies for sardine. The squares on the left hand side represent decisions, the circles represent the main uncertainties on population processes and states.

Expected outcomes of fishing strategies

The expected outcome of the different combination of fishing strategies and controls were obtained following the steps below (Figure 5.3). Starting conditions for simulations were set to be consistent with the observed status of the fishery in the late 1970s.

- 1) A number of alternative strategies in each strategy type (catch or effort control) was defined by test runs of the model and also by using historical data from the fishery. Specifically in the case of strategies of effort control, effort levels applied between 1977 and 1983 (Chapter 4) were used as reference points to define alternative fishing strategies. An age at first capture of 1.5 years (approximate age of first maturity) was used as auxiliary measure to effort control.
- 2) Simulations were run for 10 years having as starting conditions the average spawning stock biomass between 1977 and 1983 from VPA (~250,000 tons), and a dome-shaped regime of environmental conditions as proposed by Bakun (1996) for the 1980s (see Chapter 4) .
- 3) The expected outcome of a given fishing strategy was calculated as the average of the 10 years runs obtained in 1000 Monte Carlo simulations, weighted by probabilities of parameters, models and variables used in the model.
- 4) The performance of each fishing strategy is defined by the expected average catch, catch variability, and the frequency of cases (simulations) in which the spawning stock was driven

below the historical lowest size, that is approximately 50,000 tons. This frequency was used as a measure of the probability of stock collapse.

Predictions of stock recovery

Simulations were carried also to examine the expected responses of the stock to strategies of stock rebuilding after the collapse. Stock biomass and exploitation rates for the late 1980s were used as starting conditions for simulating biomass recovering trajectories using the same procedure outlined in Figure 5.3.

Spawning stock per recruit

Data on survival, maturity and reproductive output at age (Table 5.2) were used in the analysis of spawning per recruit

$$SPR_{A50\%} = \sum_{i=0}^{3.5} (l_i f_i R_i)$$

where $SPR_{A50\%}$ is the number of spawners produced per recruit for a given combination of age at first capture ($A_{50\%}$) and exploitation rate ($E=F/Z$; [0.1]); l_i is the survivorship to age i ($l_i=l_0s(1-V_iE)$), l_0 is the survivorship to age 0 (=1), $s = \exp^{-M}$, M is the instantaneous natural mortality rate; V_i is the age specific vulnerability, and R_i is the age specific reproductive output. V_i is a function of the age at first capture and a concentration parameter ($b=10$), i.e.

$$V_i = \frac{i^b}{A_{50\%}^b + i^b}$$

The reproductive output weights the relative reproductive contribution of an age class be accounting for differences in relative fecundity and frequency of spawning (Parrish et al., 1986). SPR is expected to decrease with E , and is normally expressed as the percentage of the SPR value calculated for an unfished stock (%SPR; Goodyear, 1993).

Table 5.2. Percentage of individuals mature and the reproductive output (A) at age for *Sardinella brasiliensis* (source Cergole, 1994). The reproductive output (A) was calculated using the equation proposed by Parrish et al. (1986) to *E. mordax*. The equation was adjusted so that the relationship $A_i = 0.0000432W_i^{2.64}$ generates a factor A=1 when the weight $W = 45g$, the approximate mean weight at age at first maturity

Age	0	0.5	1	1.5	2	2.5	3	3.5
%Mature	0	0	0.5	0.75	1	1	1	1
A	0	0	0.83	1.00	1.95	3.21	5.19	10.58

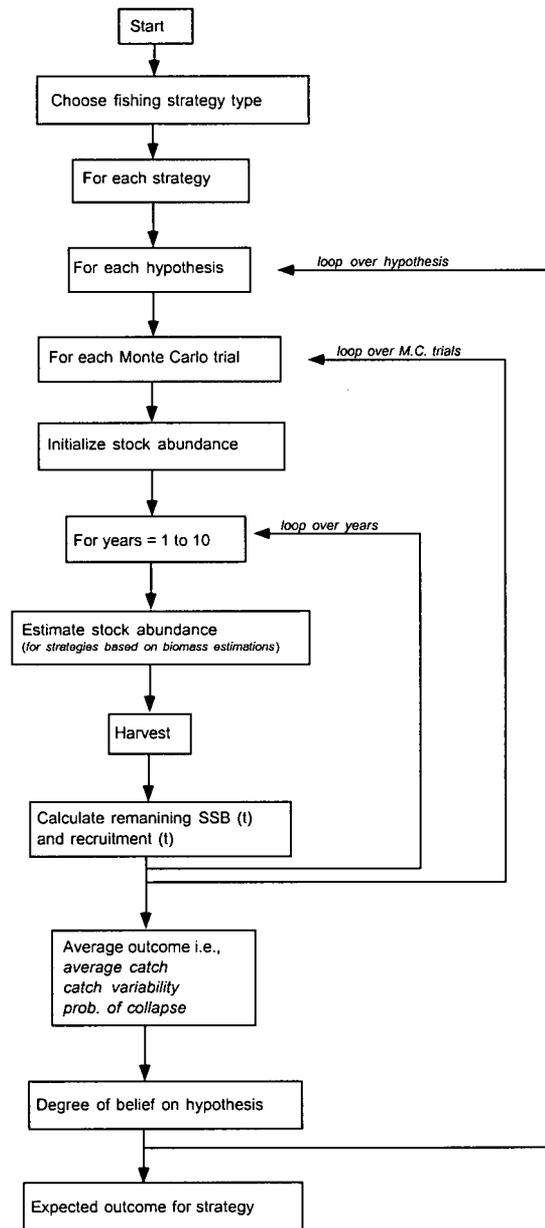


Figure 5.3. Monte Carlo simulation procedure used in the evaluation of the outcomes of fishing strategies using a single-species approach.

Multi-species approach with Ecosim

A trophic model of the Southeastern shelf ecosystem (Fig. 4.4; chapter 4) is used in this section to evaluate fishing strategies for sardine when the population is placed in an ecosystem structured by trophic (i.e., predator-prey) relationships. The model has 22 trophic groups, and tracks changes in number and biomass of three groups (sardine, triggerfish and weakfish) that were split between juvenile and adult pools. Ecosim (Walter et al., 1997) was used to evaluate the predicted effects of short-term harvest strategies on the main harvested species in the ecosystem, and also to assess optimal fishing rates for the sardine stock. Model details are given in chapters 2 and 3.

Uncertainties were accounted for the type of control of trophic relationships in the ecosystem, which has been shown to influence the magnitude and direction of changes in the ecosystem when subjected to fisheries (Chapter 2). Three hypotheses are considered to have the same degree of belief:

- a) *bottom-up control*, where the amount of prey available to predators is limited so that the mortality rate of a species in the ecosystem is largely independent of the abundance of predators.
- b) *top-down control*, where a larger part of prey biomass is vulnerable to predation, and mortality rate is largely dependent on the abundance of predators.
- c) *“wasp-waist” control* (Bakun, 1996; Cury et al., in press), where the abundance of small pelagic fish control both their predators and prey. Following Cury et al., the interaction between small pelagic fish (sardine, anchovy, and other forage fish) and their prey (phyto and zooplankton) is assumed to be top-down controlled, while the interaction between small pelagics and their predators is bottom-up controlled. Top-down and bottom-up control were set in the model according to the scenarios a and b above.

Trophic control hypotheses were combined with two contrasting assumptions about the maximum relative foraging time of apex predators in the system. The combination of hypotheses thus produced 6 different models used in the analysis of fishing policies.

To examine the short term effects of fishing strategies, dynamic simulations were run for 5 years according to fishing scenarios that halve, completely stop, and double the fishing rates of the four major fleets in the region, i.e., Purse seiners, Bottom trawlers, Shrimp trawlers, and Pole-and-line vessels. Scenarios 1, 2 and 3 represent fishing strategies solely directed to the Purse seine fleet, resulting in a 50% decrease, 100% decrease, and a 100% increase in F for sardine in 5 years, respectively. Strategies were also tested where all fleets (Purse Seiners, Bottom trawlers, Shrimp trawlers, and Pole-and-line vessels) are decreased by 50% (scenario 4); decreased by 100%, i.e., all fisheries closed (scenario 5); and increased by 100% (scenario 6) during a 5 years period. No by-catch is included in the model, as the objective of the simulations was to investigate the likely effects of changes in fishing mortality rates for the target species.

To assess the optimal fishing mortality for the sardine stock, simulations were run for 10 years and the average sardine yield compared among constant fishing rates.

Valuing new information: the Expected Value of Perfect Information

The quantitative decision analysis described above provides information useful for the computation of risks associated with harvest decisions, either in terms of the expected consequences of a given action or in terms of the odds of obtaining an outcome different from that prescribed as the most probable. That in turn allows evaluation of how well decisions can be made with present available information and uncertainties. Simulation results are thus used to evaluate the benefits of reducing uncertainties on the processes relevant for the decision problem. The objective of this analysis is to calculate the expected value of a decision made with perfect information about each of the hypothesis is true. This value, termed the expected value of perfect information (EVPI), represents the maximum, or upper bound, on what we should be willing to pay for research that will generate new information that reduces uncertainties.

Two steps are necessary to calculate the EVPI (Walters, 1986; Morgan and Herion, 1990). First the expected value of a decision made with perfect information must be calculated. Imagining that we could forecast which state of nature exists, so that we could choose the optimal action for that state, then the value of a decision made with perfect information would simply be the forecasted result of that decision. However, at this point in time we are uncertain about which

state of nature exists, so the expected values of outcomes for each optimal action for each possible state of nature must be weighted by the probability of occurrence of those states. Therefore the expected value with perfect information (EVWPI) is calculated as

$$EVWPI = \sum_i [p(i) \cdot \text{Max}(i)]$$

where, $p(i)$ is the probability of state i occur, and $\text{Max}(i)$ is the best outcome for state of nature i . To calculate the expected value of perfect information, then EVWPI needs to be subtracted from the maximum expected value from a decision analysis made under uncertainty, i.e. that takes uncertainty into account (EIU).

$$EVPI = EVWPI - EIU$$

In this sense, EVPI indicates the total cost or value loss resulted from being uncertain. In the present analysis the expected value of perfect information is computed with both modeling approaches using the probabilities placed on each hypothesis or model, and the conjunct of decisions outlined above. For the single species approach, EVPI is computed for two types decisions: in the choice of an optimal exploitation rate; and in the choice of an optimal effort level. For the multi-species approach EVPI is computed for the choice of optimal fishing rates for sardine. The objective to be maximized in each case is the average catch in the time period specified.

