Assessing the effects of internal (trophic structure) and external (fishing and environment) forcing factors on fisheries off Central Chile: basis for an ecosystem approach to management

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DECLARATION

This thesis documents original research carried out as PhD student at the Zoology Department, University of Cape Town from November 2004 to February 2007. The results presented in this thesis are my own, except where otherwise acknowledged in the text.

The work presented in this thesis, either in part or full, has not been presented for any other degree at the University of Cape Town or any other University.

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Sergio E. Neira Alarcón

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Date

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Long ago, my mother told me that as a child I almost drowned in the cold waters of Cocholgue, a small beach near Concepción (my hometown) in Chile. Although I do not recall this key moment, my fascination for the sea may have well started that day. As a result, I got engaged in the study of marine biology and ecology. This PhD thesis represents the most remarkable achievement in my career (until now).

The work presented in this thesis is entirely my own. However, as no fish (nor scientist) is an island, the final version of this document greatly improved through the interaction with people and institutions to which I am deeply indebted for their advice, support and encouragement.

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I take full responsibility for any mistake and deficiency that may remain in this thesis.

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Sergio Neira

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ABSTRACT

Human perception of sea fisheries has evolved from an inexhaustible resource paradigm towards a generalized concern on the degraded state of fish stocks and ecosystems. Accordingly, fisheries science and management are expanding from the traditional single-species approach towards an ecosystem approach to fisheries. Marine communities are organized as webs of interactions that are affected by external natural (climate) and anthropogenic (fishing) forcing, with their relative effects poorly known, but hypothesised to strongly depend on internal food web structure (i.e., who eats and controls whom).

This thesis approaches relevant ecological considerations for an ecosystem approach to fisheries in the upwelling ecosystem off central Chile (33ºS-39ºS). The main objective is to assess the effects of internal (trophic structure) and external (fishing and environment) forcing factors at the fish stock and food web level in the study area. The methodology includes i) the construction of snapshot and dynamic food web models to test hypothesis of changes in the food web in the last century, and the relative contribution of fishing, trophic controls and bottom-up environmental variability to those changes, ii) the computation and analysis of a set of ecosystem indicators to test hypotheses of changes in different aspects of the exploited community (mean trophic level, age and length at maturity, network properties and system variability), iii) the analyses of the relationships between time series of abundance of species with known trophic interactions (Chilean hake-red squat lobster and Chilean hake-small pelagic fish) to test hypothesis of top-down and bottom-up control versus alternative hypotheses of fishing and/or environmental control in the same populations, and iv) simulation experiments to test hypotheses of ecosystem change and recovery under fishing and environmental forcing.

Models and indicators are constructed using data series of abundance, catches, production, consumption and diets of the main functional groups in the study area. Snapshot and dynamic food web models are constructed and analyzed using the Ecopath with Ecosim software version 5.1 and routines therein.

The observed trends in indicators and model results are in accordance with what is theoretically expected in stressed ecosystems (shift towards a food web dominated by short-lived, low trophic level and high turnover rate species), and suggest that the food web could be in a state that is more susceptible to external forcing. Fishing and the environment (bottom-up anomaly in PP) may have affected the upwelling ecosystem off central Chile both at the stock and at the food web level between 1970 and 2004. The effects of these forcing factors may have been mediated by trophic controls operating in the food web. There is also evidence to support the hypothesis that trophic controls beyond fishing, e.g., trophic (internal) and environment (external) may operate in the analysed populations and this information should be considered in their assessment and management. While target objectives are set and agreed, it is proposed that the main objective for the ecosystem approach to fisheries should be to avoid fishing-induced regime shifts, since results from simulation experiments suggest that fishing can induce ecosystem changes of lower recovery than bottom-up forcing.

This thesis is the first attempt to analyse fisheries in central Chile from a more holistic ecosystem approach. This allowed documenting a series of ecosystem processes, interactions, dynamics and shifts in the upwelling system off central Chile. Results suggest that Chilean fisheries should not be managed based exclusively on the assumption that “each fish is an island” (i.e., using single-species approaches). Rather, the development of ecosystem-based fisheries science and management arises as the main strong recommendation for Chilean scientists, managers and stakeholders. The current lack of ecological data and limited scientific understanding impedes, for the moment, the implementation of a fully ecosystem-based fisheries management. However, this should not be used to justify inaction. Simple and effective low cost steps are proposed to facilitate the movement towards an ecosystem approach for the management of fisheries in central Chile.

Keywords: Food web modelling, Ecosystem indicators, Controls in marine ecosystems, Ecosystem states, Ecosystem shifts, Ecosystem approach to fisheries, Upwelling ecosystem, Central Chile.

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CHAPTER 1

GENERAL INTRODUCTION

This chapter describes the theoretical framework for this thesis. Human perception of sea fisheries has evolved from an inexhaustible resource paradigm towards a generalized concern on the degraded state of fish stocks and ecosystems. Accordingly, fisheries science and management have expanded from the traditional single-species approach towards an ecosystem approach to fisheries encompassing both the ecological and human wellbeing. This thesis focuses on the main ecological considerations for an ecosystem approach to fisheries in marine, and specifically upwelling, systems. Marine communities are organized in webs of interactions that are affected by natural (climate) and anthropogenic (fishing) forcing. The relative effects of each external factor are hypothesised to strongly depend on food web structure (i.e., who eats and controls whom). However, the relative effects of external forcing in food web dynamics and the strength of trophic links and interactions among target species and their prey and predators are still poorly known. The case study is the upwelling ecosystem off central Chile, a typical yet poorly studied upwelling system. The main objective of this thesis is to assess the effects of internal (trophic structure) and external (fishing and environment) forcing factors at the fish stock and food web level. The methodology includes food web models and ecological indicators. This information is then used to set a general basis for ecosystem-based management of the fisheries in central Chile. Research hypotheses to be approached are introduced along with an outline of the following chapters.

Evolution of marine fisheries: from inexhaustible fishes to pervasive stock collapse

In 1884, the famous naturalist T.H. Huxley wrote “All the great sea-fisheries are inexhaustible…nothing we can do can possibly affect them”. This quote is widely used to illustrate human perception on marine fisheries during the pre-industrialized era (Haddon, 2001). The “inexhaustibility paradigm” (Mace, 1997) was based on the high abundance of coastal fish that once astonished naturalists (such as Huxley) and fishers, and on the rather few and localized examples of human-induced depletion of marine resources.

Even though primitive fishing gears can significantly reduce the abundance of marine populations, it is traditionally accepted that massive effects of fishing started with the onset of industrialized fisheries. For example, the recovery observed in ground fish species of the North Sea after World War I and World War II indicated that fishing pressure on these marine populations was already too high (Beverton and Holt, 1957).

The increasing perception that fish are limited led to a series of scientific programs focusing on fisheries in the early 1900s (see examples in Smith, 1994). Quantitative fishery science emerged from the work of Baranov (1918), Ricker (1948; 1954) and, especially, Beverton and Holt (1957), whose dynamics of exploited populations is considered “the bible” of fisheries science (Pitcher, 1996). From its inception, this branch of ecology has been eminently applied, focusing on the estimation of fish numbers and, based on the human need for continuously harvested fish, on solving how to sustain a maximum yield (Hempel and Pauly, 2002).

Important stock collapses during the 1970s and 1980s supported early critics of the concept of maximum sustainable yield (Larkin, 1977), and new concepts such as precautionary and responsible fishing were added to the fisheries jargon. Fishery scientists were then required to provide information on the uncertainty associated with stock assessment and forecast (Anonymous, 1995). With the rise of computers, fishery science became highly sophisticated in terms of mathematical models and statistical techniques, but also less transparent and parsimonious, i.e., more difficult to be understood by stakeholders and dependent on crucial assumptions (Cotter et al., 2004).

Although technical advance revealed the role of poor data and scientific mistakes in promoting observed collapses, they do not effectively increase the understanding of the causes of failure. In fact, the “myopic” task of improving single-species assessment (suitability of underlying assumptions and alternative models, the fitting process and constrains imposed by data quality, among others) distracted attention away from the real questions (Walters and Martell, 2004).

Until the 1990s, fisheries scientists were rather contemporary in their scope perceiving the productive potential of a stock as the amount of fish present at the beginning of their careers. This shifting baseline (Pauly, 1995) implied that the perception of stock productivity decreased with successive generations. Thus, by the time global and historic overviews on fisheries emerged, the "bigger picture" was worrisome. According to the Food and Agriculture Organization (FAO) of the United Nations, the world catch increased between 1950 and the 1970s (due to growing fishing power and better statistics collection), slowed down during the 1980s and reached a plateau in the 1990s (FAO, 2005). However, Watson and Pauly (2001) showed that, due to persistent over-reporting of China's landings, the world catch has been declining at a rate of 0.36 (0.66 without anchoveta) million tons per year since late 1980s.

The world catch was then close, and probably beyond, the more robust estimate of sustainable yield, meaning that world fisheries were near their sustainable limit (Buckworth, 1998). In fact, 35% of global stocks were 'senescent' or over-fished by the late 1990s (Garcia and Grainger, 1997) and 25% of representative stocks in the global fishery collapsed between 1950 and 2000 at a relatively constant rate over time and stocks (Mullon et al., 2005). With the abundance of predatory fish reduced to only 10% of their un-fished biomass (Myers and Worm, 2003; Christensen et al., 2003), the risk of driving stocks to levels at which their reproductive capacity was impaired (i.e., depensation effect) became a major concern. The little evidence of depensation in overexploited stocks by the mid 1990s was optimistically interpreted as reversibility of overfishing (Myers et al., 1995). However, a few years later, a second meta-analysis revealed that the likelihood of fish stock recovery after strong reduction in abundance was indeed low and some times nil, even under no fishing (Hutchings, 2000). Furthermore, because fishing selectively removes the larger and fast-growing individuals first, fishing mortality is selective with respect to both species and to phenotypic variation within species. Thus, fishing is a potential source of evolutionary change for retained populations (Law, 2000).

Therefore, beyond important economic and social externalities (i.e., overcapitalization and job loss), global fisheries are facing a concerning biological and ecological crisis much more complex than just *too many fishermen catching too few fishes*. As Cury and Cayré (2001) pointed out, we rarely hear good news in fisheries these days and, in fact, fishing is now considered the main threat to marine ecosystems (Jackson et al., 2001). The future may hold even more bad news; if current trends are maintained, all exploited fish stocks could collapse by 2048 (Worm et al., 2006).

Marine fisheries, the last big-scale human activity based on the exploitation of wild stocks, are navigating troubled waters from an illusory inexhaustible past towards a possible desert (in terms of edible biomass) future. These extreme perceptions are, however, context-specific. Although heavily criticized by peers (e.g., Lankester, 1884; Longhurst, 2007), both Huxley (1884) and Worm et al. (2006) assumed that fisheries will be exploited using the fishing capacity of their time. However, while inexhaustibility was always a fallacy, degraded and collapsed fisheries are a pervasive reality.

Fishing and ecosystems: from no effects on fish to fishing-induced ecosystem shifts

We have seen how sea fisheries can reach an "ocean of scarcity" if the world fishery continues to be eroded by depletion of individual stocks. However, what have been the ecosystem-level effects of massive removal of target and non-target species?

Although fishing-induced changes in ecosystems have been long foreseen (examples in Smith, 1994 and Pauly and Christensen, 2002), traditional fisheries science considered overfishing and collapse as problems affecting single stocks only. Therefore, no major attention was paid to the effect of fishing on communities and ecosystems where stocks are embedded until early 1980s (e.g., Mercer, 1982). The cumulative evidence on the effect of fishing on ecosystems has revealed that fishing has indeed changed ecosystems from their pristine state to a present degraded condition (Jackson et al., 2001).

One of the most salient features of communities is their organization as webs of ecological interactions, among which are predation and competition. Therefore, fishing removal of target and non-target species unavoidably alters community structure, both directly and indirectly. The direct decline in abundance of retained species indirectly can result in an increase in previously controlled prey and competitors (now released from strong predation and competition) and a decrease in dependent predators (due to food shortage). Because many life history parameters are size dependent (e.g., big individuals live longer, grow slower and occupy higher position in the food web), community level changes induced by size-selective fishing are seldom random. Fishing decreases the size, trophic level and age of fish communities in a process known as fishing down the food webs (Pauly et al., 1998a). Although common in lake and rocky shore systems, food web cascades induced by overfishing are only starting to be documented also in open/pelagic marine systems (Frank et al., 2005; Daskalov et al., 2007).

In addition to changes in community structure (number and abundance of components), fishing alters ecosystem function (flows of energy and productivity), decreases genetic and trophic diversity (loss of species and trophic guilds) and disrupts habitats that offer refuge for early life stages and adults of many species, including fishery resources (Goñi, 1998; Jennings and Kaiser, 1998; Hall, 1999). All these changes may decrease ecosystem capacity to withstand and recover from external perturbations (i.e., resilience). Sustained overfishing may then trigger a regime shift towards a new state that may not be economically, ecologically and/or socially desirable (Cury and Shannon, 2004; Daskalov et al., 2007). The reversibility of such shifts is unknown and still poorly evaluated.

Ecosystem effects on fisheries

Early fisheries scientists concluded that, due to the likely null impact of fishing, observed geographical and temporal changes in marine populations must have been the expression of “natural” forces (Smith, 1994). The heavy exploitation levels observed by the time fisheries models were developed led to the assumption that fishing mortality was the main factor underlying stock dynamics (including collapse). Thus, “natural” causes, or more formally natural mortality, were relegated to a secondary place as a constant and minor effect. However, the current lack of recovery in overexploited stocks under no fishing has highlighted the major role of natural mortality on stock dynamics. The two main sources of natural variability are found in the physical and biological environments.

Scale deposition off the California Current System indicates that some pelagic and demersal species have fluctuated at centennial and millennial scales (Holmgren and

Baumgartner, 1993; Finney et al., 2002), i.e., long before the rise of industrial fisheries. In fact, sardines and anchovies oscillate in synchronous, low frequency and out of phase cycles in distant marine systems, indicating a strong link between the climate and their population dynamics (e.g., Kawasaki, 1983; Lluch-Belda et al., 1989; Schwartzlose et al., 1999; Chavez et al., 2003). Physical and biological time series revealed that decadal fluctuations of commercial stocks are sometimes the expression of large scale whole ecosystem changes, better known as regime shifts. These shifts result from natural change in the environment amplified through the food web by the physical-biological overlap (Steele, 2004).

The evidence that physiological and ecological processes such as growth, recruitment, distribution and reproduction are affected by physical variables such as temperature, salinity, etc., supports an environmentally-induced variability in stock abundance. Intra- and inter-annual variability are important for short lived species and/or year classes in long lived species, while decadal variability is more important at the community and ecosystem levels (Chavez et al., 2003; Steele, 2004).

In contrast to environmental forcing, a whole branch of ecology (trophodynamic) supports a trophic-based regulation of populations' abundance. In the marine environment, organisms occupy several trophic levels during their life spans. Thus, they must be affected, at least at some stage, by predation pressure or food limitation (Hunt and McKinnell, 2006).

Because predation in the ocean is mainly size-based, it is clear that "big fish eat small fish" (Pitcher and Hart, 1982). However, the question of who eats whom (and how much), while important to estimate predation mortality in fish stocks, does not necessarily answer who controls whom. For decades, ecologists have debated whether top-down (predator consumption) or bottom-up (food limitation) forces dominate ecosystems. The current paradigm accepts that ecosystems (and individual organisms) can be affected simultaneously by bottom-up and top-down controls (Hunter and Price, 1992).

Community trophic structure is a key ecological template on which fishing and environmental forcing act. Therefore, the understanding, quantification and modelling of controls is important for fisheries management, especially in the prediction of the response of stocks and ecosystems to fishing and environmental forcing.

Fisheries science and management: From nothing to manage to an ecosystem approach to fisheries

Accumulated experience on the exploitation of marine resources has led to some indisputable "lessons". First, although renewable, marine populations are limited. Second, exploited components are tightly related to their physical and biological environment, and their abundance depends on fishing, but also on other ecosystem components. Third, fishing generates negative ecosystem-level effects (in prey, predators and habitat) that can have negative feedbacks on fishing resources, e.g., accelerate collapse and/or prevent recovery.

How have fisheries science and management dealt with these lessons? Unfortunately, a fourth lesson is, in fact, a profound criticism of the traditional approaches used to manage fisheries. Due to their poor performance and limited scope, single-species approaches are unable to deal with the full dynamics of exploited marine populations.

Ecosystem integrity is considered crucial for fisheries sustainability and thus the consequences of mismanaging an ecosystem are far higher than mismanaging a single stock (Frid et al., 2006). Furthermore, the increasing scientific and public awareness of the negative impacts of fishing on ecosystems has expanded the focus of fisheries management beyond single-species, and the ecosystem is regarded as the appropriate integrative management unit.

A global call for a more holistic approach to fisheries has resulted in the rise of an ecosystem-based approach to management, also known as an ecosystem approach to fisheries (FAO, 2003). Although the general legal framework for the ecosystem approach to fisheries has been established through a series of international agreements, the implementation stage remains a key challenge for fisheries science and management (Hempel and Pauly, 2002).

The limited knowledge of the ocean (poor understanding of processes, interactions among components, and uncertainty in data and model behaviour among others) is normally used to highlight the impracticality of managing fisheries from an ecosystem perspective. However, the ecosystem approach to fisheries is not about how to best manage ecosystems, but how to minimize negative impacts of fishing on ecosystems while taking into account changes in the ecosystem that can affect fisheries. In this process, a balance between economic, social and ecosystem objectives must be achieved, assuring the ecological and human wellbeing (Prescott-Allen, 2001).

The ecosystem approach to fisheries must be regarded as an evolution rather than a revolution in fisheries management (Garcia et al., 2003) for which incremental steps are possible (Pikitch et al., 2004). In terms of the ecological well being, the focus should be the ecological considerations that matter for an ecosystem approach to management. A good starting point is to identify the interactions among living and non-living components of the ecosystem and how fishing and climate affect them. This is normally done by combining observed data on as many aspects of the ecosystem as possible, e.g., abundance of target and non-target species, diets, fishing activities, environmental factors, etc. These data can be used to build and test quantitative ecosystem models and indicators to reveal key ecological interactions and ecosystem states. This process will lead to a better understanding of the system that then can be combined with modelling tools to test ecosystem dynamics under alternative management and environmental scenarios. Once the main links, processes and mechanisms in the ecosystem are identified, objectives, indicators and reference points useful for fisheries management can be easier to propose and agree on (Cury and Christensen, 2005).

Models and indicators: all models are wrong, but some are interesting

Early fishery science was limited by a nineteenth century mechanistic worldview and by computational technology. In this context, the relatively simple equations of population ecology became the basis of fisheries science. Modern management objectives and questions have, however, evolved beyond single-species concerns. Therefore, single-species models, although useful, are insufficient. Almost forty years after the first edition of the “bible” for fisheries science (Beverton and Holt, 1957), Mangel and Levin (2005) argue that community ecology and not population dynamics must be the fundamental ecological science underlying fisheries.

Management is a matter of choices and, therefore, a way to explore the outcome of these choices is needed to reach informed and reasonable decisions (Walters and Martell, 2004). Choices need to be explored with a representation of reality, indicators representing the objectives pursued by management, and reference points to measure the performance of management actions (Cury and Christensen, 2005).

The representation of the “management unit” is normally a mathematical model. i.e., a coherent representation of the system and/or of processes therein, that must be able to replicate the observed trends in the variable(s) of interest over time. In this way, there is a higher degree of confidence that the most important features governing the dynamics of the “management unit” have been captured.