5.3. Results and Discussion

Single-species approach

Simulations were run for 10 years, having as starting conditions the spawning stock biomass and environmental conditions hypothesized for the late 1970s. Results are shown in figures 5.4 to 5.7. Strategies of catching a constant proportion of the stock and allowing a constant escapement produce the highest yields among the strategies tested. Changes in stock catchability with stock size decrease considerably the performance of strategies of effort control. Similarly, constant catch strategies resulted in the lowest average yield among the strategies tested. The performance of constant escapement strategies are particularly sensitive to errors in biomass

estimates. The general effect is of decrease in average yield, increase in catch variability and in the chances of stock collapse with the increase in coefficient of variation of the estimation method (Figure 5.7). The adoption of more conservative escapement levels does not reduce the relatively high chances of stock collapse when the error in the estimation procedure is larger than 30%. Variations of this magnitude are commonly observed in acoustic estimation methods as a result of variations in the adjustment of ecosounders, changes in the acoustic properties of fishes, and the efficiency with which surveys cover the complete distribution area of the stock (MacLennan and Simmonds, 1992). Misund (1997), for instance, reported differences of ca. 100% in the estimation of herring biomass obtained between surveys in the same year. Similarly, acoustic assessment of sardine biomass in the 1988 spawning season (Castello *et al.*, 1991) produced a confidence interval for stock biomass between 38 and 77 thousand tons, corresponding to a coefficient of variation in the order of 30%.

Strategies of catching a constant proportion of the stock annually are less sensitive to errors in biomass estimates. The increase in the coefficient of variation of estimations has very little influence over the expected average yield, but increase the variability of catches and the chances of stock collapse (Figure 5.6). For a harvest rate of 0.5, the chances of bringing the stock to collapse increases from less than 1% to more than 50% when cv increases from 0 to 0.5.

The expected yield under effort control peaks at ca. 350 effort units, with a probability of stock collapse of less than 20% (Figure 5.5). Figure 5.5 also represents the approximate fishing effort applied to the stock in the period from 1977 to 1983, which was very close to the predicted optimal effort level. Considering that since then the purse seine fleet has doubled in size and became more technologically equipped with sonar and power blocks, it is suggested that chances of stock collapse increased considerably during the following decade.

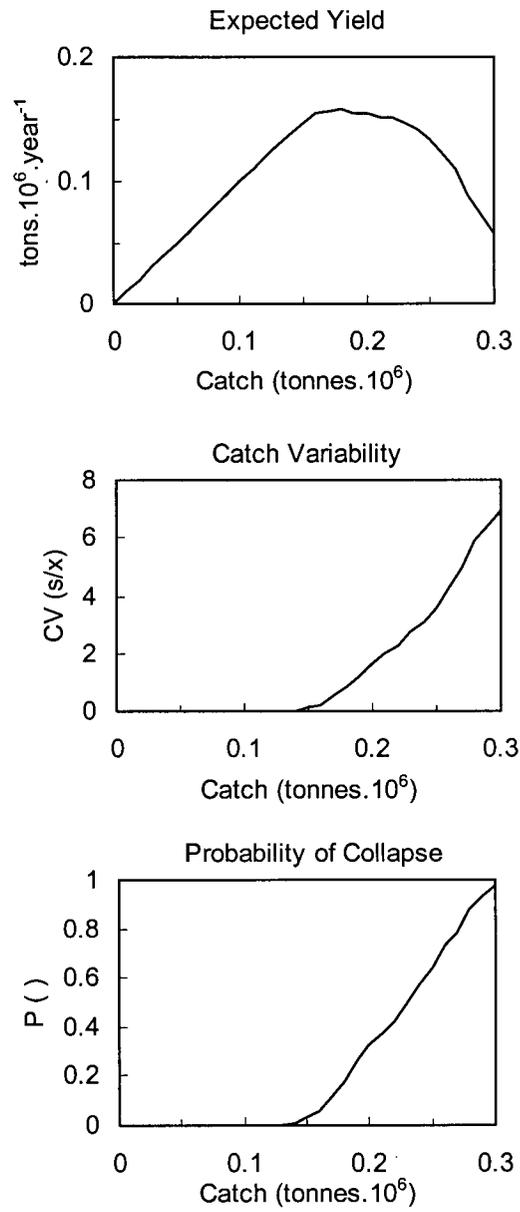


Figure 5.4. Outcomes of fishing strategy that capture a constant catch of sardine as predicted by the single species model.

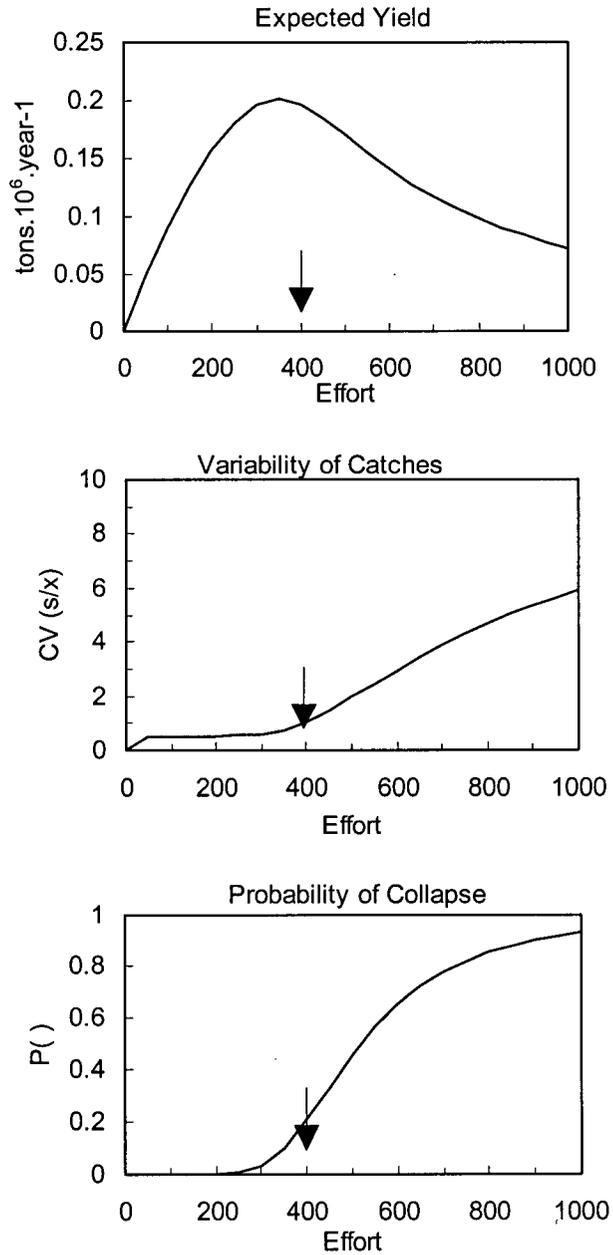


Figure 5.5. Outcomes of fishing strategies based on effort control as predicted by the single species model. The arrow indicates the approximate effort level in the period from 1977 to 1983. Effort index calculated as the product of number of trips and the mean tonnage of boats.

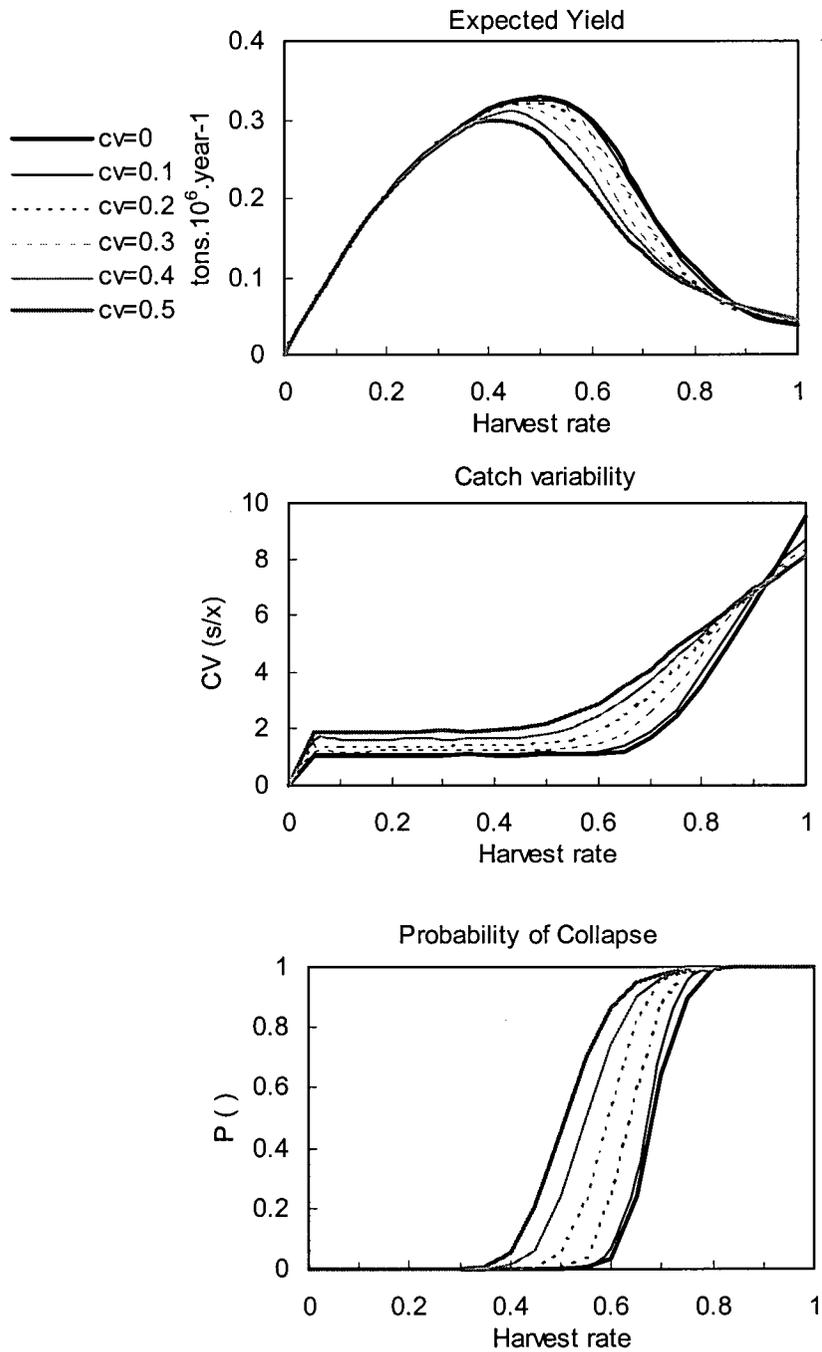


Figure 5.6. Outcomes of fishing strategies that harvest a constant proportion of the stock as predicted by the single species model. CV is the coefficient of variation of the biomass estimation procedure.

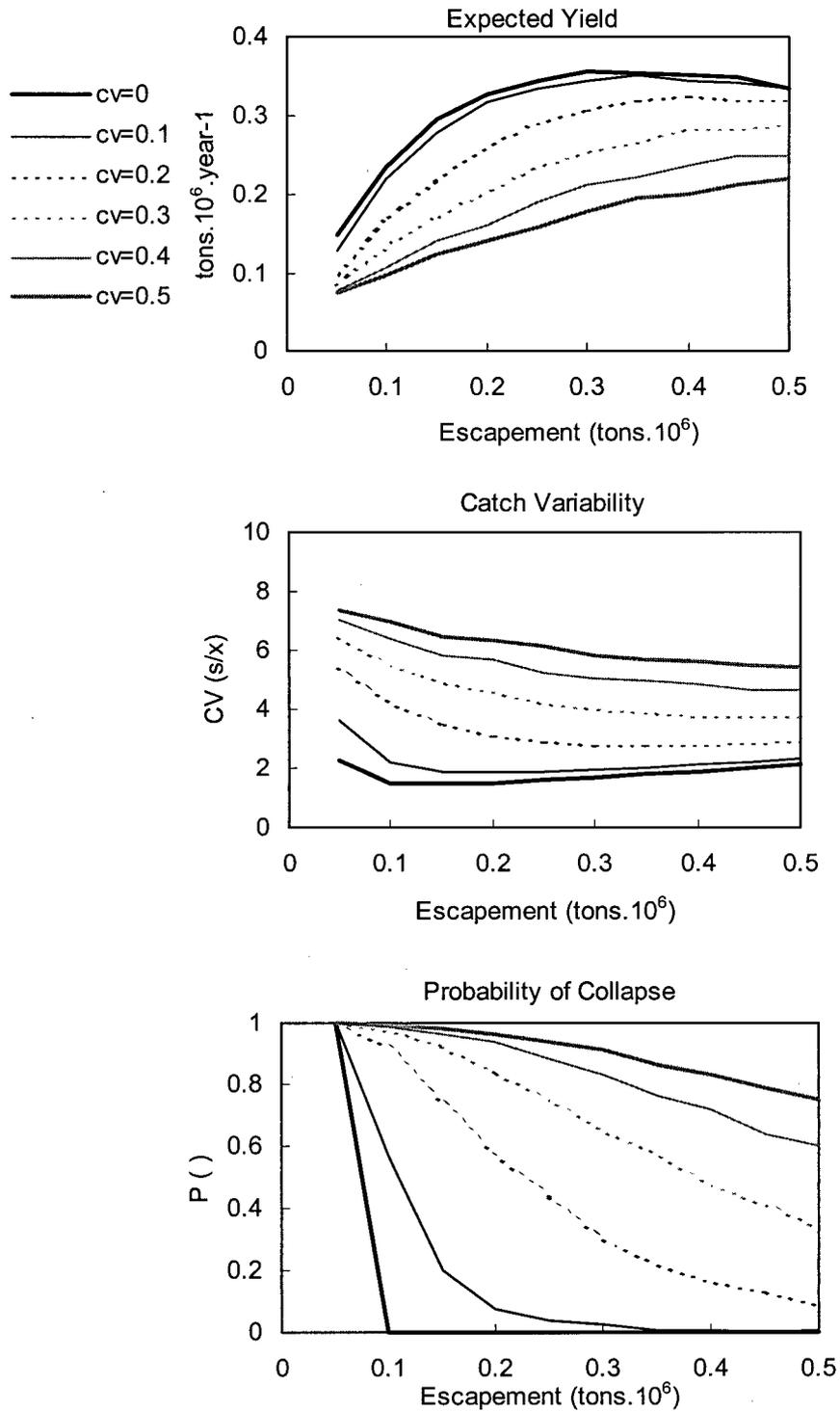


Figure 5.7. Outcomes of fishing strategies based on a constant stock escapement as predicted by the single species model. CV is the coefficient of variation of the biomass estimation procedure.

Expected Value of Perfect Information

In the present analysis the expected value of perfect information is computed for two types of decisions: in the choice for an optimal exploitation rate and for an optimal effort level. The objective is to find the fishing strategy (harvest rate or effort) that would maximize the yield from the fishery during 10 years after the collapse, i.e. after the early 1990's when the spawning stock biomass was about 70,000 tons. Uncertainties were included in three independent processes for each type of strategy (Table 5.3). Uncertainty on future environmental regimes represent a situation where decisions are made under complete ignorance on the environmental conditions and recruitment success in future years.

Table 5.3. Decision table on the choice of harvest rate and effort level for the sardine fishery.

Harvest strategy	Uncertain processes/states		
Harvest rate h=0 to 1	<u>Stock production</u> <i>3 hypotheses</i>	<u>Estimated biomass</u> <i>coefficient of variation of estimations</i>	<u>Future env. regime</u> <i>favorable or not</i>
Effort f=0 to 1000	<u>Stock production</u> <i>3 hypotheses</i>	<u>Stock catchability</u> <i>parameter uncertainty</i>	<u>Future env. regime</u> <i>favorable or not</i>

Table 5.4 shows the calculated optimal fishing strategies, the correspondent average expected yield, and the expected value of perfect information, which measures the expected gain to be obtained if we could suddenly resolve all uncertainty about each of the hypothesis is correct. Higher expected yields are predicted with constant harvest rate strategies, as has been previously suggested. With constant harvest rates strategies the expected gain of reducing uncertainties is less than 5% of the expected yield obtained when decisions are made under uncertainty. Walters (1986) suggests three reasons why the value of learning, measured as a upper bound by EVPI, is often not as large as one would intuitively expect: first, because optimal policies for each of the various hypothesis considered need not to differ substantially from the policy that provides the maximum expected value; second, stock-recruitment hypothesis may predict nearly the same yield across a wide range of harvest policies; and finally, because the optimal harvest rate tend to be close to the optimal policy for those hypothesis that were assigned high initial probabilities. The latter reason is particularly unlikely in this case considering that the three stock production hypothesis were assigned equal probabilities. It seems that in this case uncertainties on

recruitment processes and in the estimation of stock biomass have very little influence on the choice for the optimal constant harvest rate strategy.

The situation is quite different when effort control is employed. Uncertainties on stock catchability influence considerably the choice for the optimal effort level. The expected value of perfect information is in this case ca. 40% of what is expected to be obtained with a decision made under uncertainty. That indicates that research on the factors controlling stock catchability would cause a considerable improvement in the current management practice for the Brazilian sardine, more than that expected from oceanographic research aimed at increasing the ability to forecast future environmental regimes controlling recruitment.

Table 5.4. Results of the analysis of the expected value of perfect information for harvest strategies for the Brazilian sardine after the collapse.

Harvest strategy	Best h or f	Expected yield (tons.year ⁻¹)	EVPI (tons.year ⁻¹)	EVPI (%)
Harvest rate	0.4	208,015	7,800	3.75
Effort	150	85,467	34,886	40.81

Multi-species approach

Results of simulations of the effect of fishing strategies on the biomass and catches of sardine are shown in tables 5.5 and 5.6. It is predicted that closing the purse seine fishery (scenario 2) will lead to an average increase in sardine biomass ca. 6 times compared the baseline level of the late 1980s. Halving the current fishing rate (scenario 1) would lead to a biomass increase of ca. 2 times, and it is predicted to increase catch on average by 18% in five years (Table 5.6). Results vary however with the type of trophic control, being higher biomasses predicted to be recovered with top-down and wasp-waist control. In both cases releasing the fishing pressure would enable sardine to fully benefit from the available food by efficiently foraging on phyto and zooplankton. For a comparative analysis, results obtained with the single-species approach for the same short term policies are listed in table 5.7; for instance, stopping the purse seine fleet is expected to result in an increase in sardine biomass between 1.27 and 2.66 times the baseline biomass, depending on the environmental conditions prevailing during the 5 years.

Table 5.5 and 5.6 also allow for a direct comparison of the effect of decisions in other fisheries (scenarios 4, 5 and 6) on the resulting sardine biomass and catches. For the rebuilding strategies

(4 and 5) results point to smaller biomass and catch than what is predicted under the purse seine only scenarios (1 and 2). On the other hand, doubling all fisheries has a smaller effect on sardine biomass than that predicted by increasing the purse seine fleet. These results illustrate the type of indirect effects expected when fish stocks are linked by predator-prey relationships, i.e., allowing the rebuilding of species at the top of the food web cause a reduction in the benefits expected from releasing fishing pressure on sardine, specially when the fisheries target species that directly affect sardine production, either by competing for the same food resources or by being a predator. The latter situation occurs with Bottom trawl and Pole-and-line fisheries, for harvesting adult weakfish and bonito which are predators of small forage fish in the model. However the most important sardine predator group in the ecosystem model (*Other pelagic feeding fish*) is not fished by any of the fleets considered in the simulations.

Table 5.5. Relative change in sardine biomass after 5 year under different fishing scenarios. Values are relative to the Ecopath baseline level described in Chapter 3. F stands for the maximum relative feeding time of apex predators. Scenarios 1, 2 and 3 involve changes in the purse seine fleet only.

Scenario	Higher F			Lower F			Average
	Top-down	Bottom-up	Wasp-waist	Top-down	Bottom-up	Wasp-waist	
1	3.41	1.51	2.16	3.41	1.51	2.16	2.36
2	12.45	2.26	5.29	12.45	2.26	5.29	6.67
3	0.15	0.44	0.29	0.42	0.61	0.46	0.40
4	2.48	1.30	1.75	2.48	1.34	1.79	1.86
5	6.62	1.59	3.20	6.62	1.69	3.31	3.84
6	0.19	0.53	0.37	0.60	0.69	0.54	0.49

Table 5.6. Relative change in sardine catches after 5 years under different fishing scenarios. Values are relative to the Ecopath baseline level described in Chapter 3. F stands for the maximum relative feeding time of apex predators. Scenarios 1, 2 and 3 involve changes in the purse seine fleet only.

Scenario	Higher F			Lower F			Average
	Top-down	Bottom-up	Wasp-waist	Top-down	Bottom-up	Wasp-waist	
1	1.71	0.76	1.08	1.71	0.76	1.08	1.18
2	—	—	—	—	—	—	0.00
3	0.30	0.87	0.58	0.84	1.21	0.92	0.79
4	1.24	0.65	0.88	1.24	0.67	0.89	0.93
5	—	—	—	—	—	—	0.00
6	0.39	1.05	0.73	1.19	1.37	1.08	0.97

Table 5.7. Relative change in sardine biomass after 5 years under two strategies for stock recovery. Simulations carried with the single species approach with contrasting environmental conditions.