Among available models to explore ecosystem concerns, the Ecopath with Ecosim approach (Christensen and Pauly, 1992; Walters et al., 1997) has a series of advantages over other existing modelling approaches. First of all, Ecopath and Ecosim has huge network support since it is the most widely utilized approach worldwide. Most importantly, Ecopath with Ecosim has high plasticity, being capable of representing a huge number of functional groups, fisheries, and ecosystems. Ecopath with Ecosim is then capable of addressing the widest range of ecosystem-based research questions (Plagányi, 2007), and has been selected here as a suitable means of representing the “ecosystem”.

However, this approach has some drawbacks, also highlighted by Plagányi (2007). Basically, Ecopath with Ecosim is focused on the trophic interactions between target and non-target species and therefore strongly relies on assumptions of the importance of trophic relationships and the "foraging arena" formulations to represent these. Ecopath and Ecosim do not include explicit/full representations of spatial and habitat-related processes and their effects on species interactions, but this is true for many ecosystem models. Although the Ecospace module, also included in the software, is spatially resolved, it is not explored here. Although less data intensive than many modelling approaches, Ecopath with Ecosim requires data that are sometimes difficult to obtain, such as diet compositions and species abundance estimates for all functional groups.

No single indicator can represent/assess all sources of ecosystem variability. However, a large international effort has been carried out to test available quantitative indicators (Daan et al., 2005a) and some of them have been selected to track changes in ecosystem state. This thesis relies primarily on trophodynamic indicators to identify changes at the ecosystem level because they integrate a series of ecological processes and interactions. However, the link between objectives and indicators is not yet clear and the set of reference points is still in its infancy.

Characteristics of upwelling systems

Upwelling systems are highly productive areas of the world oceans sustaining globally significant landings (Carr, 2002). The major upwelling systems in the world are equally distributed in the northern hemisphere (California Current and Canary Current) and in the southern hemisphere (The Humboldt Current and the Benguela Current). These four systems comprise a small portion of the world ocean surface, but sustain almost 30% of the world marine fish catch (FAO, 2005). The source of this productivity is found in the physical process that brings nutrient rich deep waters to the surface, fertilizing the upper ocean layer and enhancing phytoplankton growth.

Fish productivity in upwelling ecosystems has attracted scientific attention in terms of the mechanisms explaining the high abundance of fish and their noticeable temporal fluctuations. In particular, two species of small pelagic fish, anchovies and sardines, have been central for the development of hypotheses on recruitment, trophic dynamics, environment-resource links, switches in species dominance, ecosystem regime shifts and trophic controls (Pauly and Tsukayama, 1987; Cury and Roy, 1989; Bakun, 1996; Durand et al., 1998; Schwartzlose et al., 1999; Cury et al., 2000; Chavez et al., 2003).

This information has led to the identification of common ecological patterns and food web features in all major upwelling areas. Because the high primary production is carried by primarily large, chain forming diatoms, food chains are rather short. Fish communities are dominated by a few species of small pelagic fish (sardines and anchovies) that, in the Pacific Ocean, alternate dominance at periods of ca 25 years (Chavez et al., 2003). The food web dynamics seem to be regulated by changes in small pelagic fish populations (wasp-waist populations) rather than bottom-up or top-down forcing. This feature has been termed "wasp-waist" control (Rice, 1995; Bakun, 1996; Cury et al., 2000) and it is characterized by a top-down control by small pelagic fish on their zooplankton prey and a bottom-up control on their dependent predators. Therefore, wasp-waist populations play a key role as nodes where the effects of fishing and the environment can be amplified leading to important changes at the ecosystem level (Rice, 1995; Bakun, 1996; Cury et al., 2000).

Food web modelling using the Ecopath approach in upwelling ecosystems started in early 1990s. Jarre-Teichmann et al. (1991) and Jarre-Teichmann and Pauly (1993) modelled the highly productive Humboldt system off Peru and its huge anchoveta fishery. During late 1990s and early 2000s, other trophic models were developed as to cover the major upwelling regions in the world, e.g. California, southern Humboldt, Namibia, South Africa, and north-west Africa (Jarre-Teichmann and Christensen, 1998; Neira and Arancibia, 2004, Neira et al., 2004; Shannon et al., 2003; Heymans et al, 2004). Comparative analysis of these models revealed that whereas the general structure of major upwelling systems is very similar, there are many system specific characteristics related to ecosystem size (e.g., energy flows) and structure (e.g., endemic groups) (Jarre-Teichmann and Christensen, 1998; Moloney et al., 2005). A huge research effort has been conducted in the Benguela Current system in last two decades from the analysis of trophic flows during the 1980s and 1990s (Shannon et al. 2003) to dynamic simulations to understand the effects of fishing on stock dynamics and shifts between sardine and anchovy dominance (Shannon et al., 2000; Shannon et al 2004a,b). More recent modelling efforts have approached the changes in the trophic structure in the southern Benguela in last few centuries (Watermeyer et al., in rev.). Cury and Shannon (2004) analysed the northern and southern sub-systems in the Benguela Current, concluding that both systems have experienced similar shifts in environmental variability, but overfishing in the northern Benguela has shifted the ecosystems to a new state, while conservative management has allowed sustainable fishing in the southern Benguela.

Although the main forcing factors behind the dynamics of upwelling ecosystems are clear, their likely antagonistic and synergistic effects have prevented full understanding of the individual and combined effects of fishing, the environment and trophic controls. It is believed that the above forcing factors can induce regime shifts (Cury and Shannon, 2004; Lees et al., 2006). However, changes in the trophic control template induced by fishing, environmental variability or both can lead to unexpected dynamics including regime shifts of unknown reversibility.

Therefore, moving towards an ecosystem approach to fisheries in upwelling areas implies the need for improved knowledge in order to answer a number of important research questions:

1. Effects of fishing on ecosystems: are ecosystems degraded compared to their past states?

2. Forcing factors: what are the relative effects of fishing, the environment and trophic structure on stock and food web dynamics?

3. Dynamic quantification of predation mortality and forage species management: who eats and controls whom?

4. Fishing and ecosystem variability: Is fishing altering ecosystem structure and processes, leading to increasing variability?

5. Ecosystem-based fisheries management: what are the objectives, indicators, reference points and control rules?

6. Ecosystem shifts and reversibility: When and why ecosystem reference points are exceeded? Does fishing or environmental variability lead to ecosystem regime shifts of low reversibility?

Case Study: The southern Humboldt System off central Chile, the least studied upwelling ecosystem

The Chilean system has followed the trend in most of ecosystems around the world by reaching, and maybe exceeding, upper limits of harvesting to accommodate the expansion of human interventions and impacts. The dramatic decrease of marine mammals in the first half of the last century due to overexploitation (Aguayo-Lobo et al., 1998) and the heavy exploitation and collapse of fish stocks in more recent decades are examples of how fishing has drastically altered biological components of this productive marine ecosystem. Nowadays, few species are not fully exploited or overexploited. The total catch in this system increased rapidly during the 1970s and 1980s and has been steadily declining after the historical maximum in the mid 1990s.

Historically, the coastal system off central Chile (Fig. 1.1.) has been one of the most productive, yet poorly studied, eastern boundary upwelling systems (Morales and Lange, 2004). However, a series of recent research efforts are changing this situation. Since the late 1990s, the main physical-chemical processes and patterns of biodiversity of the pelagic and benthic sub-systems as well as the oceanography of the Humboldt system off central Chile are becoming clearer (see Strub et al., 1998; Camus, 2001; Escribano et al., 2003; Morales and Lange, 2004; Escribano and Schneider, 2007; Thiel et al., 2007).

In terms of the communities inhabiting this area, the focus of the research has been directed to the study of basic life history parameters for the pelagic and demersal fish communities. Little attention has been paid to groups with low/no commercial value (Neira and Arancibia, 2004).

Although the geographic distribution of target species, their prey and predators can extend beyond central Chile (Fig. 1.1), fractions of these populations (stocks) are, to some extent, restricted to the study area by oceanographic, bathymetric and geographic features (Camus, 2001). In addition, the Chilean fisheries management legislation considers central Chile (33-39ºS) as a macro-area with independent and different management regime (and fishing fleets) compared to the northern and southern-austral management macro-areas. It is thus assumed that the effects of fishing mortality are independent in these areas. Therefore, although not completely enclosed, central Chile can be considered a suitable ecological and management area for ecological and fisheries studies.

The management and assessment of Chilean fisheries has been based on the traditional single-species paradigm where the exploited populations were considered isolated from their environment, which in turn, is assumed to be an inert background. However, as in the rest of the world, this kind of perception is becoming more difficult to maintain.

For example, horse mackerel (*Trachurus symmetricus*), one of the most productive single species fisheries of the world, collapsed in the mid-1990s. Red squat lobster (*Pleuroncodes monodon*), an economically valuable crustacean, was managed with extreme precaution after its collapse in the 1980s. However, after a few years of apparent recovery, the stock collapsed again in the early 2000s and the fishery has been banned since then. Chilean hake (*Merluccius gayi*), the most important fish resource targeted for direct human consumption, collapsed in 2004 without clear signs of recovery and some stakeholders are considering a moratorium on hake catches.

Since early 1990s, all these fisheries have been managed with a system of total allowable quotas set by the National Fisheries Council following the technical advice of the Undersecretary of Fisheries. This technical advice is based on a detailed analysis of the state of each resource conducted with single-species stock assessments methodologies. The analysis includes fishery-independent yearly survey data and global or structured (by age or size) models, which are in turn used to project the state of the stock under several constant catch scenarios, selecting the quota that represents the lower risk of missing a conservation goal. Although not formally developed, target reference points are related to maintain the adult stock in a certain level (assumed sustainable) respect to the non-exploited biomass. However, in spite of management based on state-of-the-art fisheries science methodologies, these fisheries are in poor condition.

Araucanian herring (also known as common sardine, *Strangomera bentincki*) and anchovy (*Engraulis ringens*) are the dominant small pelagic fishes in central Chile.

These species presented relatively low landings during the 1960s and early 1970s and even lower during the 1980s. However, both stocks built up during the 1990s, reaching high biomass levels and important landings. These decadal fluctuations may be linked to fishing pressure, but especially to the environment, as seems to be common for small pelagic fish around the world.

These examples indicate that traditional fishery theory and practice are insufficient for the sustainable management of Chilean fisheries. There is increasing evidence that exploited stocks are not isolated from their environment. In reality, they are linked to predators and prey (some of which are targeted by other fisheries), and predation mortality can be the main source of mortality, especially in juvenile stages (Neira and Arancibia, 2004; Neira et al., 2004).

Furthermore, there is increasing evidence that the ocean environment that these stocks inhabit is far from being an inert background. Inter-annual variability at the El Niño Southern Oscillation scale and the occurrence of regime shifts in the system are examples of changes at stock and ecosystem levels where fishing is not a driving force (Montecinos et al., 2003).

Alheit and Ñiquen, (2004) propose that long-term decadal variability is more important in the dynamic of the Humboldt ecosystem than the frequent perturbations associated with the El Niño Southern Oscillation. Decadal changes are expressed as shifts between anchovy and sardine regimes, which are accompanied by a whole ecosystem restructuring from phytoplankton to the top predators. These regime shifts are caused by decadal periods of warm/cold anomalies in sea surface temperature related to the approach/retreat of warm subtropical oceanic waters to the South American coast off Peru and Chile. Periods of mainly negative temperature anomalies are dominated by anchovy (i.e., 1950-1970; 1985 to the present) while warmer periods (i.e., from 1970 to 1985) are sardine dominated (Alheit and Ñiquen, 2004). The same authors propose that transition periods (turning points) from one regime to the other have occurred in 1968-1970 and 1984-1986. These decadal warm/cold periods drastically alter community structure and species composition in the entire Humboldt Current, resulting in adverse/favourable physical and trophic conditions for important pelagic fish species such as anchovy and sardine, but also for prey and predators located in all levels of the food web (Alheit and Ñiquen, 2004).

There are, however, additional sources of variability producing unknown results (e.g., climate change). On the one hand, the interplay between fishing, the environment and trophic controls in determining the dynamics of exploited populations and the food web and induce changes of state is increasingly recognized. Further, global climate change may affect the ways in which El Niño Southern Oscillation and decadal shifts affect ecosystems and upon which the effects of fishing are superimposed.

Previously, a few research efforts have been carried out to analyse food web structure and ecosystem-effects of fishing in the southern Humboldt off central Chile. Specifically, Neira and Arancibia (2004) and Neira et al. (2004) analysed food web structure, trophic relationships and energy flows, concluding that food web structure off central Chile is similar to those in major upwelling areas (e.g., low system maturity, short food chains, low transfer efficiency and energy flows dominated by the pelagic realm). Predation mortality is an important component of total mortality in the Chilean system, especially in recruit and pre-recruit groups. Arancibia and Neira (2005) analysed ecosystem effects of fishing off central Chile, informing a significant decline in the mean trophic level of landings. This trend may reflect “fishing down the food web process” (sensu Pauly et al., 1998a) rather than bottom-up effects of El Niño Southern Oscillation (Arancibia and Neira, 2005).

Milessi (2005) simulated the influence of environmental changes, fishing and trophic relationships in the food web of the coastal system off central Chile, using an Ecopath model constructed by Neira and Arancibia (2004). Results indicate that both bottom-up changes in phytoplankton and top-down effects of fishing can reverberate through the whole food web. Milessi (2005) also approached the effects of the microbial food web or “microbial loop” in the structure and flows in the system, finding that extra-production from the microbial loop only reached zooplankton groups (mostly copepods) without strongly affecting fish biomass. However, Milessi (2005) did not analyse these results under a fisheries management approach nor the impacts on overall system resilience.

Obviously, single-species approaches and models cannot be held responsible of all the problems affecting the main fisheries in central Chile. In addition to management *per se* limitations, e.g., lack of enforcement, illegal landings and discarding, etc., management is vulnerable to external pressure. Catch quotas are normally higher than technically advised due to political and economic pressure exerted by stake holders represented at the National Fisheries Council (Arancibia and Neira, 2003; Arancibia and Neira, in press).

Therefore, fisheries of central Chile seem to need a broader scope of analysis beyond short-term economic sustainability of individual fisheries. The scope offered by the ecosystem approach to fisheries may help improving fisheries management by aiming the ecosystem and social well being as well.

The main objective of this thesis is to assess the effects of internal (trophic structure) and external (fishing and environment) forcing factors at the fish stock and food web level in the upwelling ecosystem off central Chile using available ecosystem models and indicators to set the basis for an ecosystem approach to fisheries management in this highly productive food web.

Organization of the thesis

This thesis is organized in two main parts and a total of eight chapters. Chapter 1 (general introduction) leads to Part A (Chapters 2 to 5) which investigates changes in the upwelling ecosystem of central Chile both at the stock and food web levels. This is done by assessing the relative roles of fishing, bottom-up forcing and trophic interactions (controls) in observed changes. Part A aims to understand the main forcing factors (and their relative effects) affecting food web dynamics in the studied system. Because trophic interactions and food web structure are basic characteristics of marine ecosystems, in this thesis the “ecosystem” is idealized as a food web, i.e., a network of interactions based on direct (prey/predators) and indirect (food competition) trophic links. Spatial and habitat features are also important characteristics of marine ecosystems affecting food webs. However, due to the lack of information, they are not treated in this thesis. Part A has a strong modelling focus, but some chapters deal with observed patterns and the analyses are driven by time series data. A balance between observations (mainly catch and biomass data) and model results was used to calculate ecosystem indicators to assess ecosystem state. Data sources, models and indicators are fully introduced when first used.

Part B (Chapters 6 to 8) addresses issues concerning the implementation of an ecosystem approach to fisheries in central Chile. Objectives, indicators and reference points are reviewed in Chapter 6 with emphasis on upwelling ecosystems and the Chilean system in particular. A critical point for the ecosystem approach to fisheries is avoiding negative irreversible fishing-induced regime shifts, in which ecosystems are unable to provide services society expects (e.g., food and revenue), and Chapter 7 approaches this issue by using a model to investigate which factors (fishing or bottom-up forcing) are more likely to induce non-reversible regime shifts. Chapter 8 synthesises Parts A and B and further elaborates the steps to be followed in the development of an ecosystem approach to fisheries plan.

Chapters and hypotheses addressed in this thesis are described below.

Chapter 2. Assessing changes in the southern Humboldt in the 20th century using food web models

As will be detailed in Chapter 2, large scale fishing activities in Chile started in the late 1800s early 1900s based first on large mammals. Demersal trawlers targeting Chilean hake and benthic crustaceans began fishing in early 1950s, while the exploitation of pelagic fish stocks rose in the 1960s (anchovy and Araucanian herring) and 1970s (horse mackerel and hoki). After reaching a peak in the mid 1990s, total landings have been steadily declining and sequential stock collapses are being witnessed. It is hypothesized that community structure has changed since the start and development of industrial fishing in the southern Humboldt, with the direction of changes being in accordance with what is expected from ecological theory and observed changes on stressed ecosystems (Odum, 1985).

Chapter 3. Analysing changes in the southern Humboldt ecosystem for the period 1970-2004 by means of dynamic food web modelling

Food web changes can be forced by fishing pressure and environmental changes, likely mediated by ecosystem trophic structure. Because these aspects of the ecosystem are dynamic and synergistic, they cannot be evaluated through snapshot food web models. In Chapter 3 a time-dynamic food web model is fitted to time series data of biomass, catches and fishing mortality to test the hypothesis that the dynamic of stocks and the food web have been affected by fishing, bottom-up forcing and internal trophic structure between 1970 and 2004. Specifically, it is hypothesised that fishing has played the most important role in the system.

Chapter 4. Interactions between exploited stocks, fishing mortality and ocean temperature in the southern Humboldt: who controls whom?

Estimates of predation mortality and forage species management are key ecological considerations that could be included in an ecosystem approach to fisheries management. The issue of who eats whom (evaluated in diet analysis and snapshot food web models) does not necessarily reveals who controls whom in a food web. If predation is an important process in the southern Humboldt, then the hypothesis tested in this chapter is that beyond fishing and environmental controls, there are trophic controls operating among fishery resources with prey-predator interactions. In terms of food web structure, the hypothesis is that the number of species across animal groups in the southern Humboldt has a wasp-waist pattern as postulated by Rice (1995) and observed by Cury et al. (2000) in the southern Benguela ecosystem.

Chapter 5. Identifying and understanding ecosystem changes in the southern Humboldt Current System using ecosystem indicators

Because of their multivariate nature, ecosystems need to be analyzed using a battery of indicators to identify different ecosystem processes, interactions, states and levels of exploitation. A set of ecosystem indicators is developed from model and actual data in this chapter is used to analyze the southern Humboldt system off central Chile over the past five decades. The hypotheses tested are that the increase in fishing effort/catch led to i) a decrease in the trophic level of the catch (TLm), ii) a decrease in the magnitudes of network properties, and iii) an increase in the turnover rate of the community. However, iv) these changes have not affected system variability, property primarily driven by decadal changes in the environment (i.e., regime shifts).

Chapter 6. Ecosystem-based objectives, indicators and reference points for fisheries management in upwelling ecosystems.

The global call for an ecosystem approach to fisheries has forced fishery science to consider whole-ecosystem properties in addition to the status of particular species as motivation for management decisions. The development of ecosystem-based objectives, ecosystem indicators and ecosystem reference points play a key role in this process. Previous work has proposed and evaluated a series of ecosystem indicators in the most important upwelling ecosystems in the southern hemisphere (i.e., the Benguela Current System and the Humboldt Current System). However, the definition of ecosystem reference points has not been fully evaluated, and limit reference points (ecological thresholds) remain unknown or poorly understood. In Chapter 6, a review of literature, empirical data and model results is conducted for marine ecosystems, with emphasis on upwelling systems in the southern hemisphere. The aim is to review and propose ecosystem-based objectives and reference points for available ecosystem indicators.

Chapter 7. Mechanisms affecting the behaviour of ecosystem-based limit reference points in an upwelling food web model.

Although bottom-up forcing and overfishing are known to induce shifts in ecosystem states, system changes and their reversibility under each factor are still poorly understood. Therefore, understanding when and why limit reference points are approached and exceeded is a key element in predicting ecosystem responses to fishing and climate change. Furthermore, analyzing fishing and environmental effects is important to understand ecosystem switches to new (not necessarily desired) states and whether these switches will be reversible. In this chapter, dynamic food web simulations are conducted to test the hypothesis that fishing rather than bottom-up forcing is more likely to induce irreversible shifts in ecosystem states.

Chapter 8. General discussion and synthesis: What lessons can be learned from this analysis and how can this information be used in fisheries management?

This chapter synthesizes the findings of previous chapters. Results of part A are revisited to propose the main changes in the ecosystem under study. The aim is to integrate results on the internal ecosystem structure (food web structure, main links and interactions) and the relative effects of the main external forcing factors, to arrive at an understanding of how these factors interact and cause changes in ecosystem structure and dynamic of the Chilean ecosystem. Part A and Part B are used to highlight key aspects that should be considered in the implementation of an ecosystem approach for the management of fisheries in central Chile.

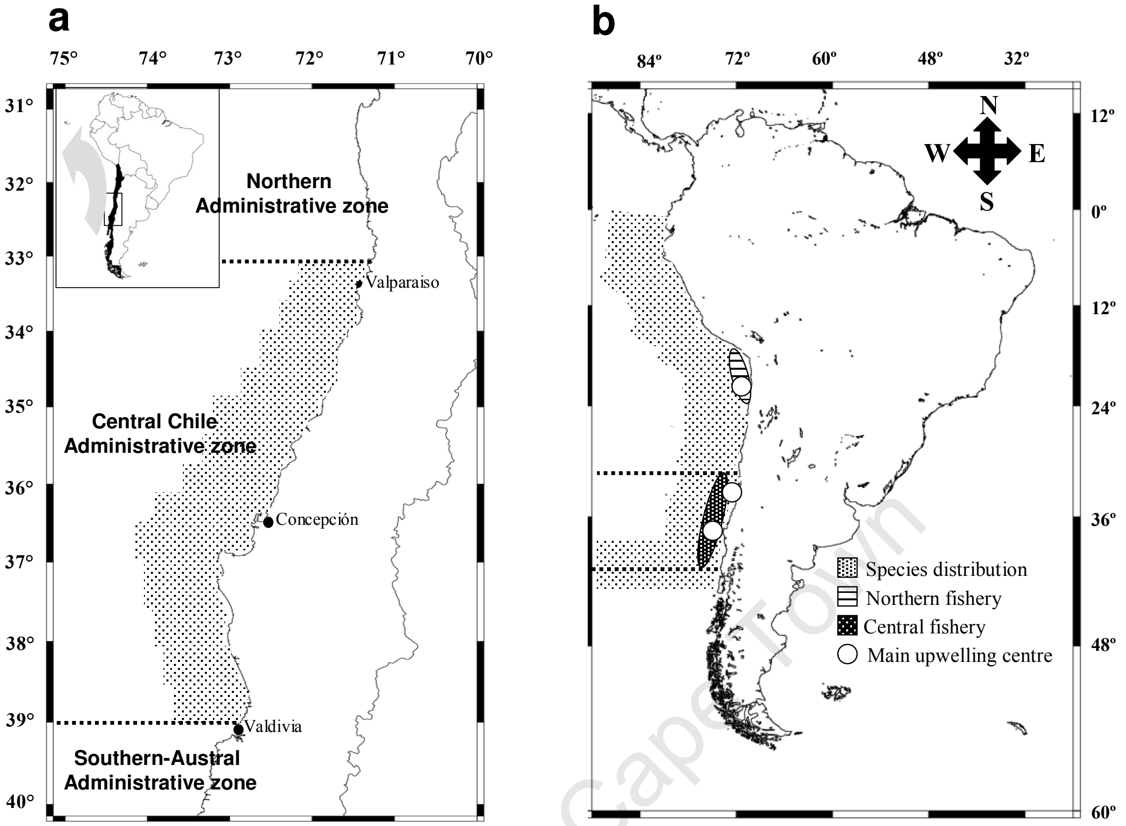

Figure 1.1. Study area, the southern Humboldt upwelling system off central Chile. a) coast of South America and the Humboldt Current System (schematized by the grey arrow) extending from 44ºS up to Equator and the Galapagos Islands. This system is characterised as a predominant northward flow of surface waters of sub Antarctic origin and by strong upwelling of cool nutrient-rich subsurface waters of equatorial origin. The Study area, the upwelling system off central Chile (33º-39ºS) is shown as a close up; b) Approximated geographic distribution of the main fishery resources exploited by fishing fleets off central Chile (see Froese and Pauly, 2007), main fishing zones and main upwelling centres (22º-24ºS; 32-34ºS and 36-38ºS). Doted lines represent the limits of the three main macro-zones in terms of fisheries management in Chile.

CHAPTER 2

ASSESSING CHANGES IN THE SOUTHERN HUMBOLDT IN THE 20th CENTURY USING FOOD WEB MODELS

Abstract

This chapter assesses changes in the southern Humboldt system (33ºS-39ºS) in the 20th century by constructing and comparing food web models representing four historical periods: i) pristine (<1900s), ii) altered by removal of marine mammals (1950), iii) development of industrial fisheries (1992), and iv) the current state (2005) when main stocks are fully or overexploited. Models are constructed with a standard structure in terms of functional groups using the Ecopath with Ecosim (EwE) software version 5.1. Model components include: the fisheries, cetaceans, sea lions, marine birds, cephalopods, large-sized pelagic fish (swordfish), medium-sized pelagic fish (e.g., horse mackerel, mackerel, and Pacific grenadier), small-sized pelagic fish (e.g. anchovy and Araucanian herring), demersal fish (e.g. Chilean hake, black conger-eel), benthic invertebrates (red squat lobster, yellow squat lobster, pink shrimp) and other groups such as zooplankton, phytoplankton and detritus. Input data are gathered from published and unpublished (grey) literature. Inter-model comparison is based on individual and community indicators calculated with network analysis. The biomass of target species (with the exception of small pelagic fish) and top predators decreases in more recent models. Although predation mortality is the main cause of total mortality for the majority of the groups in all models, fishing mortality of target species is high in the 1992 and 2005 models. This has led to a decrease in the importance of predation removal of the most important fish stocks compared with fishing, which is verified as the main predator in the system in the current state. Changes in system energetics could have resulted in loss of productivity by increased flow into detritus. Prior to heavy fishing, long-living and high-trophic level species were abundant compared to the most recent models where species with small body size, short life span and low trophic level dominate. These fishing-induced trends are in accordance with what is theoretically expected in stressed ecosystems and, if correct, the food web could be more susceptible to external forcing and negative ecological interactions.

Keywords: southern Humboldt, food web reconstruction, Ecopath with Ecosim, ecological network analysis, trophic interactions, upwelling system.

Introduction

Interactions between humans and the marine environment have a long history. Gathering and fishing were probably one of the first anthropogenic activities impacting coastal ecosystems (Nicholson, 1979). With time, other human activities linked to the sea (e.g., transport, trading, and exploitation of new sources of energy, among others) were significant for the development of human societies, but also important stressors for marine ecosystems.

Regardless of these ancient bonds, anthropogenic impacts on many marine ecosystems have become significant only since the industrial era (Pauly et al., 1998a; Caddy and Cochrane, 2001; Valdemarsen, 2001; Christensen et al., 2003; Myers and Worm, 2003). More powerful ships equipped with improved technology (refrigeration, navigation and fish detection systems) and fishing gears transformed humans into successful predators able to catch almost anything that is abundant and/or valuable in the sea (Smith, 1994; Pauly et al., 2002). As a result, the world fish catch increased from 2 million tons in 1850 to a maximum of 95.5 million tons in 2001 (McGoodwin, 1995; FAO, 2005). This fast growth was possible by first exploiting unregulated coastal resources and then by expanding the geographic and bathymetric range of fleets to new resources (Watson and Pauly, 2001). In this process, almost every important stock has been driven to collapse (Beverton, 1998), many of them without clear signs of recovery (Hutchings, 2000).

Fishing removal of target and non-target species (the category of by-catch accounts for one fourth of the world catch) has directly and indirectly altered the food webs where fisheries are embedded. Fishery-induced impacts extend far beyond target and by-catch species, decreasing the length (Bianchi et al., 2000; Daan et al., 2005b) and trophic level (Pauly et al., 1998a) of fish assemblages, along with habitat destruction (Jennings and Kaiser, 1998; Trimmer et al., 2005). Evidence of trophic cascades found in open marine ecosystems (Daskalov, 2002; Frank et al., 2005; Daskalov et al., 2007) could indicate that humans are starting to impact the world ocean as in a big lake. Fishing has degraded and simplified marine ecosystems towards food webs dominated by species with high turnover rate, short body size, short life span and low trophic level.

As fishing is increasingly considered the main threat to marine ecosystems (Jackson et al., 2001), traditional fisheries management is experiencing a worldwide crisis due to the limited ability of single-species models to assess the effects of fishing on ecosystems and the effects of the environment (physical and biological) on fishery resources (McGoodwin, 1995; Buckworth, 1998; Botsford et al., 1997). Consequently, the ecosystem approach to fisheries (EAF) has been emerging as a new paradigm recognizing that if fisheries are meant to be sustainable, then wider ecosystem considerations must be explicitly considered in management (FAO, 2003).

The understanding of ecosystem changes, with fisheries included as an important component, is a key component of EAF and, along with conservation of biodiversity and sustainability, ecosystem reconstruction is considered a major goal for EAF (Pitcher and Pauly, 1998; Pitcher 2001; 2005). Although it is unlikely, even under sustainable fishing pressure, that ecosystems can be reconstructed to, for example, their pristine state (we do not know how ecosystems were in the past, and some components could be already extinct), historical ecosystem-based reference points can potentially increase our understanding of ecosystem dynamics and the roles of fishing and other forcing (i.e., environmental variability) in driving ecosystem change. This understanding is important when assessing the current status of ecosystems and in developing strategies aimed to reconstruct ecosystems and/or alleviate negative impacts caused by external and internal forcing (Pitcher 2001; 2005).

However, little attention has been paid to the state of harvested populations (communities) beyond comparatively recent times. This is because fisheries scientists have been rather contemporary in their scope, disregarding historical trends and precedents, and tending to perceive the productive potential of a stock as the amount of fish present at the beginning of their careers. This baseline change (so-called “shifting baseline”, *sensu* Pauly, 1995) implies that the perception of the productive capacity of stocks (and ecosystems) decreases with successive generations.

Although reconstructions of time series of exploited species can be indicative of past ecosystem changes, retrospective analysis based only on biomass, catch and effort data can be misleading since, generally, these data are more related to the behaviour of the human predator rather than the natural prey (Heath, 2005). In addition, fishery-induced changes in ecosystem components can be delayed for several years (Daan et al., 2005b). Therefore, in addition to abundance and fisheries-based indices, there is also a need for flux-based and food web metrics in order to gain insights into mechanisms by which climate and fishing might affect marine food webs.

Food web models and network analysis are useful for following and assessing the pathways through which energy flows up and down the food web, and for comparing the relative magnitudes of these flows through, for example, the benthos, plankton, predators and fisheries, and how fishing alters them (e.g., contributions in Christensen and Pauly, 1993; Pauly and Christensen, 1995). Network and food web based metrics are key measures of ecosystem structure and function (Garrison and Link, 2000; Cury et al., 2005a), conveying useful information in the process of translating our understanding of ecosystem dynamics, patterns and processes into fisheries management.

The southern section of the Humboldt Current System off central Chile is a typical eastern boundary ecosystem, supporting one of the highest levels of primary productivity recorded for the open ocean (1.7 gCm^{-2} y^{-1}; Daneri et al., 2000), and globally significant landings (>4.5 million tons in 1995). Despite this high biological productivity, the state of exploited stocks is far from being healthy (Cubillos et al., 1998; Arancibia and Neira, 2003). In fact, the main target species have been fully exploited or overexploited for years, leading to a series of recent stock collapses, e.g., for horse mackerel (1998), red squat lobster and yellow squat lobster (1999), and Chilean hake (2004).

When analyzing the whole food web, Arancibia and Neira (2005) observed a significant decrease in the mean trophic level of the catch which indicates a likely change in community structure induced by fishing. In addition, small pelagic fish, species hypothesized to play a key role in all major upwelling systems as “wasp-waist” populations (Rice, 1995; Cury et al., 2000; Cury et al., 2005b), have been under increasing fishing pressure, and a recent and unexplained outbreak of jumbo squid (*Dosidicus gigas*) in the system has been associated with steep declines in some demersal and pelagic fish species (SSP, 2004a; Arancibia and Neira, in press). Sources and consequences of these changes are poorly known, but it is unlikely that they can be fully understood from a single-species perspective. Rather, a more holistic approach is needed. Unfortunately, little is known about the ecosystem status of the southern Humboldt system before and at the beginning of heavy industrial fishing.

Future ecosystem-based strategies applied in the southern Humboldt will rely on historical reference points to compare the performance of management strategies. In this study I assess changes at the functional group and food web levels in the southern Humboldt by constructing and comparing Ecopath models representing four historical periods: i) the pristine state (<1900s); ii) the altered state induced by removal of big marine mammals (1950); iii) the heavy industrial fishing period (1992); and the present state (2005) when individual stocks and the whole food web are considered significantly altered by fishing (Arancibia and Neira, 2003; Arancibia and Neira, 2005a,b).

Methods

Study area

The southern Humboldt system off central Chile extends from 33ºS to 39ºS and from the coastline up to 30 nautical miles offshore, covering approximately 50 000 km^2 (Fig. 2.1). This geographical unit corresponds to the "Mediterranean District" of the Humboldt system, that is ecologically independent from the "Peruvian Province" and the "Southern District" located northward and southward, respectively (Camus, 2001). The main oceanographic and biogeographic patterns that characterize the southern Humboldt are: a rather narrow continental shelf (<30 nautical miles), a strongly seasonal upwelling period (September to March) and high levels of primary productivity (Strub et al., 1998; Daneri et al., 2000; Escribano et al., 2003).

The marine environment along central Chile is very diverse due to the presence of four main water masses: Subtropical Surface Water (STSW), Subantarctic Water (SAW), Antarctic Intermediate Water (AAIW), and Equatorial Subsurface Water (ESSW) (for a review see Strub et al., 1998). Wind driven coastal upwelling brings the ESSW to the surface in the coastal zone, causing a persistent and characteristic shallow oxygen minimum zone (> 0.5 mL O_2 L^{-1}).

Based on the correlation between the low frequency coastal modes and the Pacific and Atlantic sea surface temperatures (SST), Montecinos et al. (2003) suggest that coastal SSTs comprise two main large-scale climate processes affecting the southern Humboldt. At the inter-annual scale the main source of variability is the El Niño Southern Oscillation cycle, whereas on a long-term scale, an inter-decadal oscillation occurs at a basin-wide, and maybe even global, scale.

In terms of biological components, the southern Humboldt sustains a diverse food web. Large diatoms dominate the phytoplankton group most of the year (Avaria and Muñoz, 1982), while the zooplankton is dominated by herbivorous copepods and euphausiids. Jellyfishes also constitute an important group in the plankton domain (Palma and Rosales, 1995). Macrocrustaceans are significant benthic components and some species such as red squat lobster (*Pleuroncodes monodon*), yellow squat lobster (*Cervimunida johni*) and pink shrimp (*Heterocarpus reedi*) are important fishery resources. The fish community is dominated by pelagic species. Small pelagic fishes such anchovy (*Engraulis ringens*) and the endemic Araucanian herring (*Strangomera bentincki*) are present at high biomasses in the southern Humboldt and dominate landings. These species feed on phytoplankton and zooplankton (Arrizaga et al., 1993). Although the horse mackerel (*Trachurus symmetricus*) performs large-scale migrations in the Pacific Ocean, it is a major fishery resource off Chile, where it feeds mainly on euphausiids (Miranda et al., 1998). The demersal fish community is dominated by the Chilean hake (*Merluccius gayi*) both in biomass and landings. Hake inhabits mid-depth waters (200-400 m) and feeds on euphausiids, galatheid crustaceans and small pelagic fishes (Meléndez, 1984; Arancibia, 1989; Cubillos et al., 2003). This species also exhibits a highly cannibalistic behavior (Arancibia et al., 1998). The current status and basic ecology of top predators such as marine birds, sea lions and cetaceans are poorly known, but it is likely that their abundances are low compared to those at the start of the industrial fisheries in Central Chile (Aguayo-Lobo et al., 1998).

The southern Humboldt ecosystem also represents an independent management unit, comprising the main fishing ground for the Chilean purse seine and trawling fleets, both industrial and small scale operations, and accounting for approximately 75% of the total landings in Chile (Neira and Arancibia, 2004; Neira et al., 2004). The other 25% of the total catch comes from northern Chile. The main species in northern Chile are

Spanish sardine (*Sardinps sagax*), anchovy (*E. ringens*), horse mackerel (*T. symmetricus*) and mackerel (*Scomber japonicus*). However, these are separate stocks, or at least are managed as that, from those off central Chile and thus fishing activities in northern Chile do not affect how fishing mortality is represented in the modelled region.

Expansion of the fisheries in central Chile during the last century

Four main periods in the history of human exploitation of marine resources in the southern Humboldt can be identified:

A. Pristine Period (<1900)

The first fishing activities were likely associated with the "*Huentelauquen*" culture, and have been traced to the Pleistocene-Early Holocene period (i.e., 10400 to 9000 years ago). Archaeological evidence indicates that this group gathered a wide range of coastal marine taxa such as molluscs (mainly bivalves), echinoderms (sea urchins), crustaceans (decapods and barnacles) and seaweeds, due to their easy accessibility on rocky and sandy beaches. However, they also caught coastal fish, marine mammals and sea birds (Báez et al., 2002). This survival fishery seems to have remained unchanged for millennia since no significant changes are recorded for the Colony (1534 to 1810) and early Independent Republic (>1818) periods. This is considered to be the pristine state, when fishing activities were for survival, mainly local, and basically concentrated on the shores. This period finishes with the start of big-scale fisheries in central Chile based on the exploitation of marine mammals (Aguayo-Lobo et al., 1998).

B. Altered period: removal of marine mammals (1900-1950)

After millennia, aboriginal fishing along the Chilean coast was gradually displaced by North American, British and, for a very short time, French ships that operated from Talcahuano (36° S) to New Zealand from 1830 to 1835. Although several attempts to build a Chilean whaling company were made after the Independence war against the Spanish Crown (>1818), post-war hostilities impeded continuous fishing activities. The first Chilean whaling company ("Compañía Chilena Ballenera") was created only in

1871 with a fleet of six ships that operated in the whole South Pacific Ocean (Véliz, 1961). Although two new companies ("Matheiu & Macaña" and "Juan Macaya & Hijo") were created in the following decades, the whaling fleet was still a small-scale activity with limited catch power. "Juan Macaya & Hijo" was subsequently upgraded to an industrial fleet that operated in central Chile, especially during the migration of cetacean species to central Chile during the breeding season. Fishing effort on cetaceans was most intense between 1920 and 1982, when about 40 thousand individuals of sperm whale (*Physeter catodon*), fin whale (*Balaenoptera phisalus*) and blue whale (*B. musculus*), among others, were officially caught. Based on the poor condition of exploited stocks, many of which were seriously depleted, the authority banned whaling in central Chile in 1983 (Aguayo-Lobo et al., 1998).