Future. regime	Stop fishing	Halve fishing
Bad	1.27	0.82
Good	2.66	2.20

Table 5.8 and 5.9 compare the predicted results of closing (scenario 4) and doubling (scenario 6) all fisheries on the biomass of the main harvested species in the ecosystem. Predicted changes in anchovy biomass are also shown. Closing all fisheries positively benefit all harvested groups with the exception of marine shrimps, anchovy and triggerfish. Conversely, doubling the current fishing rates negatively affect all groups in the system but marine shrimps and anchovy, which are predicted to have a net biomass increase in almost all trophic control hypotheses tested. Having small and fast growing groups such as marine shrimps benefiting from the overfishing of higher order consumers is not surprising given that reducing all predators in the system is expected to increase the abundance of preys, as has been the case with overfished tropical marine ecosystems (Pauly, 1979; Christensen, 1998). Also the higher turnover rates of marine shrimps allow them to withstand higher exploitation rates than that supported by slow growing fishes. The most affected groups are in both scenarios adult weakfish, rays and skates, and sardine. These species are either heavily fished (weakfish and sardine) or not being predated in the system (rays/skates and weakfish) so that a release in fishing will lead to a prompt increase in biomass; or are slow growing species (rays and skates) so that an increase in fishing will rapidly reduce their biomasses. Figure 5.8 illustrates these generic effects for a bottom-up control.

Table 5.8. Relative change in biomass of main harvested species in the Southeastern Brazilian Bight as predicted by Ecosim after 5 years with all fisheries closed. F stands for the maximum relative feeding time of apex predators. Shaded are groups that show a decrease in biomass.

<i>Groups</i>	<i>Higher F</i>			<i>Lower F</i>			<i>Average</i>
	<i>Top down</i>	<i>Bottom up</i>	<i>Wasp-waist</i>	<i>Top down</i>	<i>Bottom up</i>	<i>Wasp-waist</i>	
Bonito	1.67	1.52	1.59	1.67	1.47	1.59	1.59
Adult Weakfish	14.45	4.53	4.57	14.44	4.50	4.54	7.84
Rays/Skates	5.01	4.14	4.13	5.01	4.14	4.13	4.43
Croaker	1.40	1.24	1.25	1.40	1.23	1.25	1.30
King Weakfish	1.27	1.48	1.50	1.27	1.41	1.46	1.40
Triggerfish	1.05	0.91	0.88	1.05	0.91	0.88	0.95
Marine shrimps	0.00	0.49	0.50	0.00	0.51	0.52	0.34
Anchovy	0.89	0.87	0.87	0.89	0.90	0.88	0.88
Sardine	6.62	1.59	3.20	6.62	1.69	3.31	3.84

Table 5.9. Relative change in biomass of main harvested species in the Southeastern Brazilian Bight as predicted by Ecosim after 5 years with all fishing fleets doubled. F stands for the maximum relative feeding time of apex predators. Shaded are groups that show an increase in biomass.

<i>Groups</i>	<i>Higher F</i>			<i>Lower F</i>			<i>Average</i>
	<i>Top down</i>	<i>Bottom up</i>	<i>Wasp-waist</i>	<i>Top down</i>	<i>Bottom up</i>	<i>Wasp-waist</i>	
Bonito	0.63	0.65	0.65	0.64	0.66	0.66	0.65
Adult Weakfish	0.12	0.31	0.31	0.22	0.37	0.37	0.28
Rays/Skates	0.20	0.20	0.20	0.20	0.20	0.20	0.20
Croaker	0.69	0.78	0.78	0.73	0.80	0.80	0.76
King Weakfish	0.63	0.81	0.81	0.75	0.85	0.85	0.78
Triggerfish	0.27	1.02	1.02	0.33	1.02	1.02	0.78
Marine shrimps	0.37	1.39	1.38	1.26	1.51	1.51	1.24
Anchovy	1.07	1.14	1.15	1.36	1.22	1.26	1.20
Sardine	0.19	0.53	0.37	0.60	0.69	0.54	0.49

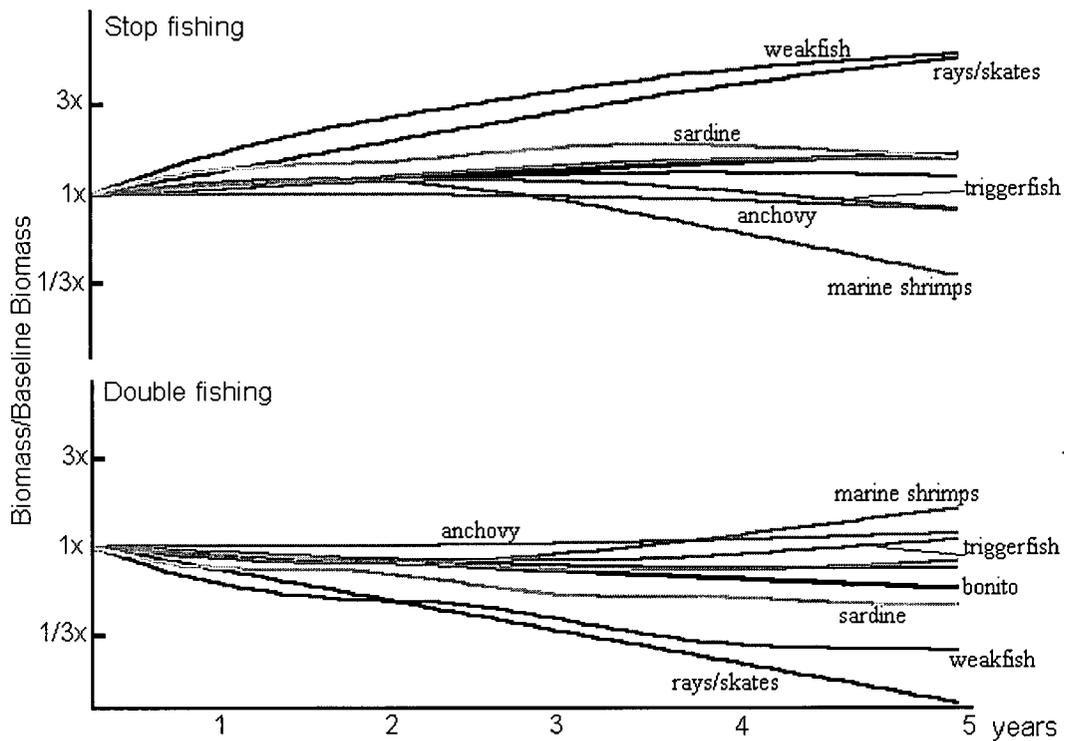


Figure 5.8. Dynamic simulation of fishing scenarios where all fishing is closed (upper panel) and doubled (lower panel) in 5 years. Simulation ran under a bottom-up trophic control.

Figure 5.9 compares the expected yield of sardine under constant fishing mortality rates. Results vary with the type of trophic control; higher yields are predicted with top-down control; top-down and wasp-waist control predict lower optimal fishing rates ($F=0.3 \text{ year}^{-1}$) compared to bottom-up control ($0.9 < F < 1.2 \text{ year}^{-1}$). Assuming lower maximum foraging time of apex predators result in the model predicting higher yields for fishing rates higher than the Ecopath baseline. This result has to do with the functional representation of consumption rates in Ecosim, where food consumption per time varies proportionally to the decrease in availability of resources and its is limited by a maximum foraging time. Decreasing the availability of preys (e.g. sardine) relative to the baseline level leads to an increase in the time apex predators spend feeding to balance the deficit in food intake; the end result being the increase in predation mortality when the stock is overfished. The higher the maximum foraging time the lower the yield obtained from the prey species. In one case, bottom-up control, the choice for the maximum foraging time directly influenced the predicted optimal fishing rates for sardine.

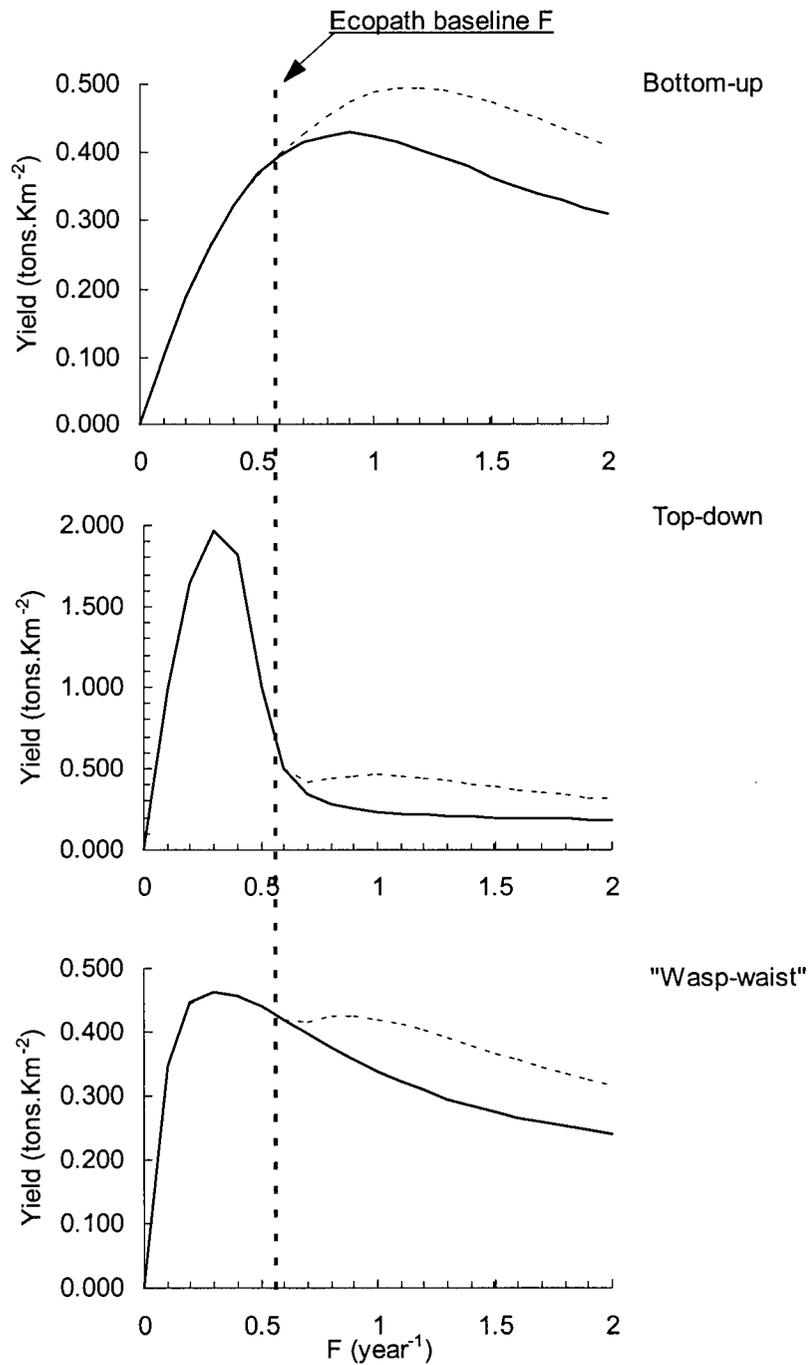


Figure 5.9. Predicted average yield (10 years) of sardine under fishing mortality rates (F). Dashed line across graphs indicates the baseline F for sardine in the original Ecopath model (chapter 4). In the graphs the continuous line represents the predicted yield expected when the model allows for higher maximum relative foraging time of apex predators in the system. The dashed thin line represents results with lower maximum relative foraging time.