The common sea lion (*Otaria flavescens*) is by far the most conspicuous species of otariids inhabiting Chilean coasts (Siefeld et al., 1999). Time series data of catches and abundance for this species in the study area are scarce. The first records indicate intensive harvesting activity during the early 1900s. For example, at one site (Santa Maria Island, 36ºS), 52 thousand individuals were caught between 1921 and 1922 (Osgood, 1943). Nowadays, the common sea lion population in the study area is estimated at only 17 thousand individuals (Anonymous, 1997). Culling has been prohibited in the study area since the early 1980s.

C. Altered period: heavy industrial fishing (1950 to late 1990s)

Industrial fishing targeting fish and benthic crustacean species in central Chile started by the end of the decade of the 1940s, when demersal trawlers directed their effort to the catch of common hake. Landings quickly increased up to 80 thousand tons per year by the mid 1950s.

The industrial pelagic fishery started activities in the 1960s, targeting mainly two species of small pelagic fish, Araucanian herring and anchovy. At the same time, an industrial fleet was also operating on medium-sized pelagic fish, horse mackerel (*Trachurus symmetricus*), with significant landings only from 1975 onwards (Figs. 5.2a and 5.3).

D. Significantly altered Period (>2000s)

The maximum catch levels in the study area occurred during the mid 1990s with a historical peak of 4.5 million tons in 1995, after which total landings have been decreasing steadily. This situation is explained by the collapse of important stocks such as horse mackerel in 1998, red squat lobster and yellow squat lobster in 1999, and more recently Chilean hake in the early 2000s.

The time scale of each model is the year. This is because in central Chile trophic studies have been conducted in a punctuated rather continuous way over the last few decades, with 1992 and 2005 representing years with the best available data. During these periods (1992 and 2005) no major oceanographic perturbations occurred in the southern Humboldt, thus interannual variability can be assumed minimal. The models representing the system in years 1950 and >1900s are more hypothetical and the yearly scale is more practical since there are no further data as to build models that average a time period of several years.

Modelling approach

I constructed three new food web models and used a previously constructed model representing the system in the early 1990s (Neira and Arancibia, 2004) to represent food web structure in the southern Humboldt during the four described periods. Models were constructed using a standard structure (Neira and Arancibia, 2004; Moloney et al., 2005). The functional groups considered in each model are: phytoplankton, zooplankton I (microzooplankton), zooplankton II (mesozooplankton, represented by copepods), zooplankton III (macrozooplankton, represented by euphausiids), gelatinous zooplankton (salps and jellyfishes), macrobenthos (represented by red squat lobster; and yellow squat lobster), anchovy, Araucanian herring, mesopelagic fish, horse mackerel, hake, pelagic fish I (medium-sized pelagic fish represented by hoki *Macrouronus magellanicus*), demersal fish I (benthic feeding species), demersal fish II (pelagic feeding species), condrichthyans (mainly skates), pelagic fish II (large-sized pelagic fish represented by swordfish *Xiphias gladius*), cephalopods (squid *Loligo gahi*; jumbo squid), sea lion, sea birds (penguins, pelicans, cormorants), cetaceans (odontocetes, misticetes, killer whales and dolphins) and detritus.

These groups were selected in order to have a representation of all trophic levels in the studied food web. In some cases, functional groups are disaggregated to the species/age group level because they are abundant and have commercial value (data are available). Others represent more an aggregated taxonomic level because no data are available for all components. In those cases, data of one representative and/or more abundant species are used to characterize the group.

Considering the cannibalistic behaviour and the strong ontogenetic changes in diet of Chilean hake (Arancibia, 1987; Arancibia et al., 1998), this group was split into juveniles (small) and adults (large). According to Arancibia (1987), small hake includes age group 0 to 3 year-olds (≤35 cm total length), while large hake are 4+ year-olds (≥36 cm total length).

Having the same standardized structure is requirement for comparisons between models. However, this might have resulted in loosing important structural changes over time. For example, the pristine state may have had groups that are no longer present in the study area. Therefore, it is desirable that such visible changes were included in the modelling since they are important indicators of system alteration. However, there is no evidence of species extinctions/outbursts and/or dramatic changes in distributions of species indicating that they are no longer/appeared in the system. Therefore, no subtraction/addition of groups was performed in any model.

Models were constructed using the Ecopath with Ecosim version 5.1 software (EwE; Christensen and Pauly, 1992; Walters et al., 1997). EwE models represent direct and indirect trophic relationships in any food web by splitting the production of each group (i) into its components:

$$\text{production}_i = \text{catches}_i + \text{predation mortality}_i + \text{biomass accumulation}_i + \text{net migration}_i + \text{other mortality} \quad (1.1)$$

or,

$$P_i = Y_i + B_i * M2_i + BA_i + E_i + P_i * (1-EE_i)$$

where P_i is total production, Y_i is total fishery catch, B_i is biomass, BA_i is biomass accumulation $M2_i$ is total predation rate, E_i is net migration rate (emigration - immigration), and P_i (1-EE_i) is other mortality ($M0_i$) with EE_i the ecotrophic efficiency which represents the total fraction of the production that is either eaten by predators or exported from the system, including in the form of fishery catch.

By assuming that i) no migrations and export occur (catch is the only export), and ii) steady state conditions apply for each group (BA_i=0) during the modelled periods, a system of linear equations is solved:

$$\boldsymbol{B_i * P/B_i + EE_i - \sum_j (B_j * Q/B_j * DC_{ij}) - EX_i = 0} \qquad (1.2)$$

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

Following Winberg (1956), the second main equation in EwE expresses the mass balance for each group i of the system as:

$$Q_i = P_i + R_i + U_i \qquad (1.3)$$

where Q_i is prey consumption, both inside and outside the system (imports), P_i must be eaten by predators, exported from the system or contributed to detritus, R_i is respiration, and U_i is unassimilated food.

To run the model, each group requires estimates of B_i, P/B_i, Q/B_i, DC_{ij}, EX_i, assimilation efficiency and EE_i. Nevertheless, one of the parameters (B, P/B, Q/B or EE) can remain unknown for each group, since it can be estimated (together with respiration) from the solutions to the system of linear equations. Values of the gross efficiency of food conversion (GE), which corresponds to the Production/Consumption ratio (P/Q), can be used as alternative inputs to Q/B. In Ecopath, primary production represents (is defined as) net production, and therefore disregards respiration.

Therefore, for the phytoplankton group it is not necessary to enter Q/B or P/Q values. Data sources and estimation methods used to calculate input parameters for the model representing the heavy industrial fishing period are fully described in Neira and Arancibia (2004) and Appendix 1.

For groups in models representing the current state (2005), the food web under removal of big marine mammals (1950) and the pristine (<1900s) periods, I assumed the values of input parameters used in the model constructed by Neira and Arancibia (2004), except in the following cases: For the current state model, B_i, P/B_i, and DC_{ij} are collected from survey data directed to the assessment of biomass in demersal (Chilean hake), small pelagic (Araucanian herring and anchovy) and medium pelagic fish (horse mackerel, hoki), and benthic invertebrates (red squat lobster, yellow squat lobster, pink shrimp) in the study area. Y_i was obtained from the statistics of the Chilean National Fisheries Service “Servicio Nacional de Pesca” (www.sernapesca.cl).

For the system under removal of big marine mammals, B_is for target species such as Araucanian herring, anchovy, Chilean hake, horse mackerel, squat lobster and pink shrimp were obtained from available time series from the Chilean Undersecretary of Fishing (Arancibia et al., 2003). The catches of the same species were obtained from “Servicio Nacional de Pesca”. In the absence of population estimates for cetaceans and sea lions, I assumed that B_i for these functional groups corresponded to the biomass levels in the early 1990s (Neira and Arancibia, 2004) plus the sum of the catches for these groups during the period 1950 to 1992 obtained from Aguayo-Lobo et al. (1998) and Siefeld (1999). Following Neira and Arancibia (2004) and Neira et al. (2004), B_i and Y_i in species that are a by-catch in the fishery of Chilean hake, are estimated under the assumption of constant ratios for [biomass of by-catch species]/[biomass of hake] and [catch of by-catch species]/[catch of hake]. This approach is simple but helpful in arriving at approximate estimates of biomass for non-target species. This is important since these species also suffer fishing mortality due to discard and no other data are available.

For the pristine state model, the biomass of top predators (cetaceans and sea lions) was calculated as the biomass of these groups in the 1950s model plus the sum of the catches from 1900 to 1950. As no biomass estimates exist for fish species during this period, I allowed the model to calculate the minimum biomass of all intermediate trophic levels needed to satisfy the food requirements of top predators in the model. This was done by assuming an EE=0.99 for each group, the only exemptions being jelly fish and phytoplankton where EE=0.15 and EE=0.3 were assumed. This is because jelly fish are considered dead-ends in terms of trophic pathways and it has been estimated that in the Humboldt System around 70% of primary production sinks within a short time (Walsh, 1981).

Checking the mass-balance in each group

Models were balanced by checking the values of EE_i and of the gross efficiency of food conversion (GE_i). EE_i ranges between 0 and 1, while GE_i, which is equal to P_i/Q_i, ranges between 0.1 and 0.35. Following criteria presented in Christensen et al. (2000), when inconsistent values of EE_i or GE_i were obtained, changes in input data B_i, P_i/B_i or DC_{ij} were performed until acceptable runs were obtained, i.e. $EE_i<1$ and $0.1<GE_i<0.35$.

Network Analysis

Network analysis routines based on Ulanowicz (1986) and Ulanowicz and Kay (1991), incorporated in EwE, were applied to balanced models to calculate system properties and flow indicators based on theoretical concepts of Odum (1969) and Ulanowicz (1986). An EwE routine originally proposed by Ulanowicz (1995) was used to aggregate the food web into discrete trophic levels (*sensu* Lindeman, 1942), allowing assessment of biomass, flow distributions and trophic transfer efficiencies (TTE) among those discrete trophic levels.

Changes in biomass distributions among functional groups were assessed using the Shannon and Simpson diversity indexes (see Magurran, 2004).

Results

Changes required to balance each model and tables showing the balanced models are presented in Appendix 1 (Tables 2 and 4) and Appendix 2.

Changes at functional group level

Biomass

Trends in the biomass of functional groups in each modelled period are shown in Figure 2.2. They must be carefully interpreted since the four points (models) are unequally spaced in time. The groups that present an increasing trend in biomass across models are: phytoplankton, zooplankton I (not shown), zooplankton II, zooplankton III, small pelagic fish (anchovy and Araucanian herring), mesopelagic fish, pelagic fish I, and cephalopods. Among these groups, anchovy, Araucanian herring and pelagic fish I are fishery resources, while cephalopods constitute an ephemeral fishery. On the other hand, the following groups show a decreasing trend: macrobenthos, hake (large), hake (small), demersal fish II, pelagic fish II, sea lions and cetaceans. All these groups have been directly impacted by fishing because they represent either target (hake, pelagic fish II, sea lions, cetaceans) or by-catch (demersal fish II) species. The biomass of jellyfish, horse mackerel and demersal fish I do not present a clear trend across models.

When considering only the biomass values that were entered in the model as input parameters (grey bars in Figure 2.2), the only increasing trends are those of anchovy, Araucanian herring and cephalopods. The biomass of horse mackerel, hake (large), hake (juveniles), chondrichthyans and demersal fish I show a decline from 1992 to the present model (2005).

Mortality coefficients

Mortality coefficients calculated by EwE for each functional group in each modelled period are presented in Figure 2.3. In both the pristine (>1900) and 1950 models, predation mortality (M2) is the most important source of total mortality in most functional groups. Exceptions are phytoplankton, jelly fish, pelagic fish I, chondrichthyans, pelagic fish II, sea birds and cetaceans. However, in the model representing 1950, fishing mortality (F) is the main source of total mortality in cetaceans and also an important source of mortality in sea lions, hake (adults), demersal fish (I), horse mackerel, small pelagic fish and macrobenthos.

Fishing mortality is important both at functional groups and food web levels in the model representing 1992. Pelagic fish (anchovy, Araucanian herring, horse mackerel, pelagic I, pelagic II, and demersal fish (hake, demersal fish I, demersal fish II, chondrichthyans) were heavily fished during this period. Benthic invertebrates (macrobenthos) have low F contributions, but this is because they were recovering from previous overfishing, while no F applied to sea lions and cetaceans because their fisheries were already banned.

In the model representing the current state of the system (2005), no fishing pressure is observed in macrobenthos (because the fishery on squat lobsters has been banned since 2001). A reduced F is observed in small pelagic fish, pelagic fish I and demersal fish species. F is still very high in horse mackerel and hake despite the fact that these species are considered overfished. Cephalopods are under increased fishing pressure, mainly due to the recent outbreak of jumbo squid yielding > 150 thousand tons in 2005. However, it is expected that this situation will not last since outbreaks of jumbo squid are normally of short duration (Fernández and Vásquez, 1995).

Changes in predators' consumption and fishing removal

A comparative analysis of the total production of small pelagics, horse mackerel and hake removed by their predators and fisheries in the four modelled periods is presented in Figure 2.4. In the case of small pelagic fish, hake is the main natural predator in all periods, and sea lions play a secondary role in terms of consumption. Other predators removed a relatively small amount of biomass in all periods. The main natural predator for horse mackerel is sea lions in the >1900 and 1950 models, while sea lions, predatory fish and hake are important in 1992 and 2005. Cetaceans, birds and cephalopods are secondary predators for horse mackerel in all models, but sea lions and hake (cannibalism) are the main predators of hake in all models, except for 2005.

Obviously, no significant fishing removal occurred in the pristine model. Fishing removed only a marginal amount of production of the main fish components in the 1950 model, but became the main source of production removal in models representing 1992 and 2005 (Fig. 2.4). This is explained by the increase in fishing effort (increasing total landings from 90 thousand tons in 1950 to >1.9 million ton in 2005) and by the decline in the abundance of top predators, specifically sea lions. The above means that the fishery today represents the main predator for the main target species in the system.

Changes at the food web level

Aggregated trophic food web

Results obtained from the aggregation of the food web in discrete trophic levels are presented in Figure 2.5. In all models, total biomass (B_T) and total throughput (T_T) per discrete TL sharply decrease as TL increases. Most of the system B_T and T_T is concentrated in TL< TL V. Trophic transfer efficiencies (TTE) are small in low (TL I => TL II) and high (TL IV=> TLV) TLs, while large TTEs are found in intermediate TLs (TL II => TL III => TL IV), probably an artefact of high EE. When comparing models, B_T and T_T are higher in the models representing the pristine state and the year 1992. Although TTEs among discrete TLs do not change in a consistent way, and remain similar across models, the mean TTE increases from the pristine model to the more recent ones, mainly owing to the increases in TE between TL IV and TL V.

System attributes

Global metrics of energetics in the food web are presented in Figure 2.6. The sum of all respiratory flows, sum of all flows into detritus and total primary production/total biomass ratio decreased from the 1900 model to the 1950 model and then increased in 1992 and 2005. Total primary production/total respiration ratio was lower in >1900 model and higher but of similar magnitude in 1950, 1992 and 2005 models. This may indicate a change in the flows of energy and loss of primary production in the most recent models.

Overall metrics of food web structure in the four models are presented in Figure 2.7. The system supported the highest catch in the 1992 model, decreasing in 2005. The mean trophic level of the catch decreased from 1950 to 1992 and remains almost the same in the recent model, indicating that the exploited fish community is dominated in the more recent models by species located in lower trophic levels. The Finn's path length and Finn's cycling index have similar values in the last three models and all are higher than the value of these indicators in the model representing 1900. This may indicate that the trophic distances between prey and predators have increased as well as nutrient cycling. The system biomass/production ratio, which can be interpreted to represent the longevity of the organisms in the food web, decreased from the pristine and 1950 models to the more recent models, indicating a change in the food web from a community dominated by long-lived organisms to one dominated by short lived organisms. The food web has also changed from one where the biomass was evenly distributed among functional groups towards a community dominated by a few abundant functional groups, as indicated by the Simpson and Shannon diversity indices.

Discussion

The lack of historical information and the limitations in our understanding of ecosystems makes the reconstruction of past food webs difficult. The combination of general ecological principles and best guesses used in this chapter to approach different historical periods in the food web can be criticized on a number of levels. However, models can never be perfect, and criticisms on assumptions and their effects (e.g., constant versus variable diets and ecotrophic efficiencies across models) will point to future research directions. This chapter could be regarded as first step in a series of attempts to try to understand past and present states of the marine food web off central Chile, and the forcing factors behind these change of state. Future research studies should focus on improving estimates of input data in order to relax assumptions such as constant diet composition, abundance, production and consumption of different groups in the past as well as exploration of model sensitivity to uncertainties in input data.

Changes at individual stock/functional group level

Model results indicate that biomass in lower TLs could have increased towards the most recent models. Conversely, the biomass of target species, non-target species and top predators followed a decreasing trend, except those of small pelagic fish and cephalopods. This could mean that fishing has decreased the biomass of many groups located in higher TLs of the food web, either directly (by targeting) or indirectly (by removing important prey items).

In the case of small pelagic fish, they seem to operate as wasp-waist populations in the major upwelling ecosystems (Rice, 1995; Bakun, 1996; Cury et al., 2000; Cury et al., 2005b; Bakun, 2006). This hypothesis states that this group controls both predators and prey, while their dynamics are not controlled either by prey or predators. However, both environmental forcing and fishing affect small pelagic fish and the effects are propagated through the food web both up and down. In turn, cephalopod species do not represent a formal fishery in central Chile due to their mostly unpredictable dynamics, and it is expected that their outbreaks and declines are not related to fishing, but to their opportunistic behaviour as predators and to environmental conditions (Arancibia et al., 2006a).

The decline in predatory fish and top predators has reduced the importance of “natural” predation in the food web. This situation, along with increasing fishing mortality in recent decades (Fig. 2.3), has led to a change in predator structure in the most recent models, when the fishery becomes the main source of removal of biomass of target species and, therefore, the most important predator in the system (Fig. 2.4). The impact of observed changes in the roles of predators and fishing in the recovery of species located in higher trophic levels is potentially important, as the fishery is removing the biomass of prey species that, if left at sea, could facilitate the recovery of top predators and predatory fishes. Declines in predator biomass could have a negative effect in terms of the system’s response to outbreaks of opportunistic species (such as jumbo squid and others). While predators can eventually regulate outbreaks, the fishery normally does not do so because many opportunistic and invasive species either do not have commercial value, or the lag between the outbreak and the response of the fishers normally precludes the development of a fishery. This is the case of jumbo squid, where landings have increased only recently. The lack of predator regulation could be an additional explanation for the unusually long presence of jumbo squid in the southern Humboldt in recent years.