Differences in production rates with each hypothesis do not imply however that much gain is expected to be obtained by reducing uncertainties on the operating type of trophic control in the system; the expected value of perfect information (EVPI) indicates in this case a gain of only

7.36% over the optimal decision that takes uncertainty into account, which is to fish at a F of 0.3 year⁻¹. This value, which would also indicate an optimal harvest rate of approximately 0.3, is similar to that calculated with the single-species approach ($h=0.4$; Table 5.4) under a different set of constraints.

The type of trophic control may however influence the transient responses of the ecosystem and consequently the output of a different set of fishing strategies. Predicted ecosystem response to overfishing sardine, for instance, raises concerns on the definition of minimum escapement levels and on the possible effects of pulse fishing strategies commonly adopted for small pelagics. Pulse fishing strategies, which basically rely on intensively fishing a stock to the point of overfishing and then let it recover before a new regime of intense fishing is initiated, have been applied to small pelagic stocks mainly as a result of the activity of Distant Water Fleets (WWF, 1998). Some authors have in fact suggested that management of small pelagic stocks should be targeted to favor recoveries when favorable environmental conditions prevail, rather than try to prevent depletion which is normally accompanied by unfavorable environmental conditions (Beddington and May, 1977). The objective of promoting stock rebuilding is also intrinsic to escapement thresholds, defined by Quinn II et al (1990) as “the population level below which the stock may be unable to rebuild its optimal level over an acceptable period of time”. Figure 5.10 exemplifies the type of response obtained in Ecosim when sardine is subjected to pulse fishing strategies. When the system is completely bottom-up controlled the stock is predicted to bounce according to the intensity of fishing, with minimal ecosystem-wide effects. When the system is top-down controlled, pulse fishing can however impose more drastic ecosystem effects and cause a delayed response of the sardine stock to the release in fishing pressure.

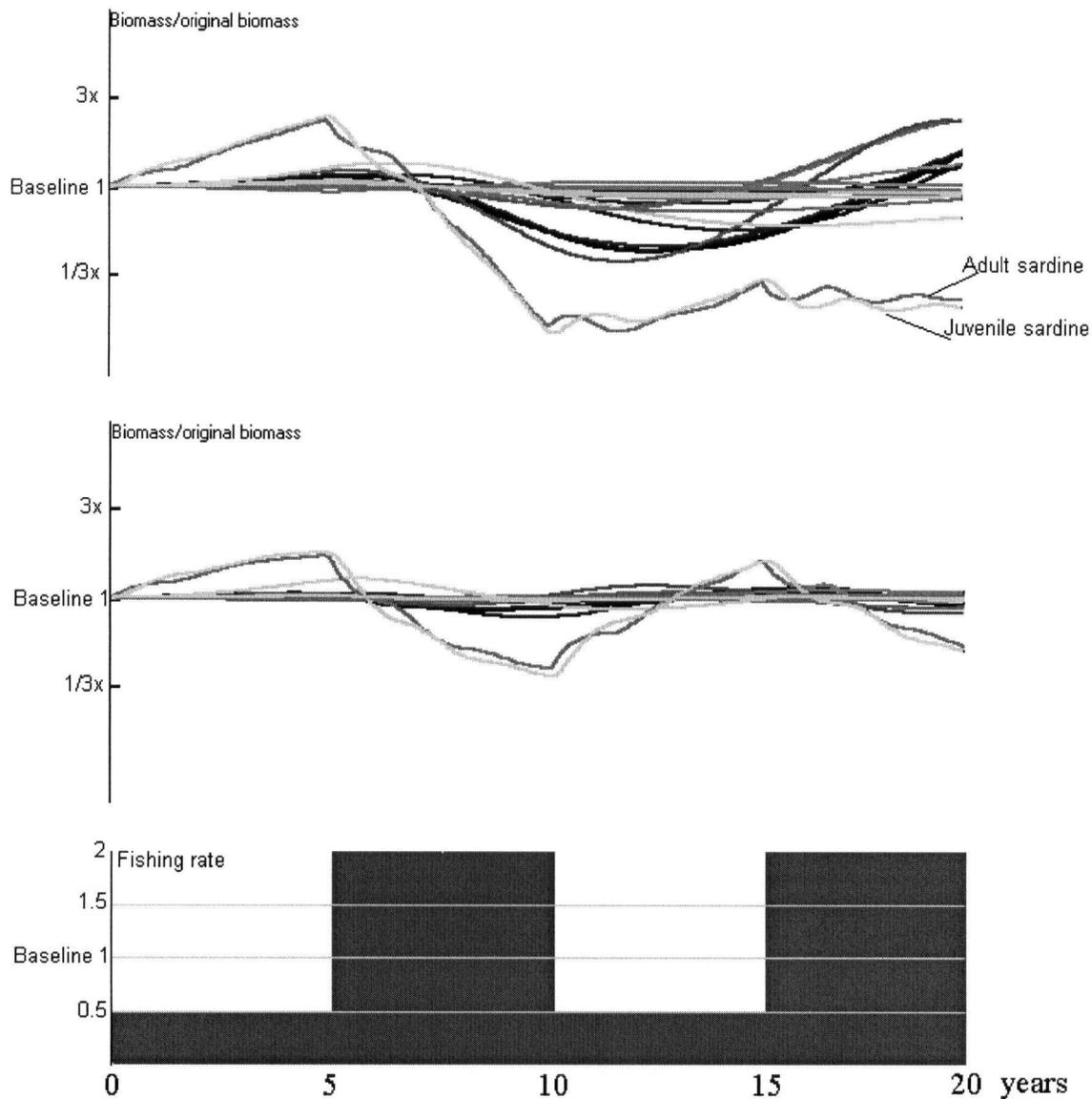


Figure 5.10. Example of a pulse fishing strategy for sardine; upper panel refers to a top-down scenario, lower panel refers to a bottom-up scenario. All trophic groups are represented to show the scale of system wide effects of fishing under the two trophic control hypothesis.

Conclusions from model simulations

Policies of effort control currently applied in the management of the Brazilian sardine are particularly inadequate in avoiding stock collapse due to the combined effect of a large fleet capacity, changes in catchability with stock size, and the variability in production rates driven by environmental regimes. The prospect of reducing uncertainties in the output of harvest decisions, and in effect reduce the chances of stock collapse, for fisheries controlled by effort

limitation is still restricted by the proper understanding of stock catchability. That will imply, in the case of the Brazilian sardine, that more effort should be put on evaluating the current fleet capacity, estimating the catchability of the stocks at contrasting stock sizes, and analyzing the population spatial dynamics (spatial range) and its interaction with the dynamics of effort allocation by purse seiners. In the latter context, two concurrent lines of thought are currently developing. MacCall's (1990) approach describes the spatial dynamics of schooling pelagic stocks according to a density dependent habitat selection model where a direct relationship between stock abundance and stock area is created by differences in habitat suitability (which is the result of environmental conditions combined with effects of local competition). His hypothesis has some interesting corollaries useful for fisheries assessment, particularly that stock area could be a good indicator of the population state and thus could be used together with catch rates in the stock assessment. This approach has been successfully applied to the Pacific sardine, when the population was small and difficult to assess with conventional techniques (Barnes et al., 1992). A second approach (Pitcher, 1997) suggests that shoaling behaviour alone can cause range collapse in the absence of significant environmental gradients in space and time. If validated, this approach raises the prospect of obtaining cost-effective diagnostics of range collapse by monitoring behavioural parameters of shoaling fish. The consideration of stock spatial attributes into fisheries research will require the gathering of auxiliary information not only from surveys but also from the fishery activity such as time searching, density of schools, school size, inter-school distance, etc.

The adoption of precautionary measures in the management of the fishery with effort control will demand an effective reduction in the effort and fleet capacity at least to the level observed during the late 1970s. Also, strategies of effort control are more likely to succeed if accompanied by auxiliary measures of control of the minimum age of recruitment to the fishery. Figure 5.11 shows the reproductive potential of the stock (measures as %SPR) for different combinations of age at first capture and the exploitation rate. When the first spawning age class (approximately 1.5 years) is effectively protected the total reproductive potential of a cohort is only slightly reduced with increasing fishing pressure. The combination of high natural mortality rate and early maturity makes the stock highly dependent on the first spawning age classes, which usually make the bulk of the reproductive capacity in many small pelagic stocks (Fig. 5.11c). In this sense protecting the first spawning age classes can help prevent early collapses of the stock, and encourage more rapid responses to favorable environmental conditions. Mace and Sissenwine

(1993) analysis of replacement thresholds indicated that to persist, i.e. for successive generations replace each other on average, small pelagic populations must maintain an average 40 to 60% of their unfished spawning per recruit (%SPR). This relatively high %SPR led the authors to infer low resilience of these stocks to fishing mortality, since a small reduction in SPR would compromise the future replacement of the stock. Clearly, exploitation must be lower in order to maintain the stock for lower ages at first capture (see 40 to 60% bands, Fig. 5.11a,b). But protecting the first spawning age class (1 to 1.5 years) provides the stock with high resilience, in the sense that a broader range of fishing mortality rates could be sustained without substantially diminishing the capacity of the population to react to favorable oceanographic events. For stocks with a dominant controlling influence by environmental regimes, that seems to be the most appropriate strategy that could be supported on biological grounds (Winters *et al.*, 1985). Yet, such strategy is probably untenable under most conditions for pelagic species due to the difficulty in controlling the age at entry in the fishery.