Although the role of environmental variability in causing observed changes in the biomass of functional groups was not explored in this study, it is well known that interannual (El Niño Southern Oscillation) and decadal (regime shifts) variability occurs in the Humboldt system (Montecinos et al., 2003). Alheit and Ñiquen (2005) show evidence of a regime shift affecting the southern Humboldt as a whole in the last five decades. In turn, EwE modelling presents evidence of a shift in environmental conditions affecting the southern Humboldt (see Chapter 3). Both studies indicate that before the mid 1980s, the system was warmer with reduced upwelling and primary productivity, while from the mid 1980s to early 2000s, the system became colder due to increased upwelling, and consequently, primary productivity could increase. If this bottom-up process affected the whole food web, it should have resulted in an increase in the biomass of the main target species during the last decades. However, this is only the case for small pelagic fish and cephalopods. Therefore, it is likely that the decline in the main stocks could have been caused by fishing rather than bottom-up factors, since model results indicate food (plankton and forage fish) was more available in the system in recent models (Fig. 2.2).

Future work should aim at disentangling better the predation effect among some functional groups. For example, combining toothed whales and baleen whales in one functional group (cetaceans) is not ideal and may have resulted in some problems for the analysis. The assumed diet composition resembles that of toothed and killer whales, which are thought to be more abundant than baleen whales off central Chile. This aggregation led to a balancing problem for the 1900 and 1950 models where a change in input parameters was necessary to remove over consumption of sea lions by cetaceans. On the other hand, functional groups such as chondrichthyans and pelagic fish II are not preyed upon in the model and thus their biomass dynamics will be driven by their prey groups. Likewise, predation mortality caused by these functional groups could have a disproportionate effect on a particular prey group. Negative consequences of poor specification of sources of mortality could have strong impacts on Ecosim predictions, especially when the "other mortality" coefficient is made sensitive to forage time adjustments.

Community and food web levels

In Table 2.1, I present general trends expected in stressed ecosystems (*sensu* Odum, 1985) and indicators used here to test these trends. In terms of system energetics, the P/R (production/respiration) ratio became unbalanced, increasing from the pristine towards recent models. Similar trends are observed in the P/B and R/B (maintenance:biomass structure) ratios. The amount of unused primary production increases in the most recent models, as indicated by increased flows into detritus.

There is no indicator derived from Ecopath that can be used to test trends in nutrient cycling. This is because bacteria are not included in the models and the plankton is modelled on an annual time scale, which is not the most appropriate for plankton dynamics. Also, the currency of the model is wet mass instead of nutrient (i.e., nitrogen, phosphorous, sulphur). However, and according with what is theoretically expected, horizontal transport increased as result of higher TTE in the most recent models (Fig. 2.5). Vertical cycling of wet mass in the model, represented via Finn's cycling index, did not decrease as theoretically expected (*sensu*, Odum 1985). In fact, the Finn's cycling index increases across models (Fig. 2.7). However, the interpretation of this index is apparently not as simple as the author originally conceived, with an increase of recycling as a system matures. In fact, the opposite trend may be the case, as suggested by Wulff and Ulanowicz (1989).

Community structure changed towards a food web with an increased proportion of "r" strategists (B/P ratio) located in lower trophic levels. Although energy flow to higher trophic levels declined (Fig. 2.5) food chains did not shorten (Fig. 2.7). In Chapter 5 it is shown that the mean size of horse mackerel, hake, anchovy and Araucanian herring has decreased in the last 20 years in the southern Humboldt. This means that small and young individuals dominate the size structure of these populations. Therefore, along with a reduced reproductive capacity, these populations might be more and more dependent on good recruitment, which, in turn, strongly depends on environmental conditions. Diversity (in terms of an even distribution of biomass among functional groups) decreased over time, and the system seems to be dominated now by a few highly abundant species/functional groups, as indicated by Simpson´s and Shannon´s diversity indices.

In terms of general (eco)system-level trends (not assessed with mass balance models), Odum (1985) hypothesized that stressed ecosystems should become more open to environmental input and output. In addition, succession should be interrupted and revert to earlier stages, with a lower efficiency of resource use. Negative ecological interactions should increase in stressed ecosystems (e.g., parasitism), while mutualism and other positive interactions decline. It is expected that functional properties (such as community metabolism) are more robust (homeostatic-resistant to stressors) than species composition and other structural properties. Therefore, it is expected that early warning of stress will be more easily seen at the species level (i.e., cetaceans, sea lions, hake, Fig. 2.2), since shifts in system level indicators are more difficult to detect in large ecosystems (e.g., Cury et al. 2005a; Shin et al. 2005). Stress should move the system away from maturity (sensu Odum, 1969). Christensen (1994) and Christensen (1995) explored in a quantitative way the behaviour of some goal functions for ecosystem development and its relation to ecosystem maturity. No clear conclusion arose in terms of an optimal goal function for ecosystem development, but ascendancy (sensu Ulanowicz, 1986) and maturity seem to be correlated with a potential measure of system stability. Therefore, when stress is detectable at the ecosystem level there is cause for alarm, since it could be a signal of breakdown in homeostasis (Odum, 1985).

However, it is also possible that some differences among models may as well be artefacts induced by lack of data and assumptions on input parameters in early periods as some biomass and diet composition estimates for early periods are not available. In fact, some of the peculiarities observed in the 1950 model could also be explained by the removal of top predators (whales and sea lions) which reduced the need for “food resources” in the system. By assuming high ecotrophic efficiencies, the model estimated minimal B_i for prey groups which may have led to lower biomasses on the basal trophic levels. This might have resulted in a decrease in total flows as well as an increase in trophic transfer efficiency, since the massive removal of fish stocks by fishing, as another top predator, was starting. Future work could explore alternative parameterization (e.g., biomass, production and diet composition estimates) in periods in which data are scarce, and how it affects model outputs. In terms of diet compositions, they could be, for example, assigned based on estimates of prey selectivity and/or, based on the assumption that no selectivity exists, and then prey proportion in predators’ diet is proportional to prey abundance in the “environment”.

Results of this chapter indicate that in the southern Humboldt, the changes in biomass of the most important target and non-target species that occurred in the last century (many of them induced by overfishing of top predators, demersal and pelagic fish species and benthic crustaceans) had a noticeable impact at the food web/community level, as indicated by the trend of the various indicators across models. These trends indicate that the southern Humboldt ecosystem is under stress and more undesirable and unpredictable changes could be expected in the short- to medium-term (see general ecosystem trends in Table 2.1).

Although of concern, these results should be taken carefully and regarded as hypotheses still to be tested. Specifically, results derived from the two models representing the pristine (>1900) and the removal of top predators (1950) models, are driven by assumptions in input parameters, while models representing the more recent periods (1992 and 2005), when the fishery was more intense, are data driven. When considering only the last two models, important changes in functional groups (i.e., anchovy, Araucanian herring, horse mackerel, hake, demersal fish II, chondrichthyans and cephalopods) and the system are still found, and the changes are in accordance with Odum's theory of stressed ecosystems (Odum, 1985). These changes may have been caused by management actions (overfishing in some fish species), environmental changes (strong El Niño event in 1997-98) and a combination of both.

Snapshot models, as constructed and analyzed here, are useful in assessing whether changes in individual components (especially biomass and catches, the ones must readily available) may result in changes at the system level. Although fishing derived indicators showed important changes among models, it is not possible to evaluate the effect of other forcing factors in explaining biomass changes in key functional groups (e.g., physical variability, trophic controls). Therefore, results obtained here must be combined with those obtained from the fitting of an Ecopath model to time series (Chapter 3), before arriving at general conclusions on the relative effects of fishing, environmental variability and trophic controls in this food web. In addition, other ecosystem indicators, e.g., size-based, physical factors, etc., to be analyzed in Chapter 4, need to be considered together with trends found here in network and food web indicators to get reliable indications of patterns of change of these indicators, which can be used to set reference points useful for fisheries management in central Chile.

Table 2.1. Trends expected in stressed ecosystems (Odum, 1985), and the Ecopath-derived indicator(s) used to evaluate them. The tick mark indicates that the trend in Ecopath-derived indicators is in accordance with the expected theoretical trends.

Trends expected in stressed ecosystems	Ecopath derived indicator	Trend
Energetics		
1. Community respiration increases	Sum of all respiratory flows	✓
2. P/R (production/respiration) becomes unbalanced (< or > 1)	Total primary production/total respiration	✓
3. P/B and R/B (maintenance:biomass structure) ratios increase	Total primary production/total biomass Total respiration/biomass	✓
4. Importance of auxiliary energy increases (exomatic metabolism)		
5. Exported or unused PP increases: Sum of all flows to detritus increase	Sum of all flows into detritus	✓
Nutrient cycling		
6. Nutrient turnover increase		
7. Horizontal transport increases and vertical cycling of nutrients decreases (cycling index decrease)	Finn's cycling index	✓
8. Nutrient loss increase (system becomes more "leaky")	Sum of all flows into detritus	✓
Community structure		
9. Proportion of "r" strategists increases	Mean trophic level of the catch and longevity spectrum average size (B/P)	✓
10. Size of organisms decreases	System B/P ratio average size (B/P)	✓
11. Life spans of organisms decrease	System B/P ratio average size (B/P)	✓
12. Food chains shorten because of reduced energy flow at higher trophic levels and/or greater sensitivity of predators to stress	Finn's mean path length and Mean length of pathways	✓
13. Species diversity decrease and dominance increases: if original diversity is low, the reverse may occur; at the ecosystem level, redundancy of parallel processes theoretically declines	Simpson's and Shannon's diversity index	✓
General (eco)system-levels trends		
14. Ecosystem becomes more open (i.e., input and output environments become more important as internal cycling is reduced)		
15. Autogenic successional trends reverse (succession reverts to earlier stages)		
16. Efficiency of resource use decrease		
17. Parasitism and other negative interactions increase, and mutualism and other positive interactions decrease		

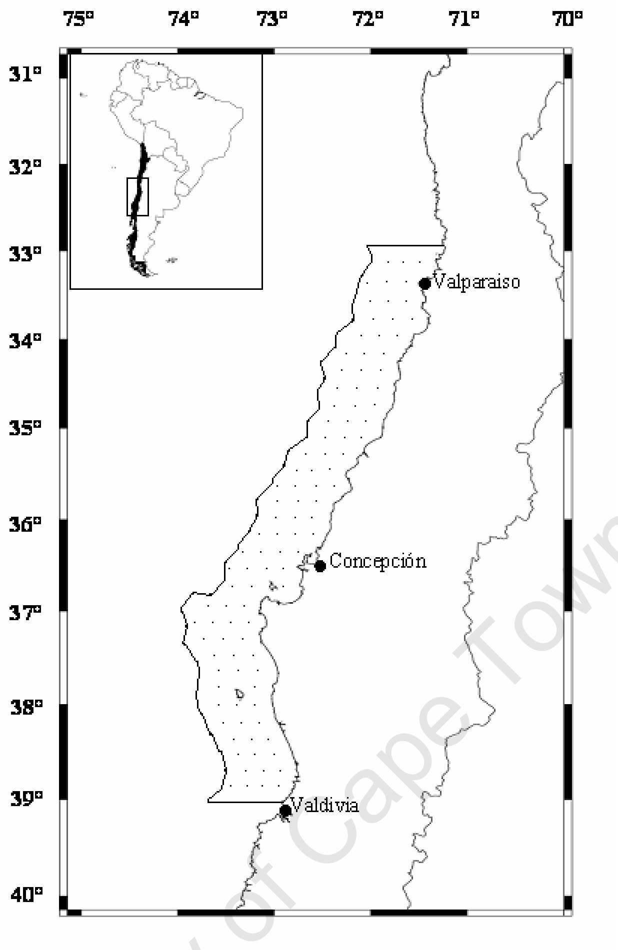

Figure 2.1. The southern Humboldt Current System off central Chile, extending from 33ºS to 39ºS and from the coast to 30 nautical miles offshore with a total area of approximately 50 000 km^2.

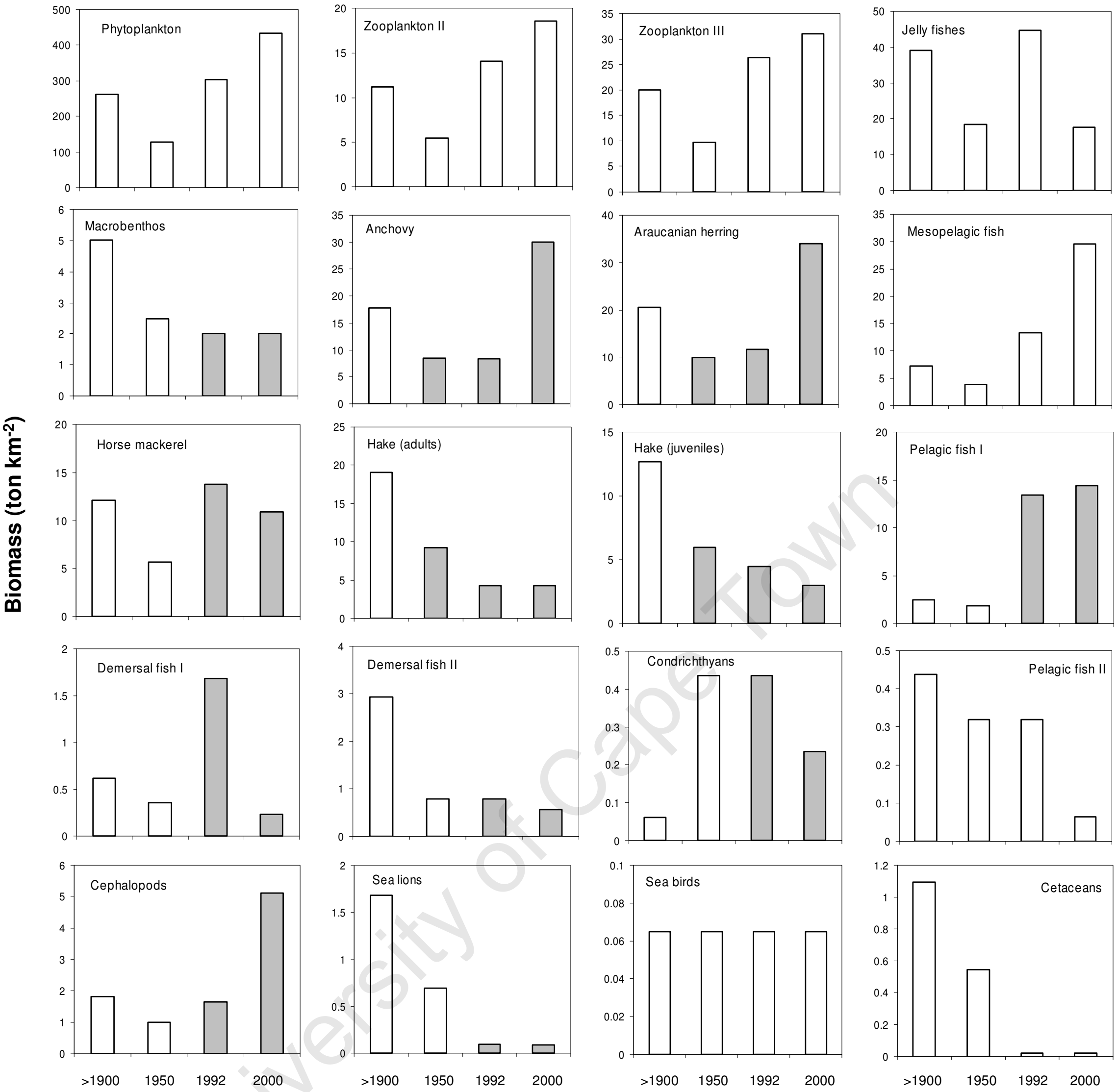

Figure 2.2. Comparison of the biomass of functional groups in the southern Humboldt ecosystem in four modeled periods. Grey bars are biomass values entered to the model as input parameters. White bars are model estimates. Zooplankton I is not shown in the figure.

Figure 2.3. Comparison of the different coefficients of mortality calculated for each functional group in the upwelling system off central Chile from results of four food web models representing different time periods. Key: Z=total mortality; F=fishing mortality; M2=predation mortality; M0="other mortalities", independent of fishing and predation.

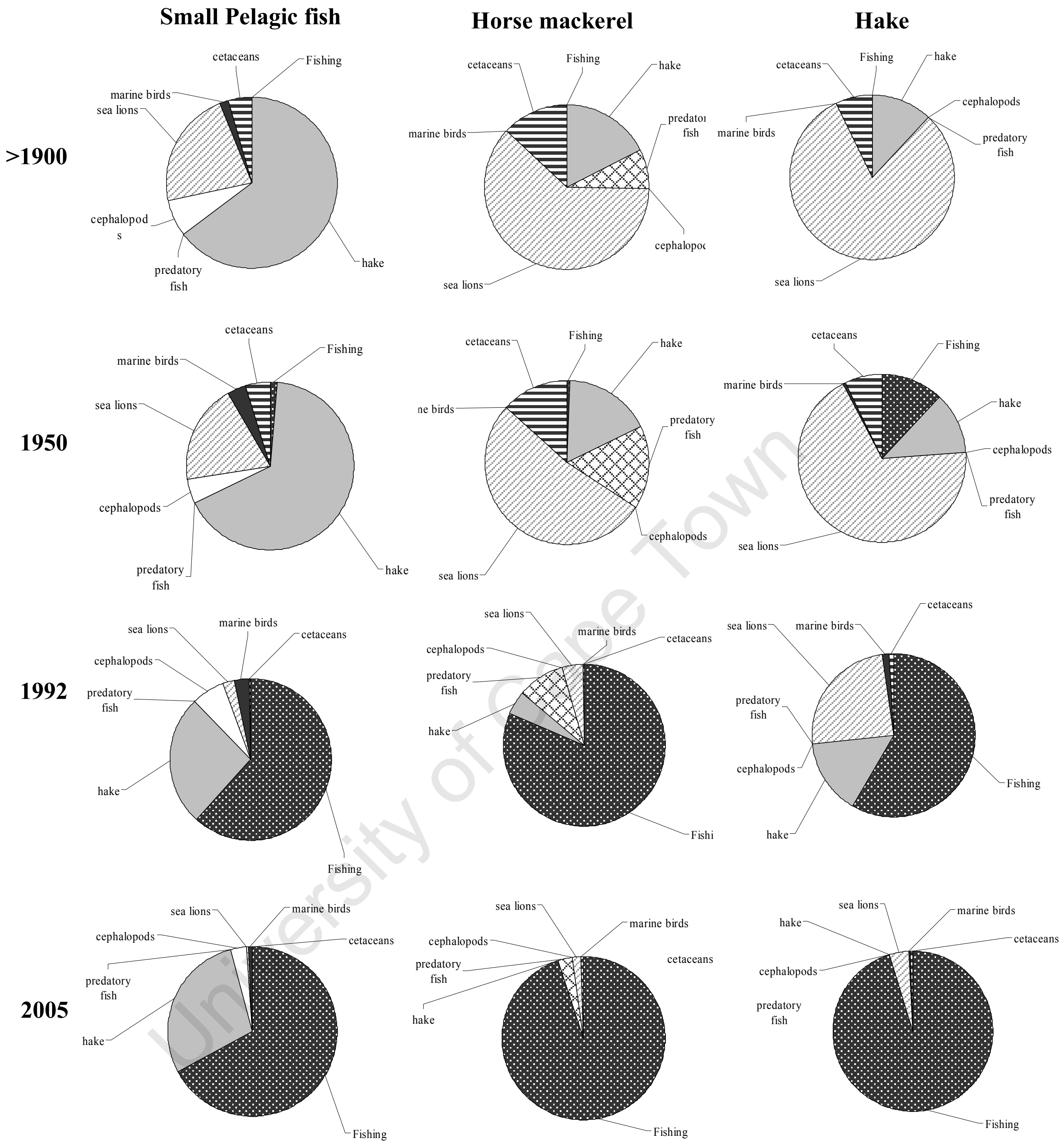

Figure 2.4. Allocations of total production small pelagic fish, horse mackerel and hake to their predators and fisheries in the upwelling ecosystem off central Chile in four food web models representing different time periods.