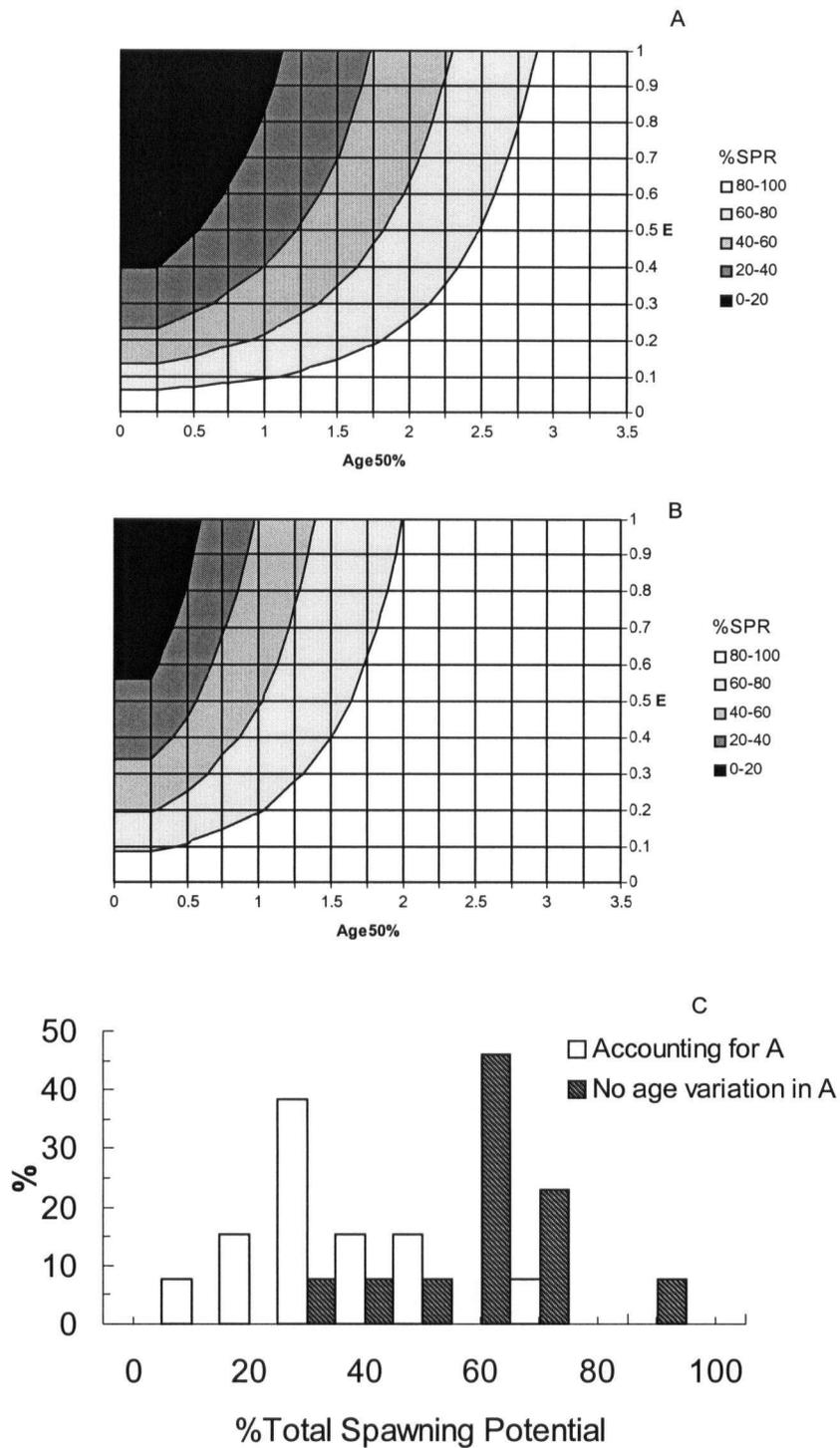


Figure 5.11. Percentage spawning per recruit (% SPR) for equilibrium exploitation rate (E) and age at first capture ($A_{50\%}$). A) taking into account the age specific reproductive output (A); B) if reproductive output were constant with age; C) percentage contribution of sardine, *Sardinella brasiliensis*, first spawning age classes (ages 1 to 1.5) to the total reproductive potential of the stock. The y-axis represents the percentage of years from data compiled between 1979 to 1989 (Cergole, 1993).

Better trade-offs between average catch, catch variability and the probability of collapse can be achieved with strategies of catch control, such as the one obtained with a constant harvest rate

policy. Under this type of policy the expected yield of a best decision made under uncertainty on the productivity of the population is within a 10% difference from the expected result of a best decision made with complete knowledge about future environmental regime controlling recruitment or the type of control of trophic relationships. The predicted optimal harvest rates are very conservative compared to the ones usually applied to small pelagic stocks, but are consistent with the sustainable fishing rates defined by Patterson (1992). Optimal harvest rates between 0.3 and 0.4 are obtained according to the modeling approach used, and appear to be conditioned by two set of independent processes traditionally overlooked by fisheries assessment: in the single species approach conservative fishing rates result from the possibility of sub-optimal environmental conditions represented in the model by low frequency regimes in recruitment success. In the ecosystem model more conservative fishing rates are predicted for sardine when predation is a major mechanism controlling production at lower trophic levels. The response of the system to the interaction of both processes (trophic and environmental) still need to be evaluated. Constant harvest rate strategies are considered very robust strategies to cope with the inherent uncertainties created by climatic effects on marine fish populations (Walters and Parma, 1996). They are usually implemented by fishing control systems that rely on annual biomass estimates and on simple feedback rules that specify the proportion of the adult stock, or the total allowable catch, to be harvested each year. The success of catch control systems is however dependent on the accuracy of the stock assessment which often suffers from large uncertainties in parameters and variables (e.g. catch at age, relative index of abundance) used in the estimation procedure. The critical information for the success of catch control systems is therefore the frequency and accuracy of stock abundance estimates, which may call upon a combination of data from surveys (e.g. acoustic assessments of spawning biomass and recruitment), better monitoring of catch composition (age and size) used in virtual population analysis, tagging experiments, and may as well rely on the active participation of resource users in data collection (Walters and Pearse, 1996).

Improvements in the understanding of biological and oceanographic processes controlling sardine production seems mostly needed if the fishery is to be managed by escapement thresholds. The possibility of depensation at low spawning stock sizes complicates the definition of escapement policies for increasing the risk of shifts in stability domains. Environmental effects can have in this case either a positive or a negative impact by pushing the overfished stock in or out of a stability domain, or even by shifting the boundary of stability domains. In

this situation a precautionary strategy that aims to diminish fishing and allow the stock to recover may not be very informative since the recovery of the stock might be interpreted both as a result of reduced fishing mortality or due to the occurrence of better environmental conditions; on the other hand, the failure of the stock to recover might be interpreted both as a result of depensation or due to a less favorable environmental regime. The trophic model provides in this case a tool to test and formulate different hypotheses about the possible causes of depensation and multiple ecosystem stability domains, such as the effect of increasing predation mortality with decreasing stock size. The testing of these hypotheses in the field will require data on recruitment, juvenile fish survival and abundance of potential predators; yet, in most cases the correct identification of mechanisms will be problematic due to the confounding effect of other environmental factors on juvenile survival. In the model of the Southeastern Brazilian shelf ecosystem the *Pelagic feeding fish* group is the most important sardine consumers. Pelagic feeding fish is, however, one of the less documented trophic components in the system. The group was originally included in the model to represent demersal fish species that actively feed on the pelagic system, such as weakfish and hake (Soares et al., 1993; Rocha et al., 1998), but may as well include a diversity of other demersal and pelagic species also targeted by fisheries and with important role at the top of the food web. A short list of other pelagic feeding fish species include sharks, cutlass fish, *Trichiurus lepturus*, and pelagic predators such as *Auxis* spp. and *Sarda* sp. A better characterization of this group, which will require data on biology and feeding habits, may lead to a more complete and accurate characterization of the effect of fisheries on the southeastern shelf ecosystem.

The evaluation of harvested strategies for the Brazilian sardine considered only the biological and ecological trade-offs involved between two types of widely applied fishing strategies, namely input (effort limitation) and output (catch limitation) controls. It was out of the scope of this work to discuss the likely socio-economic consequences of adopting one or other type of strategies and controls, neither was the objective of the analysis to examine all the possible combinations of strategies and controls for this fishery. Nonetheless, the results obtained here are expected to enrich this discussion which will require, to be effective, the active participation of resource users.

On the choice of a modeling approach

A central question for fisheries assessment today is on how to evaluate and communicate the consequences of alternative fishing policies to marine resources and ecosystems. For a quantitative analysis the question consequently concerns the choice for the modeling approach.

Models have many possible purposes and uses, and no one model is right for the entire range of uses. In principle, the choice for which type of approach to be used depends on the type of products or outputs it is expected from the analysis, i.e., on what type of information is needed for deciding among harvest decisions. Costanza et al. (1993) suggests three criteria for judging model performance: *realism* (simulating system behavior in a qualitatively realistic way); *precision* (simulating behavior in a quantitatively precise way); and *generality* (representing a broad range of system's behavior with the same model). No single model can do well on all three of these criteria, and the choice of which objective to pursue depends on the fundamental purposes of the model. In modeling complex systems tradeoffs must be made among realism, precision, and generality. For instance, when seeking for generality, models must give up some realism and/or precision. High precision (quantitative correspondence between data and model) will often sacrifice realism and generality. When the goal is to develop realistic assessments of a system, generality and precision must be relaxed. High realism models are concerned with accurately representing the underlying processes in a specific system, rather than with precisely matching quantitative behavior or being generally applicable. Costanza et al. (1993) argued that in many types of system modeling, the desired outcome is to accurately determine the overall magnitude and direction of change, trading off realism for some moderate amount of generality and precision.

Conventional fisheries stock assessment models strive for quantitative precision when describing time series of population abundance, calculating catch quotas, or predicting the consequences of policy options. Cochrane (1998), for instance, pointed to the need of an "ecosystem operating model" in management procedures for multi-species resources. A management procedure is defined as a set of rules which specify how a management recommendation is set and what data are used for this purpose (Butterworth et al., 1997). Rules are selected based on their anticipated

performance as estimated by simulation on an operating model of the resources and fishery. Successful implementation of formal management procedure for multi-species or ecosystem management will require from the operating model (Cochrane, 1998): *precision*, so that the expected system response to a management strategy is quantitatively similar to that predicted by the model; *realism* in simulating adequately the fishery-resources interactions; the incorporation of *all* sources of uncertainties to enable robust forecasts of ecosystem responses to a management strategy; and the output of meaningful performance criteria.