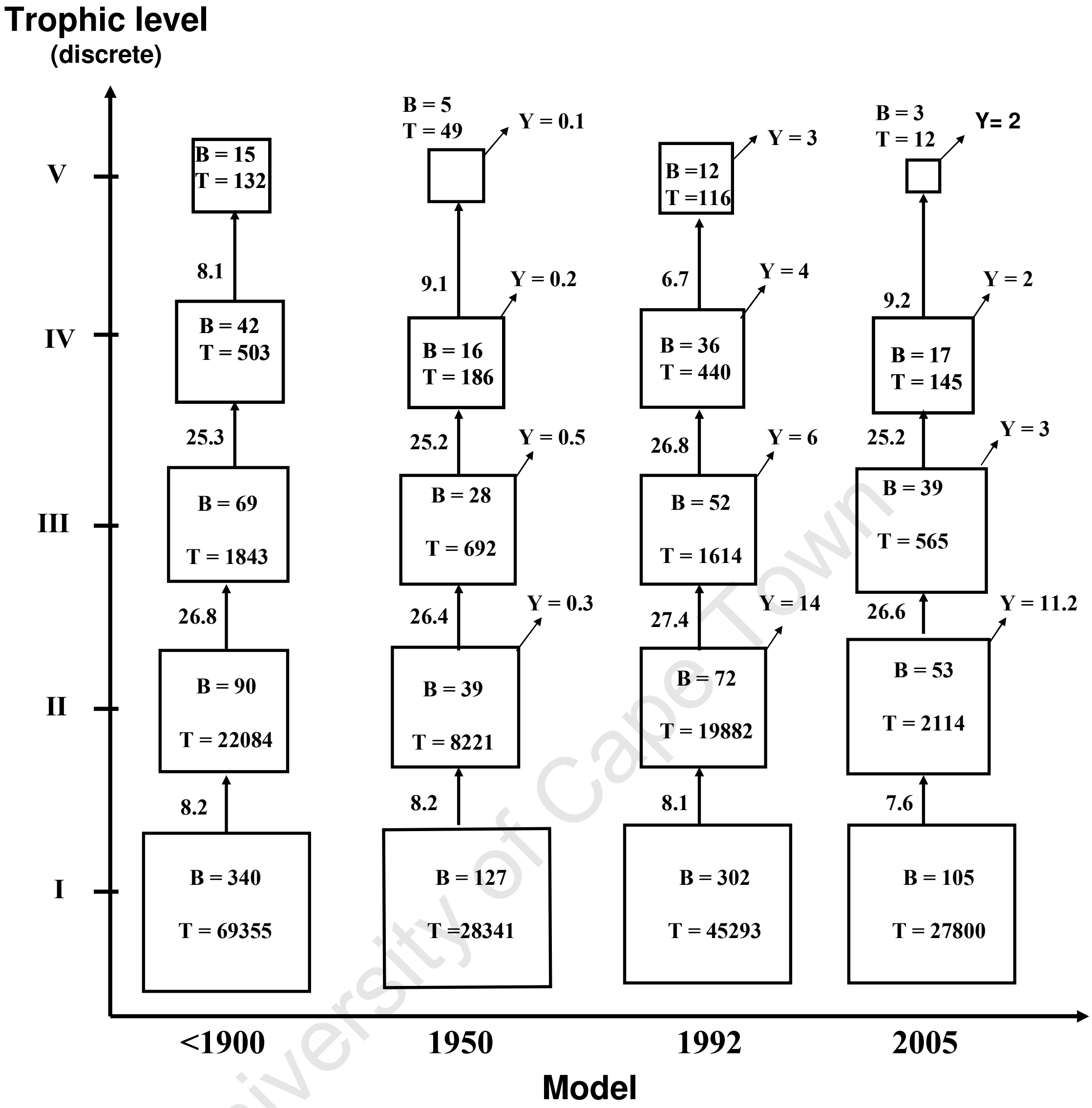

Figure 2.5. Representation of the food web of the southern Humboldt system into aggregated trophic levels. The size of boxes is proportional to the logarithm of the biomass. B=Biomass expressed in ton km^{-2}, T=Throughput expressed in ton km^{-2} year^{-1}, Arrows=Trophic transfer efficiency between aggregated trophic levels expressed as percentages. Boxes are not relative between models, but only within each model. Box size is relative to B in TL I in each period.

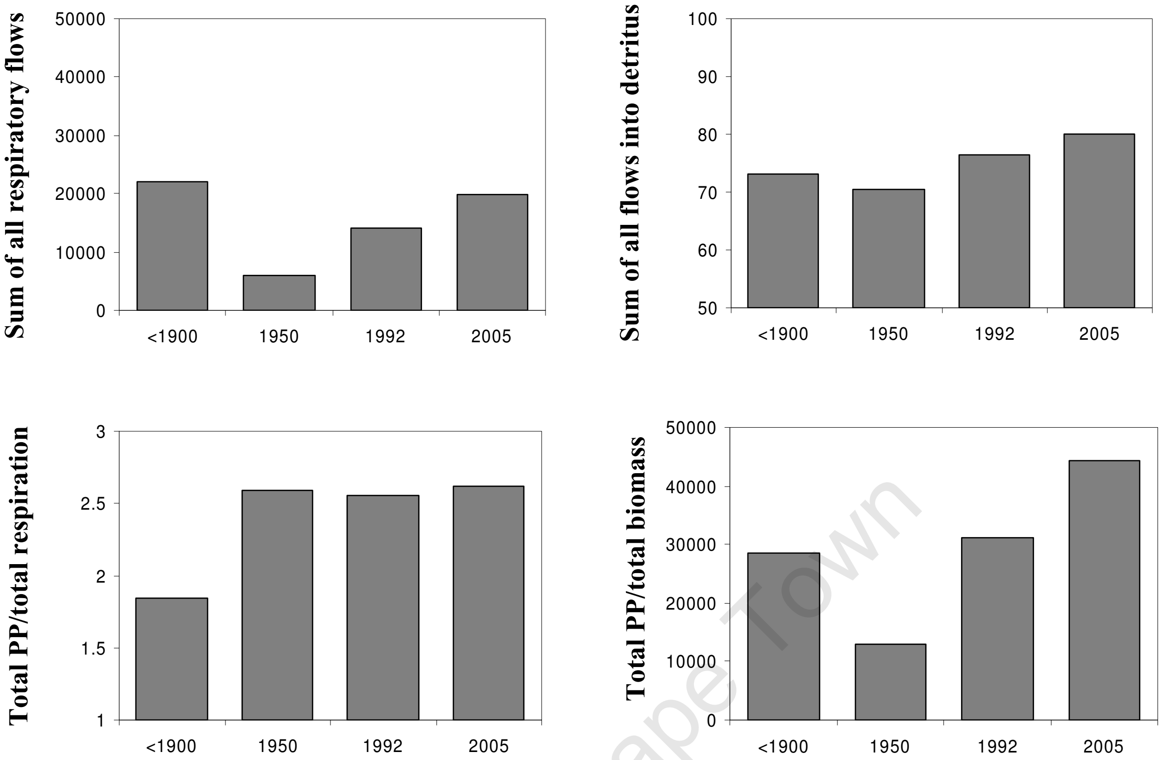

Figure 2.6. Metrics of energetic processes characterizing the food web in the southern Humboldt during the four modeled time periods. Units: Biomass expressed in t km^{-2}; Production, respiration and flow to detritus expressed in t km^{-2} y^{-1}.

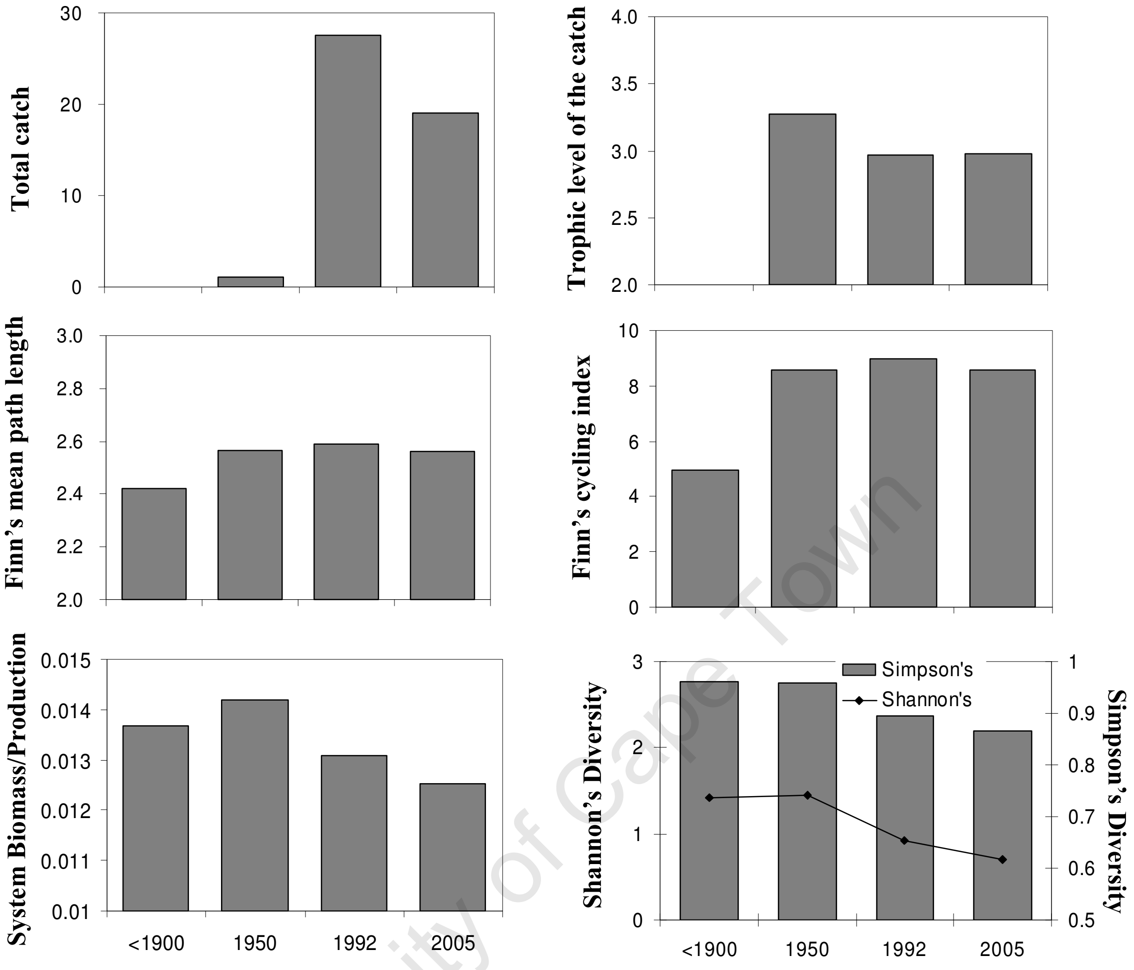

Figure 2.7. Metrics of food web structure characterizing the food web in the southern Humboldt during the four modeled time periods. Units: Total catch (ton km^2 y^{-1}); Trophic level of the catch (units of trophic level); Finn's mean path length; Finn's cycling index (% of flows); System biomass/production (y).

CHAPTER 3

ANALYZING CHANGES IN THE SOUTHERN HUMBOLDT ECOSYSTEM FOR THE PERIOD 1970-2004 BY MEANS OF DYNAMIC FOOD WEB MODELLING

Abstract

A 22-group Ecopath model representing the southern Humboldt (SH) upwelling system in the year 1970 is constructed. The model is projected forward in time and fitted to available time series of relative biomass, catch and fishing mortality for the main fishery resources. The time series cover the period 1970 to 2004 and the fitting is conducted using the Ecopath with Ecosim (EwE) software version 5.1. The aim is to explore the relative importance of internal (trophic control) and external (fishing, physical variability) forcing on the dynamics of commercial stocks and the food web. Wide decadal oscillations are observed in the biomass of commercial stocks during the analyzed period. Fishing mortality explains 21% of the variability in the times series, whereas vulnerability (v) parameters estimated using EwE explain an additional 14-20%. When a function affecting primary production (PP) is calculated by Ecosim to minimize the Sum of Squares of the time series, a further 28% of variability is explained. The best fit is obtained by using the fishing mortality time series and by searching for the best combination of v parameters and the PP function simultaneously, accounting for 69% of total variability in the time series. The PP function obtained from the best fit significantly correlates with independent time series of an upwelling index (UI; $r=0.47$, $p<0.05$) and sea surface temperature (SST; $r=-0.45$, $p<0.05$), representing environmental conditions in the study area during the same period of time. These results suggest that the SH ecosystem experienced at least two different conditions in the last three decades: i) from 1970-1985 a relatively warm period with low levels of upwelling and PP, and ii) from 1985-to present a relatively cold period with increased upwelling and PP. This environmental variability can explain some of the changes in the food webs. Fishing (catch rate) and the environment (bottom-up anomaly in PP) may have affected the SH both at the stock and at the food web level between 1970 and 2004. The vulnerability setting indicates that the effects of external forcing factors may have been mediated by trophic controls operating in the food web.

Keywords: Ecopath with Ecosim, fishing patterns, physical forcing, regime shifts, southern Humboldt, trophic controls.

Introduction

Fishing is a partly-managed human activity that currently is believed to represent a major threat to marine ecosystems (Jackson et al., 2001). Technology applied to shipping, navigation, stock detection and fishing devices (Valdemarsen, 2001) transformed human abilities, so humans could become efficient and dangerous predators, able to capture almost anything that is abundant and/or valuable in the sea (Pauly et al., 2002). This behaviour has disrupted many ecosystems through changes in marine food webs and destruction of physical habitat (Jennings and Kaiser, 1998; Pauly et al., 1998a; Daan et al., 2005b). Although worldwide decreases in fish stocks are strongly correlated with the start of the industrial fishing era (Hutchings, 2000; Myers and Worm, 2003), physical factors are widely recognized to play an important role in fish population dynamics (Cushing, 1982). Marine populations showed fluctuations even before the start of fishing, revealing a strong link between their dynamics and environmental variability (Shackleton, 1987; Schwartzlose et al., 1999). Marine ecosystems also undergo large-scale, decadal fluctuations and regime shifts, which seem to be driven by climate forcing (Hare and Mantua, 2000; Stenseth et al., 2002; Chavez et al., 2003; Steele, 2004), but some have been also related to overfishing (Cury and Shannon, 2004; Lees et al., 2006; Daskalov et al., 2007).

Predation mortality is the main source of total mortality in marine ecosystems (Bax, 1991; 1998) and fishery removal of predatory species has revealed putative trophic cascades (top-down control) in the ocean (Stenek, 1998; Dulvy et al., 2004; Frank et al., 2005; Daskalov et al., 2007). On the other hand, wasp-waist control exerted by small pelagic fish (*sensu* Cury et al., 2000) seems to be a characteristic feature in upwelling ecosystems (Cury et al., 2005b). This indicates that marine populations are also regulated by the behaviour of predators, total consumption and prey availability. Therefore, the effects of fishing and physical forcing on living groups and food web structure can strongly depend on who eats whom, and more significantly on who controls whom (Shannon et al., 2000; Hunt and McKinnell, 2006).

Upwelling ecosystems are productive areas of the world oceans where fishing, environmental shifts and trophic controls are key processes (Schwartzlose et al., 1999; Chavez et al., 2003; Cury et al., 2005b). However, the relative importance of each factor on food web dynamics is poorly understood and quantified. In particular, the southern section of the Humboldt system -off central Chile- is one of the least studied upwelling systems of the world (Morales and Lange, 2004). Although species replacement, trophic controls and fishery-induced changes at the ecosystem level are likely to affect the whole ecosystem (Yáñez et al., 1992; Neira et al., 2004; Arancibia and Neira, 2005a, Alheit and Ñiquen, 2004), single-species approaches dominate fisheries management in Chile.

The global call for an ecosystem approach to fisheries (FAO, 2003) implies the adoption of a wider and holistic view in management, necessitating consideration of multi-species and climate effects. Ecopath with Ecosim (EwE; Walters et al., 1997; Christensen and Walters, 2004) is a family of models that has been applied to many different regions around the world (see www.ecopath.org), allowing global assessments of aquatic food webs and ecosystem effects of fishing (e.g., Pauly and Christensen, 1995; Pauly et al., 1998a; Pauly et al., 2002; Christensen et al., 2003). The dynamic Ecosim model allows users to fit food web models to observed data and, in the process, evaluate the relative effects of fishing, trophic relationships and bottom-up forcing on observed dynamics (Christensen and Walters, 2004; Christensen et al., 2005).

In this chapter an Ecopath model representing the upwelling system off central Chile in 1970 is constructed and projected forward in time using the Ecosim routines. The model simulations are fit to available time series of biomass, landings and fishing mortality for the main commercial fish stocks. The aim is to analyze the relative importance of fishing mortality, predator-prey interactions (through prey vulnerability) and bottom-up forces (through changes in primary productivity) on observed stocks and food web dynamics.

Methods

The study area corresponds to the southern section of the Humboldt (SH) system off central Chile, from 33ºS to 39ºS and from the coast to 30 nautical miles offshore, covering a total area of 50 000 km^2. The geographic, oceanographic, ecological and fishing features of this sub-system have been described in Chapter 2. The area consists of a narrow continental shelf, seasonal upwelling and high primary, secondary and fish production. As a consequence, the main Chilean purse seine and trawling fleets operate in this area, supporting most of the landings in Chile. As descried by Neira et al. (2004), pelagic fish stocks of anchovy (*Engraulis ringens*), Araucanian herring (*Strangomera bentincki*) and horse mackerel (*Trachurus symmetricus*) dominate the pelagic fish community, both in biomass and landings. Important flows are also present in the demersal and benthic domains mainly associated with Chilean hake (*Merluccius gayi*), the main demersal fish component. Hake has strong trophic interactions in the system, mediated by cannibalism and including predation on anchovy, Araucanian herring, euphausiids, benthic invertebrates (mainly red squat lobster *Pleuroncodes monodon*) and other demersal fish (Neira et al., 2004).

An Ecopath model representing the SH system in 1970 was constructed as an updated version of the model constructed by Neira and Arancibia (2004). The year 1970 was chosen because it represents the starting point for the longer time series of biomass of the main fishery resources in central Chile. The model comprises 22 functional groups, including all the main trophic components of the system with emphasis on pelagic, demersal and benthic fish species (target and non-target species), plus their main prey (zooplankton and phytoplankton) and predators (marine birds, sea lions and cetaceans) (see Appendix 1). The model includes age structure in Chilean hake as follows: juvenile hake include the age group 0 to 3 years old, whereas adult hake consist of age groups 4+ years. Input parameters for model groups are fully described in Neira and Arancibia (2004). For Araucanian herring, anchovy, macrobenthos (red squat lobster), horse mackerel and Chilean hake, biomass (B) and landings (Y) were changed to values for 1970. These data correspond to official statistics on stock biomass (estimated by standard stock assessment tools) and landings (see Table 3.1).

No changes were required to balance this Ecopath model. Routines in the EwE software version 5.1 were used to project the model variables forward in time, and forced by data series representing intensity of fishing (Table 3.1). The model was fitted using available time series of estimates relative biomass (Table 3.1).

Ecosim is the time-dynamic version of the Ecopath model and uses mass-balance results from Ecopath for parameter estimation. Differential and difference equations are used in Ecosim to simulate the dynamics of fast and slow growing groups. The model explicitly incorporates the effects of trophic controls and allows limited size/age structure.