A model with high precision would be able to describe perfectly well the quantitative changes in the variables of interest with changes in controls and strategies. Ideally, to test the precision of the model it would be necessary to contrast predicted and observed values. Alternatively, we can compare the consistency of quantitative predictions of changes in sardine biomass obtained with the two modeling approaches in the same scenario. For instance, according to the single species model closing the purse seine fishery for five years is expected to cause an increase in sardine biomass between 1.27 and 2.66 times (Table 5.7). The same scenario in the ecosystem model produces an average increase in sardine biomass of 6.67 times the baseline level. A greater consistency between models is obtained when the ecosystem model is run under a bottom-up control of trophic relationships (sardine biomass 2.26 times higher than the baseline level; Table 5.5). Walters et al.(1997) also noted that Ecosim predictions approach that of a single-species model if the trophic model is bottom-up controlled. In this sense, the precision of short term predictions may be quite similar between approaches, depending on the weight put on the trophic control hypothesis in the ecosystem model.

Realism varies between approaches. The Ecopath/Ecosim model provides a more realistic description of the resource and ecosystem by representing not only the characteristics of the sardine stock but also the trophic interactions with other ecosystem components, and the possible interactions between fishing fleets. The ecosystem model however still lack a proper representation of important fishery-resource interactions such as the effect of changes in gear selectivity, which is often one of the most applied policy variables in fisheries management, and the effect of environmental factors on the availability and recruitment success of keystone species in the ecosystem. Experience with the use of the approach to explain the ecosystem changes observed in the Bering Sea suggested for instance that environmental factors, affecting recruitment or primary production, may be more important in determining the dynamics of the

ecosystem than predator-prey interactions alone (Trites et al., 1999). Lack of realism in representing important processes and uncertainties may in this sense apply for both modeling approaches, as models will always involve some degree of simplification of the observed processes in nature. The critical question is therefore not which model is more realistic, but which level of simplification imposed when using a model is less adequate to the type of problem and policy variables in hand.

When the objective of quantitative modeling is prediction, very simple models very often outperform more complex models. For instance, Ludwig and Walters (1985) showed that non-age-structured models produce better predictions of management actions than detailed age structured models. As a rule, the increase in model details makes it more difficult to specify how the components functionally interact, and each additional model parameter becomes less well specified by the available historical data. Walters (1986) showed that uncertainty about a policy parameter is likely to be minimized, for a fixed data set, by basing its calculation on parameter estimates from a model of intermediate complexity. The increase in model complexity decreases the prediction error (increase the ability to fit historical data) but increases uncertainty on parameters used to calculate the policy of interest. In summary, the choice for model complexity depends basically on the purpose of the model and on the amount of available information, i.e., if the model is too simple there is a risk of lacking realism, whereas if the model is too complex there will be not sufficient information in data to distinguish between the possible parameter values of the model. Also, the increase in model complexity should never compromise the transparency of arguments and conclusions of the model, and ideally, should be preceded by the analysis of its likely contribution to the final qualitative argument (Walters, 1986). Therefore, prediction of the dynamics of multi-species systems or ecosystems makes single-species models of little use, but detailed models involving all important species may not be the solution either, since the sensitivity of complex models to errors in parameters needed for their construction will make them unreliable (May, 1984; Hilborn and Mangel, 1997).

From a manager's point of view, the difference between the analysis of scientific advice based on single or multi-species models may be irrelevant since the questions faced by managers concerning the quality of science and the political acceptance of regulations are exactly the same, regardless of the modeling approach (Brugge and Holden, 1991). In this respect, Brugge and Holden suggest situations where the use of multi-species models will tend to go wrong. Among

the possible operational reasons for the failure are first, when recommendations based on multi-species models differ radically or are totally contradictory to those proposed in the immediate past with single species models. As stated by Gulland (1991), new scientific advice is most likely to be used if it implies changes in current management practice that are straightforward and preferably minor. Second, if the use of multi-species models cause an increase in the complexity of both management and assessment. Complexity in the management system is likely to increase if the conflicting interests are to discuss how the relative abundance of the multiple stocks should be changed. As for assessment, data requirement will most likely increase with multi-species models. Finally, multi-species models are inclined to fail if the lack of data force extreme simplifications in overall system structure and process, thus compromising realism (an argument also constantly used against single-species models).

The achievement of a comprehensive understanding that is useful for both realism and prediction will perhaps call upon the integration of the different approaches. Not that the "truth will lie in the intersection of independent lies" (Levins, 1966), but that the combination of approaches can provide complementary valuable results. Multi-species ecosystem models produce a more complete caricature of the system, explicitly recognizing its major components and processes, which enable us: i) to visualize the broad consequences of fishing policies (e.g. removing all the prey will impact the predators) and hence provide guiding principles in which to ground ecosystem goals when defining conservative exploitation rates, catch quotas, etc.; and ii) to test and formulate hypotheses about the causes of the observed changes in marine fish populations, and about the functioning of marine ecosystems. The latter is particularly relevant in the scrutiny of research questions to which resources are to be allocated to improve the understanding of the processes affecting fish populations. The simpler structure and data requirement of single-species models, on the other hand, make them particularly useful for prediction of policy variables and monitoring purposes in the management of fisheries for single stocks, as is the case with most small pelagic fisheries. An example of the use of a combination of approaches to fisheries management is found in the case of the Pacific herring off the west coast of Canada (Vandermeulen, 1998). From the ecosystem point of view, herring is an important source of food for higher trophic level species and act as an indicator of habitat loss due to their need for relatively pristine nearshore areas for spawning. The measure and monitoring of herring spawning biomass (undertaken with a single-species model) is thought to provide an indicator of overall marine ecosystem health and the effects of decisions regarding the protection of

nearshore habitats. In the case of the Brazilian sardine the trophic model provided the means to evaluate alternative hypothesis about the causes of species switches and changing stability domains that might have followed the stock collapse, besides indicating reasons other than environmental variability to the adoption of more conservative fishing rates for the species in the shelf ecosystem.

5.4. Summary

This chapter assess the ecological risks of management decisions in the sardine fishery off southeastern Brazil with currently available information and according to two modeling approaches: a single-species and a multi-species model. It is evaluated the short and long term predictions of the impacts of harvest strategies and controls, and the relative values of reducing uncertainties on ecological processes. Better understanding of the processes controlling fishery-resource interactions are mostly needed if the fishery is to continue being managed by effort control, or if escapement thresholds have to be defined when adopting catch control strategies. An alternative set of catch control strategies, particularly feedback rules for a constant harvest rate provide better trade-offs among the ecological indicators tested and appears robust to uncertainties on the prevailing ecological processes controlling production. Consistency between modeling approaches varies according to the weight put on the hypotheses represented in each model. A complementary role is suggested for the different modeling approaches in order to balance realism and prediction. Results are used to recommend on the type of research that would most likely provide the information needed to improve the quality of decisions, and on the precautionary measures that should be adopted in face of ecological uncertainties.

Chapter 6. Conclusions

Marine fisheries have historically exploited the abundant forage fish resources as source of food and fishmeal. Small pelagics have increased in importance for world fisheries particularly during the last decades as a result of the depletion of important stocks of long-lived and high trophic level fish and the rapid increase in the demand for fishmeal for the feed industry. The exploitation pattern of capture fisheries has caused changes in marine ecosystems, evident as major shifts in the composition of species, which raises concerns on the limits of ecosystems carrying capacity to fisheries. Confronted with this reality, fisheries scientists have been faced with the need to evaluate and communicate the ecosystem consequences of fishing given an incomplete understanding of the complex dynamics of ecosystems.

The objectives of this thesis were threefold: i) to evaluate the use of trophic models in the analysis of the ecosystem responses to fishing small pelagic forage fish; ii) to diagnose the fisheries in Brazil to the fishing down marine food web phenomenon; and iii) to provide an in-depth analysis of the sardine fishery off southeastern Brazil to examine the hypotheses of ecosystem changes and stock collapse, and to evaluate how uncertainties about ecological processes influence the choice of harvest strategies and controls in this fishery.

6.1. Evaluation of ecosystem responses to fishing using dynamic trophic models.

The comparative analysis of the ecosystem responses to fishing forage fish using trophic models indicated that small pelagics can play a central role in upwelling ecosystems, changes in their abundance can have considerable consequences to species at the top and the bottom of the food web. Also, as ‘wasp-waist’ species in these ecosystems, small pelagic forage fish will sustain much more conservative exploitation rates than what has been historically applied in the cases of stock collapse. Predicted results are generally in accordance with observed qualitative changes in upwelling ecosystems with the collapse of a forage species, which were normally followed by a decrease in the abundance of top predators and an increase in the abundance of a competing mid-trophic level species. Predictions of optimal fishing rates for the species are also generally in agreement with the suggested sustainable fishing rates for small pelagics, but are very sensitive to the type of trophic control (bottom-up or top-down) between predators and prey.

Model predictions are generally sensitive to the type of dominant trophic control assumptions and also appear influenced by the quality of the data used in the mass-balance assessments. As a general rule, poor quality models will perform badly in simulations run under top-down control, when models will tend to self-simplify their structure through competition or predatory exclusion of some groups.

The trophic model also allowed the testing of hypotheses about the functioning of ecosystems, their stability and resilience when impacted by fisheries. Comparing the recovery time of systems disturbed by fisheries with the structural, energetic and homeostatic characteristics of selected models it was possible to test hypotheses about the chief mechanisms controlling the stability of marine ecosystems. Results were in agreement with Odum's theory of ecosystem development, which suggests that nutrient recycling is one the main mechanisms developed by biological communities to increase control or homeostasis with the physical environment and achieve protection from its perturbations. Systems with a high percentage of the energy recycled are usually characterized by higher stability, or ability to recover from perturbations. In this analysis models of upwelling ecosystems were by far the most unstable systems, lacking well structured recycling routes to cope with perturbations imposed on the 'wasp-waist' forage species. A second type of stability, that related to the resilience of ecosystems or their ability to respond to perturbations without shifting to a different stability domain, was analyzed when exploring the effects of fishing sardine under different assumptions about the type of trophic control and the feeding time of apex predators in the system. Results indicate the possibility of depensation in sardine recruitment rates and consequent multiple stability domains in systems characterized with strong non-linear responses of predators to changes in prey densities. In these systems resilience appears to be conditioned by thresholds in the abundance of a forage species (sardine), beyond which disturbance will lead to completely different system stable states.

Another type of prediction explored with the trophic model relates to the long term effects of fishing down marine food webs on systems that have historically sustained catches of high trophic level species but that present the potential to sustain higher yields from unexploited forage species. Simulations showed that fishing down the food web for small pelagic planktivorous fishes, while at first increasing catches in intensively exploited regions, has the potential of actually decreasing yields by interrupting major energy pathways to already overexploited, high trophic level species. The diagnosis of this generic effect, described by a

backward bending curve between catches and trophic level of fisheries, corroborates global assessments of fisheries-induced changes in marine ecosystems where fishing down the food web is an observed phenomenon.

The trophic model was also used to investigate the ecosystem effects of contrasting exploitation scenarios for the major fisheries resources in the southeastern Brazilian shelf ecosystem. Scenarios describing future options for managing fisheries in the region focused on the ecological effects of allowing the recovery of stocks or intensifying even more fishing by the main fleets. The predicted qualitative changes show that increasing exploitation will lead to a decrease in biomass of high trophic level species and an increase in the importance of low trophic level species in the ecosystem. Conversely, allowing the recovery of stocks will lead to major gains in abundance of commercially harvested species, but shrimps which are predicted to decrease in abundance. Predicted changes in sardine biomass were tested for consistency with the values obtained with a single-species model under the same scenarios. Biomass recovery values obtained with the trophic model converges to that predicted with the single-species model when the system is bottom-up controlled. However, simulations run under a bottom-up control produce very optimistic fishing mortality rates for sardine, usually above that predicted with the single-species model. Consistency between optimal fishing rates predicted with both models occurs when uncertainties on the type of trophic control are taken into account in the multi-species model. The models therefore justify the need to adopt more conservative fishing rates for the species by two interdependent reasons: in the single-species model conservative fishing rates result from the possibility of sub-optimal environmental condition controlling recruitment success in the future, while in the multi-species model conservative fishing rates are predicted for sardine when predation is considered as a major mechanism controlling production at lower trophic levels. A complementary role is suggested for the different modeling approaches in order to balance realism and prediction. Multi-species models produce a more complete caricature of the ecosystem which is useful to examine the broad consequences of fishing policies and to test and formulate hypotheses about the causes of observed changes in marine ecosystems. On the other hand, the simpler structure and data needs of single-species models make them particularly useful for prediction of policy variables and monitoring purposes in the management of fisheries for single stocks, as is the case with many small pelagic fisheries.

The analysis of the ecosystem impacts of fishing small pelagics using dynamic trophic models (Ecosim) can be expanded in several ways. A question that still needs to be evaluated is how the impacts of fishing small pelagics compares with those resulting from exploiting other groups/species in the ecosystem. A systematic comparison of the predicted ecosystem effects among exploited groups may provide a better characterization of the ecological role of these species in marine food webs. Another question to be evaluated is how sensitive are the predicted optimal fishing mortality rates of small pelagics to parameter uncertainties other than the trophic control hypotheses tested in the thesis. Other candidate parameters for analysis are the productivity (P/B) of small pelagics, the rate of effective search and consumption rates of predators in the system. Improvements of the trophic model as a tool to test and formulate hypotheses about the ecosystem effects of fishing will involve, in the specific case of the southeastern Brazilian Bight, a better representation of groups at the top of the food web, such apex fish predators, marine mammals and birds. Also, improvements in the quality and credibility of the model will occur if other scientists and local fisheries managers are fully involved in data input and evaluation of model structure. In general, model predictions are expected to be improved with prior information (hypotheses) on how trophic interaction strengths (v_{ij}) are distributed in the food web, and how environmental processes other than predation affects recruitment rates of individual trophic groups. That is expected to provide better insights on the dynamics of resilience of marine ecosystems when impacted by fisheries.

6.2. Fishing down marine food webs in Brazil

In line with some of the trends in world fisheries, marine capture fisheries in Brazil are in a state of crisis, with many of the traditionally harvested fish stocks either fully exploited or overexploited. Today, the prospect of increasing catches and recovering the status of fisheries activities rely on better management of the overfished stocks, fishing for offshore resources currently moderately exploited, and/or fishing down the food web for abundant short-lived, planktivorous fishes. Fishing down the food web is not yet an observed phenomenon in Brazil; fisheries in Brazil had a relatively constant mean trophic level of the species landed from 1950 to the early 1980s, but show a recent increase in mean trophic level caused by the combined effect of the collapse of small and mid-size pelagic species (mostly sardine) and the increasing landings of large pelagic fishes with the development of offshore fisheries for tunas and sharks.

Characteristic of Brazil is however the wide diversity of marine ecosystems and types of fishing strategies adopted regionally. In the southernmost region of the country, where the shelf ecosystem is under the influence of the subtropical convergence of Brazil and Malvinas currents, fisheries have targeted mostly high trophic level stocks of demersal and pelagic species. In the upwelling ecosystem off the Southeastern Brazilian Bight sardine has been historically the main target of commercial fisheries, and sustained the largest fishery in the country. The collapse of this fishery in the late 1980s has apparently shifted the ecosystem into one dominated by an abundant population of anchovy, *Engraulis anchoita*, that is not commercially harvested. The extent to which the collapse of sardine stock and the switch to an anchovy dominated system was the result of fishing or environmental factors is still inconclusive. It was therefore the focus of this case study to examine hypotheses of ecosystem changes and to analyze how uncertainties on the ecological processes, as captured by different modeling approaches, influence the choice of harvest strategies and controls in this fishery.

6.3. The case of the sardine fishery off southeastern Brazil

The analysis of hypotheses of ecosystem changes in response to fishing impacts relied on the identification of ecological processes controlling the dynamics of ecosystem succession and resilience. The ecosystem of the Southeastern Brazilian shelf is structured around the operation of physical-biological cycles of different speeds. Among the most documented cycles are the seasonal upwelling of the cold, nutrient-rich South Atlantic Central Water on the inner shelf, and the decadal regimes determined by multi-year variability in the intensity of physical forces controlling biological production. The latter is particularly important for the management of fisheries resources because it operates at time scales commensurate with the life span of most marine fish populations. A central question in the case study was therefore whether the collapse of the sardine stock and the apparent switches in species composition represent a natural and reversible change caused by oceanic regimes, or whether they reflect a loss of resilience of the ecosystem and a change of state caused by excessive exploitation. Literature review, model simulations and stock-recruitment data for the Brazilian sardine pointed at three generic hypotheses that could be used explain the changes in the structure of the ecosystem and the collapse of the sardine fishery. *The overfishing hypothesis* considers that fishing was the chief mechanism responsible for the collapse of the stock, so that once the intensity of fishing is

reduced the stock will recover its original abundance. *The depensation and ecosystem shift hypothesis* considers that the stock declined in response to overfishing, but the recovery is hampered by depensation in recruitment rates and a change in state of the ecosystem caused possibly by ecological and behavioral processes. Finally, *the regime shift hypothesis* considers that the stock collapsed in response to overfishing and recruitment failures caused by long-term low frequency environmental effects. This hypothesis accepts that radical fluctuations in abundance may be an intrinsic feature of small pelagics inhabiting upwelling ecosystems. If so the recovery of the stock is less dependent on managing the fishery, but on favorable environmental conditions prevailing in the future. In summary, the combined effect of both human and natural effects make it difficult to characterize the dynamics of the population and ecosystem, and to predict the results of rehabilitation measures for the stock. The combination of a third process, result of the interaction between the behavior of the fish and the dynamics of the fleet, further contributes to degrade the performance of current regulatory measures for stock rebuilding using effort control.

On the other hand, the explicit recognition of uncertainties about the ecological processes controlling the dynamics of interactions between fisheries and ecosystem may allow for a sound choice of precautionary strategies for the fishery, and a better scrutiny of research programs in which to allocate resources to improve management. Policies of effort control currently applied in the management of the Brazilian sardine are particularly inadequate in avoiding stock collapses due to the combined effect of a large fleet capacity, changes in catchability with stock size, and the variability in production rates driven by environmental regimes. The prospect of reducing uncertainties about the output of harvest decisions, and in effect reduce the chances of stock collapse, for fisheries managed with input control (e.g. effort limitation), is still restricted by the proper understanding of stock catchability. In the current situation the adoption of precautionary measures in the management of the sardine fishery will imply an effective reduction in the effort and fleet capacity at least to the level observed during the late 1970s, and a more effective control of the minimum age of fish recruiting to the fishery, which has been shown to increase the resilience of the stock to overexploitation.

An alternative set of output control strategies (e.g. catch limit), particularly feedback rules for a constant harvest rate, provide better trade-offs among the ecological indicators tested and appears robust to uncertainties on the prevailing ecological processes controlling production. On the

other hand, the performance of another type of output control strategy based on minimal escapement levels deteriorates considerably in response to errors in the estimation of stock biomass. Also, the definition of escapement thresholds is complicated by the possibility of depensation in sardine recruitment rates at low spawning stock sizes and the risk of causing shifts in ecosystem stability domains. Consequently improvements in the understanding of biological and oceanographic processes controlling production and in the accuracy of biomass estimation methods seems mostly needed if the fishery is to be managed by escapement thresholds.

The implications of this work to fisheries management were discussed in the individual chapters but will be summarized here. As 'wasp-waist' species in upwelling ecosystems, small pelagics should not be managed in isolation from other ecosystem components since changes in their abundance can have consequences throughout the food web. Their ecological role in marine food webs determines that small pelagics will sustain much more conservative fishing rates than what has been historically suggested and in effect applied in the cases of fisheries collapse. The upwelling ecosystems inhabited by small pelagics have characteristics of unstable systems, lacking well developed biological mechanisms to damp the impact of fishing and environmental factors. The characteristics of unstable systems have served as a reason for the adoption of less restrictive fishing policies for the species, and helped to perpetuate management actions that continuously failed to allow the effective recovery of collapsed stocks. Conversely, seen from another perspective, the unstable characteristics of upwelling systems will mean that variability imposed by nested physical-biological cycles is a key asset for the resilience of these ecosystems, and that management should in turn be prepared to cope with these dynamic conditions. In this respect fisheries that adopt more conservative exploitation rates for the species will be more robust to the variability and ecological uncertainties inherent in these systems, and are more likely to be successful in the long run.

Notes

1. Part of Chapter 2 is published in Vasconcellos, M.; Mackinson, S.; Sloman, K. and D. Pauly. 1997. The stability of trophic models of marine ecosystems: a comparative analysis. *Ecological Modeling* 100: 125-134.
2. Chapter 3 is based on a manuscript in press in *Fisheries Research*: Vasconcellos, M. and M. Gasalla. Fisheries catches and the carrying capacity of marine ecosystems in southern Brazil.

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