In Ecosim, the biomass changes for functional groups are a function of biomass, harvest rate, other mortalities and predator consumption (for more detailed equations see Walters et al., 1997; Pauly et al., 2000; Christensen and Walters, 2004; Christensen et al., 2005):

$$\frac{dB_i}{dt} = f(B_i) - M0_i B_i - F_i B_i - \sum_{j=1}^{n} c_{ij}(B_i, B_j) \tag{3.1}$$

where *f(B)* is a positive function of biomass B for each group *i* in the model, $M0_i$ is a non-predator mortality rate, F_i is the fishing mortality rate, and $c_{ij}(B_i, B_j)$ is a function that predicts consumption of prey *i* by predator *j*.

Predator prey interactions are assumed to be moderated by prey behaviour to limit exposure to predation, and overall food web dynamics can show either bottom-up or top-down control (Walters et al., 1997; Christensen et al., 2005).

Consumption (Q) of each group i by their predator j is estimated by:

$$Q_{ij} = \frac{a_{ij} \times v_{ij} \times B_i \times B_j \times T_i \times T_j \times S_{ij} \times (M_{ij} / D_j)}{v_{ij} + (v_{ij} \times T_i \times M_{ij}) + a_{ij} \times (M_{ij} \times B_j \times S_{ij} \times (T_j / D_j))} \tag{3.2}$$

Where a_{ij} is the rate of effective search for *i* by *j*, v_{ij} is the exchange rate for prey biomass between a vulnerable and non-vulnerable state, T_i represents prey relative feeding time, T_j the predator relative feeding time, S_{ij} a user-defined seasonal or long term forcing effects, M_{ij} a mediation forcing effect, and D_j the effects of handling time as a limit to consumption rate. In the absence of further information, the model was run assuming Ecosim default values for all parameters in Eq. 3.2. The only exception was v_{ij} that is allowed to change during the process of fitting the model to time series, see below.

The parameter v (vulnerability) is a key feature of Ecopath with Ecosim since it allows different representations of how the biomass of functional groups are controlled. The vulnerabilities (vs) represent the factor by which a large increase in predator biomass (B_j) will affect predation mortality for a given prey ($M2_{ij}$). Low vulnerability means that an increase in B_j will not cause any noticeable increase in $M2_i$. A high vulnerability indicates that if B_j is for example doubled, it will cause close to a doubling in $M2_{ij}$. This means that the dynamics of the biomasses will be stable when close to carrying capacity (where vs are low), and unstable when far below carrying capacity (where vs are high).

Ecosim models this aspect of predator prey interactions by re-expressing Ecopath base biomass in terms of two components, one vulnerable or available biomass (V), the other invulnerable or unavailable biomass (B-V) to predators (Fig. 3.1). Further, it is assumed that there is a flow (v_{ij}) of organisms from (B-V) to V. In Ecosim, v distributes from 1 to $+\infty$, with a default value of 2 (also termed mixed control). Therefore when v is high (v>>2), the rapid replenishment of V depleted by predator will rapidly drain the (B-V) fraction, thus predation control will be top-down. Conversely, if v is low (1<v<2), replacement of depleted biomass from (B-V) to V will be slow, thus the control will be bottom-up (Walters et al., 1997; Christensen et al., 2005).

Ecosim uses an iterative fitting procedure to predict biomasses to time series data. Following Shannon et al. (2004a) and Christensen et al. (2005), the following steps were used to explore the relative roles of fishing, predator-prey interactions and anomalies in primary productivity (PP) in explaining variability in the abundance time series data:

1. The time series data file was read from an Excel file and stored in the EwE data base.

2. The model was projected forward in a null case, using the catches and fishing mortalities in the balanced Ecopath model for 1970 and default vulnerabilities for all i. This allowed estimation of a baseline goodness-of-fit value (sums of squares, SS) which Christensen and Walters (2004) define as the sums of log ratios of observed and predicted biomasses, observed and predicted fishing mortalities and observed and

predicted fishing mortality rates, and the log ratios of observed and predicted catches (using all the series listed in Table 3.1).

3. The fishing rates were set to the observed values from the time series and the model was run using default vulnerabilities for all i.

4. The 15 v values to which EwE was most sensitive were calculated by slightly changing each v parameter (by 1%) and rerunning the model to assess how much the SS changed.

5. A vulnerability search based on (4) was used to estimate v values that would minimize SS.

6. A search was conducted for time series values of annual relative PP that may represent historical productivity shifts impacting biomasses through the food web (for details of this routine see Christensen et al., 2005). This step included the analysis of a probability distribution for the null hypothesis that all of the deviations between model and predicted abundances are due to chance alone, i.e., under the hypothesis that there are no real PP anomalies.

7. A final search was carried out to minimize the SS for a combination of v values and a relative PP time series simultaneously, based on (4) and (6).

Results

Fishing mortality time series contributed 21% to explain observed trends in commercial stocks and zooplankton in the SH system for the period 1970-2004. The information on fishing catches and fishing mortality is not complete (Table 3.1), and time series are needed that include data for more species and more years.

The vulnerability tuning indicated that the 15 interactions for which the v parameters had the strongest impact on the SS included phytoplankton with zooplankton III, anchovy and Araucanian herring; Zooplankton I with zooplankton II; zooplankton III with mesopelagic fish, horse mackerel and small hake; macrobenthos with large hake;

anchovy with small hake; Araucanian herring with large hake and small hake; horse mackerel with sea lion; large hake with sea lion; small hake and large hake; and detritus with macrobenthos (Table 3.2).

The estimated vulnerability settings reduced the baseline SS by 14% (in addition to the 21% explained by fishing). The search for time series values of annual relative PP that may represent historical productivity shifts impacting biomasses through the food web resulted in a further 28% decrease in the SS when vulnerabilities had been tuned, and 28% also when the anomaly in PP was estimated using default v values (v=2) for all model groups. A new estimated vulnerability setting run over fishing and the anomaly of PP reduced the baseline SS by a further 20% (in addition to the 21% explained by fishing and the 28% explained by the anomaly in PP).

The best fit to the time series (Figs. 3.2 and 3.3) was found by using estimated fishing mortalities and then jointly estimating vulnerabilities (based on the 15 most sensitive v parameters) and the anomaly in PP. This sequence decreases the baseline SS by up to 69%.

This fitting scenario resulted in a fair representation of the biomass and catches of model groups for which the time series are long, e.g., macrobenthos, Araucanian herring and Chilean hake (adults) (Fig. 3.2). However, the fit between EwE estimates and observed macrobenthos biomass do not fit data well before 1980. The model is not as good at reproducing the biomass trends for anchovy, mesozooplankton and macrozooplankton to a lesser extent (Figs. 3.2). The model explains the biomass trend for horse mackerel until the end of the 1980s, underestimates biomass until the 1990s and then overestimates biomass from the early 1990s onwards (Fig. 3.2).

The model reproduces the catches fairly well for all groups for which series are available, i.e., macrobenthos, anchovy, Araucanian herring, horse mackerel and Chilean hake (Fig. 3.3). However, the catches predicted by EwE for macrobenthos are overestimated post 1980. In the case of anchovy, catches are underestimated after 1985. For horse mackerel, EwE predicted a peak in catches approximately five years later than observed catches.

Discussion

Although the percentage of total variability explained by fishing in the analyzed time series of the SH could be considered low (21%), fishing impacts in the southern Humboldt are larger than those found in another upwelling ecosystem where a similar analysis has been conducted. Shannon et al. (2004a) found that reported fishing patterns explained 2-3% of total variability when fitting a EwE model to available time series for trophic groups in the southern Benguela system. Arancibia and Neira (2005a) found that fishing has affected community structure in the Southern Humboldt system by causing a significant decrease in the mean trophic level of the catch. Likewise, we have seen in Chapter 2 that fishing mortality increased across snapshot models representing past to present periods of the system.

It has been estimated that, for some periods, predators removed most of the production of commercial stocks and, therefore, predation mortality is the main cause of mortality in the Southern Humboldt system (Neira and Arancibia, 2004; and Neira et al., 2004; Chapter 2). However, vulnerability to predation (trophic control) was found to explain only 14-21% of the variability in the time series analyzed here. This indicates that, in marine ecosystems, the answers to questions such as "*who eats whom (and how much)?*" do not necessarily provide answers to the question of "*who controls whom?*"

The explanatory power of vulnerability parameters is low in this study when compared with results in Shannon et al. (2004a) and Shannon et al (in press) for the southern Benguela, where changes in the 15 more sensitive v parameters reduced baseline SS by up to 42%. This can be partly explained by the lack of time series for top predators and the shortness of the time series for zooplankton in the southern Humboldt system. These groups are important because they can constrain fish dynamics in food web models (Christensen et al., 2005). Therefore, it is recommended that studies aimed at reconstructing population levels for top predators and plankton groups in the southern Humboldt system should be conducted, because they can potentially increase our understanding of the dynamics of commercial stocks and the whole food web. Stock reduction analysis (Walters et al., 2006), fish scales and silicates can be good alternatives to reconstruct abundances of top predators, fish species and plankton, respectively.

The search procedure revealed that changes in the SS are sensitive to trophic relationships involving Araucanian herring and anchovy as predators (preying on phytoplankton) and prey (preyed upon by large and small hake). This seems to be in agreement with the hypothesis of wasp-waist control in upwelling ecosystems (Cury et al., 2000; Cury et al., 2005b).

However, the combination of v values for the best fit model did not indicate a clear pattern in terms of wasp-waist control, i.e., small pelagic fish controlling their predators (bottom-up) and their prey (top-down). No big deviation from the mixed control (v=2) resulted for the relation between small pelagic fish and phytoplankton.

On the other hand, the vulnerability of small pelagic fish to hake deviated from mixed control (v<2), suggesting a tendency for bottom-up control although Araucanian herring and small hake had v>>2, indicating top-down control.

These results could be related, again, to the lack of knowledge about the dynamics of trophic groups located at both higher and lower trophic levels of the food web. For example, Shannon et al. (2004a) found that a wasp-waist control pattern emerged when fitting a EwE model of the southern Benguela to time series data including good representations of the dynamics of top predators such as seals and marine birds. Therefore, a more robust conclusion about wasp-waist control in the SH system, at least from this modelling perspective, should rather wait until these kinds of data become available.

The foraging arena model (Walters et al., 1997) depicts the relationship between per-capita consumption by a predator as decreasing with the overall abundance of that predator. Therefore, an alternative way of interpreting vulnerability values is that high and low values of v indicate how far or close to carrying capacity predators were at the beginning of the simulation. High v values indicate that predators were far from their carrying capacity because their consumption per unit of biomass is higher than the Ecopath base value, while low v values indicate that predators were close to carrying capacity because their consumption per unit of biomass is lower than the Ecopath base value (Christensen et al., 2005). The high and low v values obtained from the best fitting scenario (e.g. in the case of hake and mesopelagic as predators) must be interpreted in this way. From the time series we know that the biomass of hake at the beginning of the time simulation was very low compared to late 1990s (likely far from its carrying capacity). Unfortunately, no abundance data are available for mesopelagic fish.

The model is also sensitive to the v parameter of horse mackerel (as predator) and zooplankton III (as prey). However, this interaction may be a mixed control, rather than top-down or bottom-up.

The sums of squares were also sensitive to changes in macrobenthos vulnerability (Table 3.2). Specifically, high vulnerability was observed for macrobenthos to predation by Chilean hake, which could indicate a top-down control by hake in the more traditional way to interpret v values or that at the beginning of the time series hake was far from its carrying capacity with respect to macrobenthos. This result illustrates the important role of Chilean hake as a predator in the benthic-demersal realm as already noted by Neira et al., (2004) and treated in more detail in Chapter 4.

The best fit indicated that a long-term change in PP might have affected the dynamics of groups in the SH system. No statistical evidence was found to support the null hypothesis that all of the deviations between model and predicted abundances are due to chance alone (p value<0.05), indicating that there is a consistent pattern in the deviations. This result is reinforced when the proposed anomaly in PP is compared with independent time series of sea surface temperature (SST) and an upwelling index (UI) in the SH system for the period 1970 to 2000 (Fig. 3.4). This information leads to the development of a hypothesis that there has been a change in the system, affecting all trophic levels, in the last three decades.

Previous studies have documented switches in pelagic species in the SH system (Yánez et al., 1992) and, lately, a regime shift affecting the whole Humboldt system (Alheit and Ñiquen, 2004). This "regime shift" is supported here for the southern Humboldt by analyzing observed trends of relative biomass and catches of the main stocks, the proposed anomaly in PP and physical variables in the SH system in the last 35 years. From 1970-1985 the system appeared to be characterized by a relatively warm period of reduced upwelling and PP. From 1985-to early the 2000s the system appeared to be characterized by a relatively cold period with increased upwelling and PP (Fig. 3.4).

The switch between these two periods in the SH system occurred approximately during 1985-1986, which is coincident with a proposed regime shift affecting the whole Humboldt system (Alheit and Ñiquen, 2004). This could indicate that the dynamics of the sub-systems of the Humboldt Current have been synchronized in the past three decades (Cubillos et al., 2007a).

Overall, the combination of fishing, vulnerability to predation and environmental variability affecting primary production accounted for more than two thirds of total variability in the time series (a reduction of 69% in baseline SS). These results could be indicative of the dynamics of the whole SH system since available time series correspond to groups that dominate the system both in biomass and landings (Neira et al., 2004). Future modelling exercises should be conducted as soon as longer and more accurate data become available, to improve understanding of how individual and synergistic effects of the main forcing factors act on stocks and food web dynamics in the SH system. Specifically, future research efforts should be directed to try and model the functional group horse mackerel in a more realistic way. As seen in Fig 3.2, the biomass of this group is poorly represented by the current configuration of the model. It is possible that the dynamic of this group is influenced by fishing, vulnerabilities and PP in the study area, but also by processes occurring off-shore. The spawning and recruitment of this species occur outside the study area and oceanic processes may be as important for horse mackerel dynamics as coastal ones. An alternative to model this group in the future is to apply individual forcing functions under the hypothesis that they have an effect on the biomass of this group (e.g., recruitment series and or environmental signals) and observe the gains in the model fitting as explored by Field et al. (2006) and Shannon et al. (in press) for model groups in Ecosim modelling conducted for the California and Benguela systems, respectively.

The kind of holistic approach presented here should be considered when planning long-term strategies for sustainable fisheries in the SH system. At present, the advice for management is based almost exclusively on traditional single-species approaches that do not take into account fishing impacts on ecosystem components (other than target species) and rarely, if ever, include predation mortality and environmental variability when projecting the effects of different management scenarios on exploited populations. The EwE software can be used not only as an academic tool for hypothesis testing, but as a management tool that should complement, together with other multi-species and ecosystem models, single-species advice in guiding fisheries management in the SH system.

Table 3.1. Model groups and corresponding time series used in fitting an Ecopath-Ecosim dynamic model representing the southern Humboldt system (1970-2004). Key: Sernapesca=Statictics Yearbooks from the Chilean National fisheries Service (www.senapesca.cl).

Model group	Data series used	Coverage	Used to force model dynamics	Used to compare model outputs	Reference
Macrobenthos	Total biomass (B)	1970-2004	-	Yes	Acuña et al., (2006)
(red squat lobster)	Catch (Y)	”	-	Yes	Sernapesca
	Catch rate (Y/B)	”	Yes	-	
Anchovy	CPUE	1990-2004	-	Yes	L. Cubillos pers. com.*
	Y	”	-	Yes	Sernapesca
	Y/B	”	Yes	-	
Araucanian herring	Total biomass	1970-2004	-	Yes	L. Cubillos pers.com.*
	Y	”	-	Yes	Sernapesca
	Y/B	”	Yes	-	
Chilean hake adults	CPUE	1970-2004	-	Yes	SSP (2004a)
	B spawners (model)	”	-	Yes	SSP (2004a)
	B (survey)		-	-	SSP (2004a)
	Y	“	-		Sernapesca
	Y/B		Yes		
Horse mackerel	B spawners	1975-2004	-	Yes	SSP (2004b)
	Y	”	-	Yes	Sernapesca
	Y/B	”	Yes	-	
Zooplankton II (copepods)	Density (indivs m^{-3})	1997-2004	-	Yes	Córdova et al (2005)
Zooplankton III (euphausiids)	Density (indivs m^{-3})	1997-2004	-	Yes	Córdova et al. (2005)

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Table 3.2. Vulnerability parameter setting obtained from the best fitting scenario. Shaded interactions are those found to be significant. The scale is: red (more significant) to light blue (less significant).

	Predator																				
Prey	phytoplankton	zooplankton I	zooplankton II	zooplancton III	jellies	macrobenthos	anchovy	Araucanian herring	mesopelagics	horse mackerel	hake (large)	hake (small)	pelagics I	demersal fish I	demersal fish II	chondricththyans	pelagics II	cephalopods	sea lion	sea birds	cetaceans
phytoplankton	1.2	1.2	2.0	2.0	2.0		2.1	2.0													
zooplankton I	1.0	1.0	2.0				2.0	2.0													
zooplankton II				2.0	2.0		2.0	2.0	1.0									2.0			
zooplancton III									1.0E+12	2.0	2.0	2.0	1.0	2.0	2.0			2.0			
jellies										2.0											
macrobenthos											5.2E+21	5.2E+21		2.0		2.0					
anchovy											1.0	1.0						2.0	2.0	2.0	2.0
Araucanian herring											1.0	5.2E+21						2.0	2.0	2.0	2.0
mesopelagics										2.0			2.0		2.0			2.0		2.0	2.0
horse mackerel											2.0						2.0		2.0		2.0
hake (large)											2.0			2.0					2.0	2.0	2.0
hake (small)											5.2E+21	2.0		2.0					2.0	2.0	2.0
pelagics I																	2.0				
demersal fish I											2.0								2.0		
demersal fish II																			2.0		
chondricththyans																					
pelagics II																					
cephalopods													2.0				2.0	2.0		2.0	2.0
sea lion																					2.0
sea birds																					
cetaceans																					2.0
detritus	3.7	3.7				2.4															

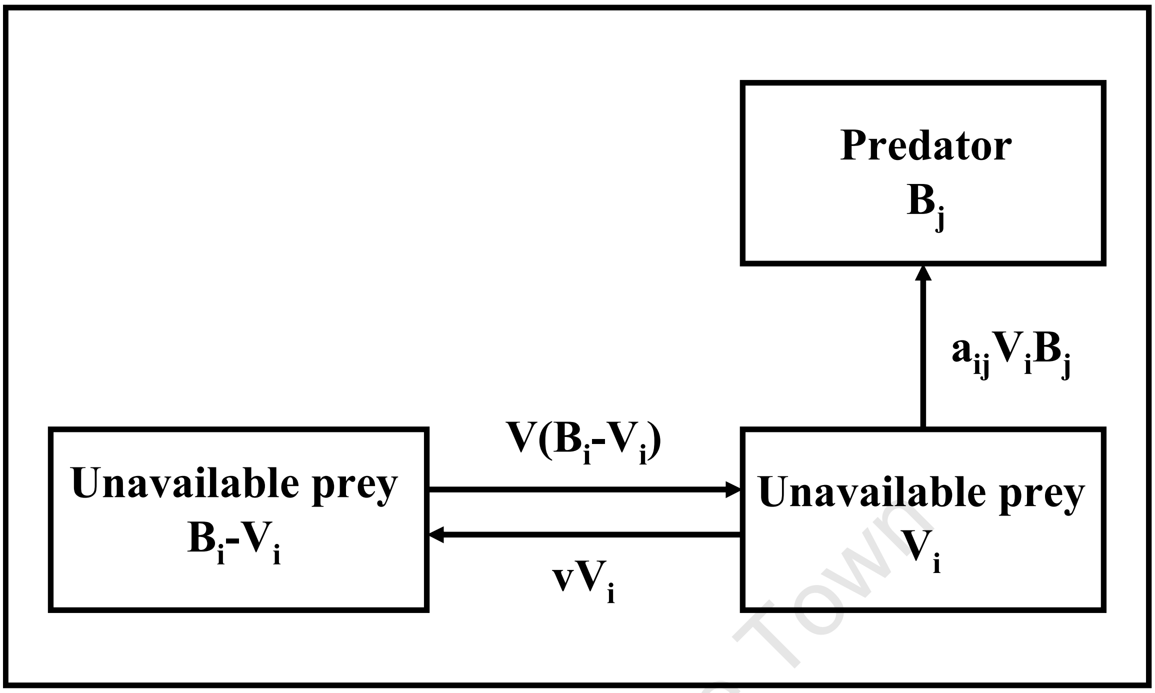


Figure 3.1. Simulation of flow between available (V_i) and unavailable (B_i-V_i) prey biomass in Ecosim. a_{ij} is the predator search rate for prey i, v is the exchange rate between the vulnerable and not-vulnerable state. Fast equilibrium between the two prey states implies $V_i = v_i/(2v + aB_i)$. Based on Walters et al. (1997).

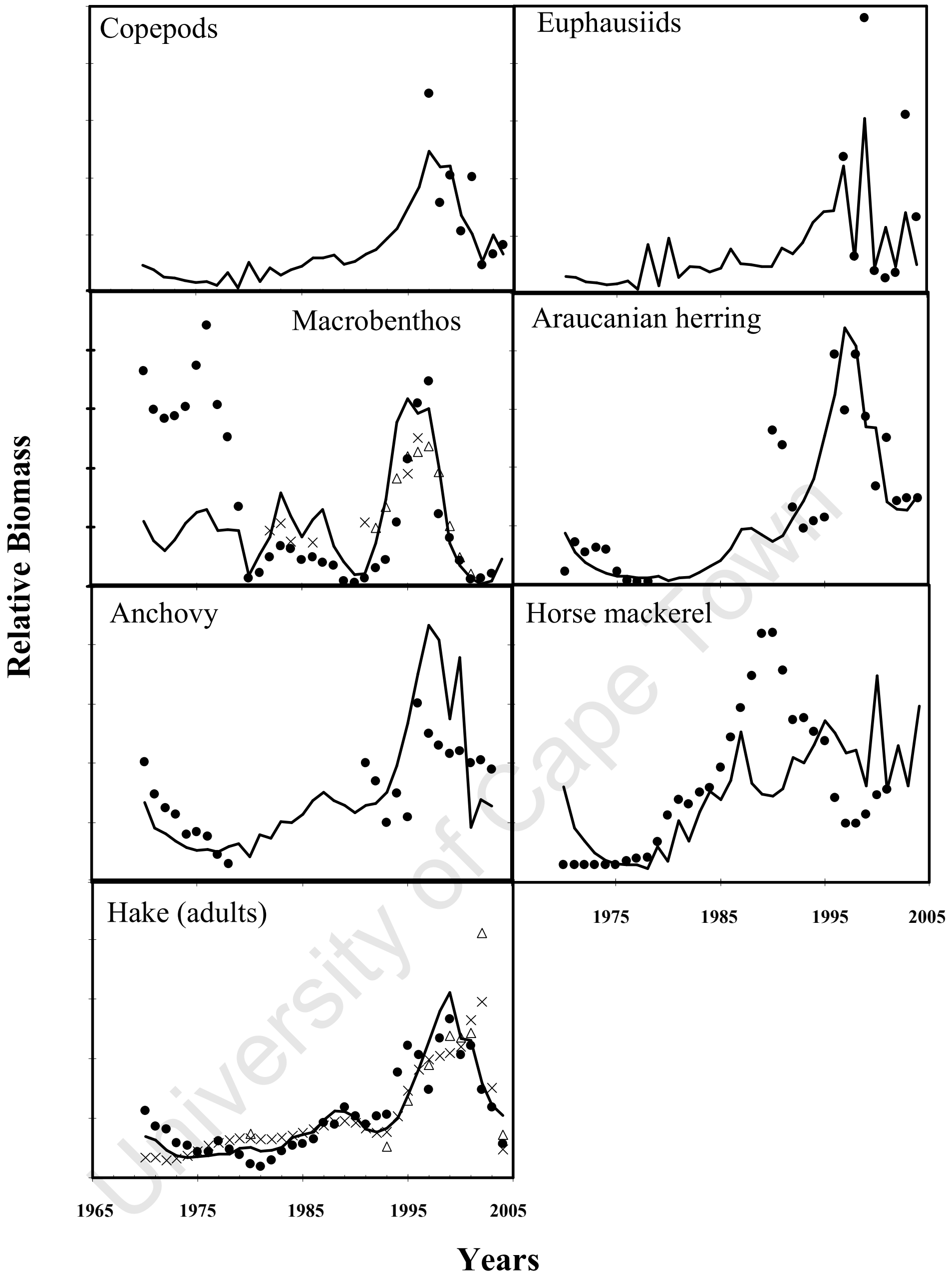


Figure 3.2. Best fit of Ecosim predicted biomass (line) to time series of observed biomass (dots) or CPUE (hake) for model groups in the southern Humboldt ecosystem off central Chile, period 1970-2004. Biomass has been made relative to biomass in the first year of simulations, i.e. 1970. Additional symbols: Macrobenthos cross and triangles=surveys. Hake cross= Spawning biomass, triangles=acoustic surveys.

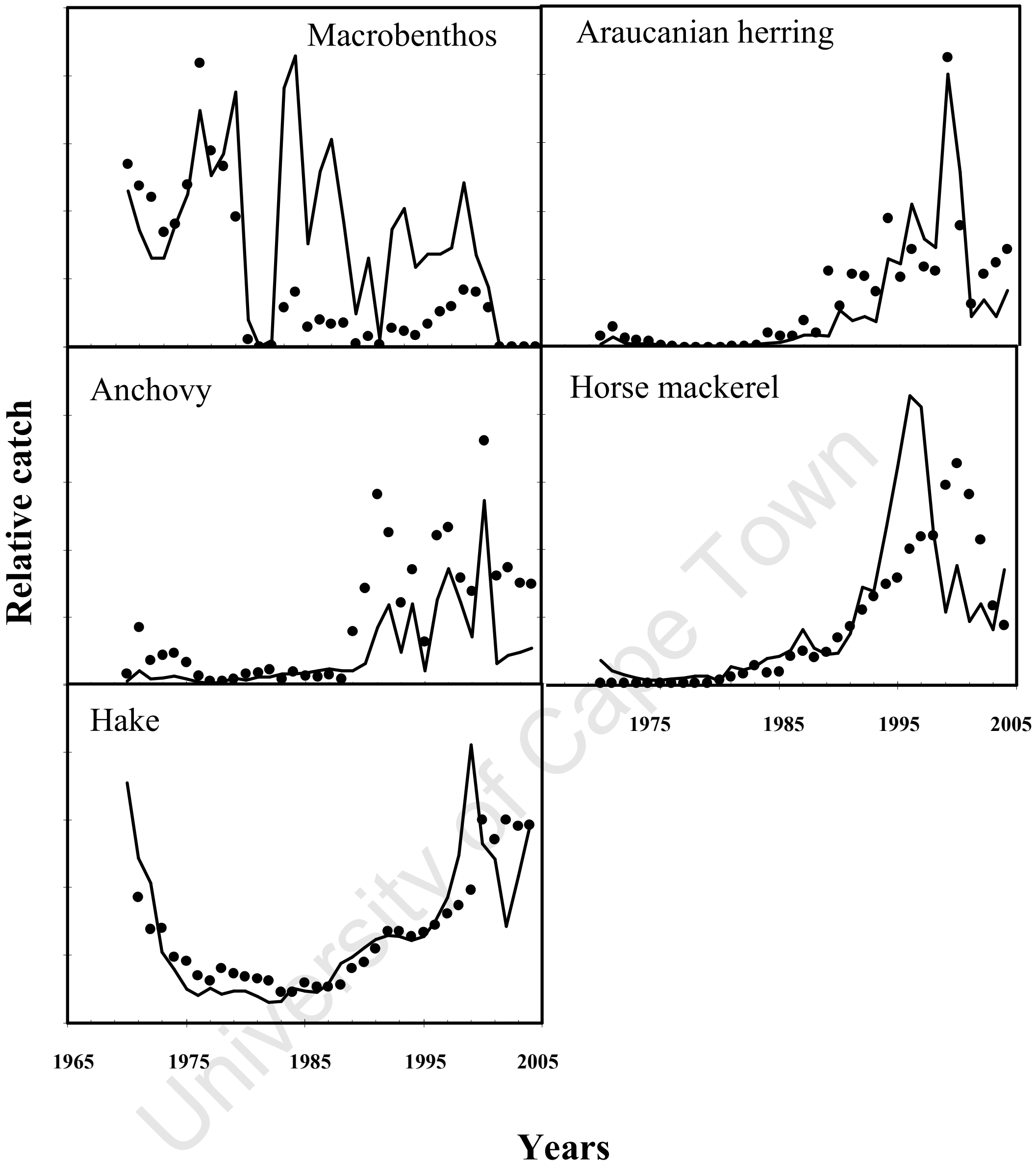


Figure 3.3. Best fit of Ecosim predicted catches (line) to time series of observed catches (dots) for several commercial stocks in the southern Humboldt ecosystem off central Chile, period 1970-2004. Catches has been made relative to the catch in the first year of simulations, i.e. 1970.

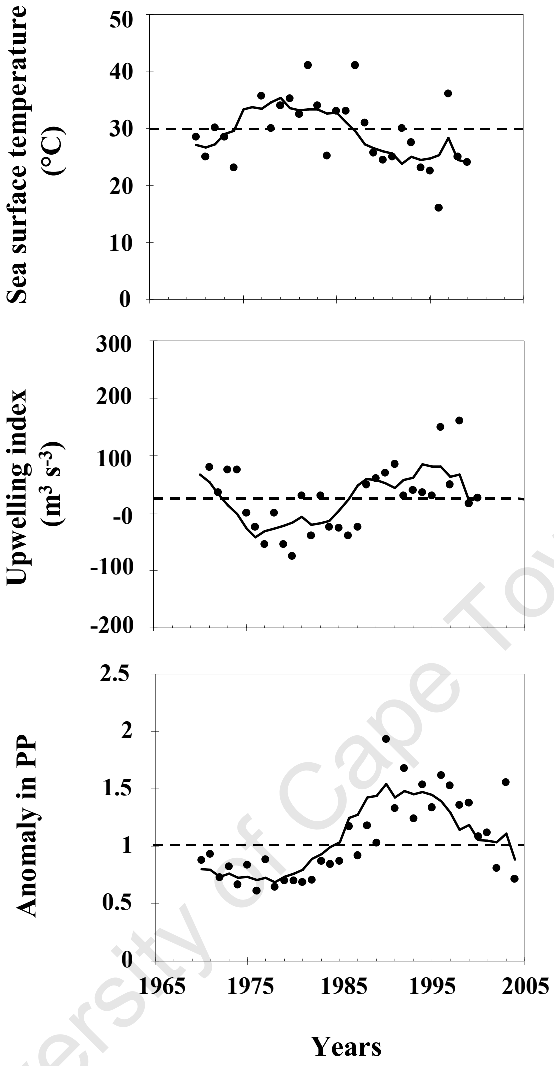


Figure 3.4. Independent time series of sea surface temperature and upwelling index measured off Talcahuano, Chile (36°42’17’’S; 73°06’44’’W) for the period 1970-2000 compared to the anomaly in primary production (PP) estimated by Ecosim to decrease the sum of squares between predicted and observed biomasses, catches and fishing mortality for the groups in Table 3.1. Key: Dots=yearly observations/estimates; continuous line=5-year running mean; punctuated line=long-term average. Spearman rank correlations: Anomaly in PP vs Sea surface temperature r=-0.45, p<0.05; Anomaly in PP vs Upwelling index r=0.47, p<0.05.

CHAPTER 4

INTERACTIONS BETWEEN EXPLOITED STOCKS, FISHING MORTALITY AND OCEAN TEMPERATURE IN THE SOUTHERN HUMBOLDT: WHO CONTROLS WHOM?

Abstract

Available data series on food web components, fishing and ocean temperature are assembled together to identify controls operating in the southern Humboldt system off Central Chile (33°S-39°S). First, the distribution of number of species, biomass and production is analysed across several animal taxa and their corresponding trophic level, aiming to identify wasp-waist functional groups. Biomass time series for two well-documented predator-prey interactions (hake-squat lobster and hake-small pelagic fish), covering the period 1990-2004, are used to test whether the temporal dynamics of these populations are consistent with "top-down" or "bottom-up" control hypotheses. These and alternative hypotheses of environmental and fishing control on these populations are explored using correlation analysis, Generalized Linear Models (GLMs) and Generalized Additive models (GAMs). The number of species across animal taxa shows a wasp-waist pattern, with a relatively high number of species in both lower and higher trophic levels, and with small pelagic fish likely playing the role of wasp-waist populations. Results from correlation analysis and GLMs support the hypothesis that trophic controls operate in the southern Humboldt system. During the analysed time period (1990-2004) the biomass of squat lobster is significantly and negatively related to hake biomass (top-down control), but not to sea surface temperature (SST) or fishing mortality (F) indicating a strong effect of predation on this group. In turn, the biomass of hake is not significantly related to the biomass of small pelagics and SST (top-down control), but have significant negative correlation with F (top-down). The biomass of small pelagic fish is not significantly affected by SST, F and hake biomass, suggesting a likely absence of top-down and environmental (bottom-up) control on this group. GAMs results suggest a strong nonlinearity in the relationship between hake and small pelagics, but not between hake and squat lobster. Overall, results presented in this chapter suggest that in addition to fishing mortality, internal (trophic) and external (environment) controls can be important in explaining the dynamics of analysed populations and this information should be explored further and taken into account in an ecosystem-based management of their fisheries.

Keywords: small pelagic fish, hake, squat lobster, controls, bottom-up, top-down, wasp-waist, upwelling system, southern Humboldt.

Introduction

Trophodynamics is the branch of ecology which considers trophic interactions to be important in determining the distribution and abundance of organisms. Since the seminal studies of Elton (1927) and Lindeman (1942), trophodynamics has been concerned with two main questions: "*who eats whom* (*and how much*)?" and "*who controls whom?*"

For decades, ecologists have debated whether top-down (predator consumption) or bottom-up (food limitation) controls dominate ecosystems (i.e., Hairston et al., 1960; White, 1978; Hunter and Price, 1992). The current paradigm accepts that ecosystems (and individual organisms) can be affected simultaneously by bottom-up (e.g., nutrient loading) and top-down (e.g., fishing and predation) controls (Power, 1992, Vitousek et al., 1997; Jackson et al., 2001, Hunt and McKinnell, 2006). Therefore, contemporary ecology aims to assess the relative strength and interactions among bottom-up and top-down forces in food webs. This information is important since it increases our understanding of observed patterns in nature (Hunter and Price, 1992) and can potentially contribute to a better management of resources in their ecosystem context.

In the marine environment, the assessment of what determines the abundance of organisms is particularly complicated since many species occupy several trophic levels during their lifespan. They are therefore affected, at least at some stage, by predation pressure or food limitation.

High diversity of species found in open marine ecosystems and environmental stochasticity affecting them were thought to dampen any strong top-down effects, favouring the dominance of bottom-up control (Strong, 1992; Jennings and Kaiser, 1998). This could be the case, for example, in the North Atlantic and Northwest Pacific systems (Richardson and Schoeman, 2004; Ware and Thompson, 2005; Chassot et al., 2007). This "bottom-up template" for communities might not be applicable to marine systems where primary production vastly exceeds consumption by grazers and/or where the coupling between phytoplankton and herbivores is weak. For example, Michelli (1999) states that changes in phytoplankton rarely reach top predators, meaning that the bottom-up control occurs only in the first links of the food web. On the other hand, changes in consumer biomass can cascade down affecting phytoplankton. Therefore, in marine pelagic ecosystems phytoplankton is thought to be primarily bottom-up controlled, while herbivores (macrozooplankton) are top-down controlled by piscivores (Michelli, 1999). The quantification of predation as the main source of mortality for many organisms, even in heavily exploited ecosystems (Bax, 1991; 1998), and the pervasive occurrence of top-down trophic cascades in lakes (Carpenter and Kitchell, 1993), rocky shores (Strong 1992), coral reefs (Dulvy et al., 2004), and marine ecosystems (i.e., Daskalov, 2002; Frank et al., 2005), support the hypothesis that predation control is important in the dynamics of closed (freshwater) and open (marine) aquatic systems.

Major upwelling ecosystems share a characteristic structural feature in that a few species of small pelagic fish (normally sardines and anchovies), being the lower trophic level that is mobile (Bakun, 2006), are responsible for passing most of the energy from lower to higher trophic levels (including predatory fish and top predators). These wasp-waist populations (*sensu* Rice, 1995) exert a bottom-up control on predators and a top-down control on zooplankton prey, and therefore upwelling ecosystems are considered to be wasp-waist controlled (Bakun, 1996; Cury et al., 2000). In turn, environmental conditions and not trophic factors (food or predation) seem to control the dynamics of wasp-waist populations.

Rice (1995), proposed the term “waist” to draw attention to the idea that in some marine ecosystems a single taxon can channel most of the energy produced in lower trophic levels of the food web to all top predators. In this regard, it is well established that thermodynamic constraints on metabolic efficiency result in classic trophic pyramids in which total number (or biomass) of individuals decreases with increasing trophic levels (Elton, 1927; Lindeman, 1942). As a consequence, a decrease in species number is expected in higher trophic levels (Duffy, 2002). However, a different pattern emerges in wasp-waist food webs, where a relatively high number of species occurs in the basal and apical trophic levels, while a low number of species is found in intermediate to low trophic levels (Rice, 1995; Bakun, 1996, Cury et al., 2000; Figs. 4.2a).

The mechanism explaining wasp-waist control may be related to "*predator-pit*" (sensu Bakun, 2006) dynamics between prey and predators. Following Bakun (2006), the "predator pit" dynamics provides a refuge from predation when prey abundance is very low. On the other hand, there is a very strong predation between prey abundance level high enough as to attract the interest of predators and the abundance level sufficient to satiate available predators. As prey abundance increases (beyond satiation point for predators), predation mortality decreases and population can then break out (see Bakun, 2006). Small pelagics tend to have shorter generation cycles than their larger and longer-living predators, and can achieve huge geographical expansions in periods of high abundance (Bakun, 2001; 2005). These characteristics allow small pelagics to rapidly shift their populations away from major predation, thus avoiding strong top-down control (Bakun, 2006). Plankton organisms, the main prey of small pelagics, lack the ability to swim and migrate long distances and cannot take advantage of their even shorter generation times, then being vulnerable to top-down control by small pelagics and other zooplanktivorous fish (Michelli, 1999; examples in Cury et al., 2000).

Under the wasp-waist template, the impacts of small pelagic fish abundance on their prey (e.g., copepods) and dependent predators (e.g., marine birds and mammals) are predictable (Cury et al., 2000). However, the direct effects of changes in the abundance of small pelagics on non-dependent fish predators and the indirect effects on the other prey of these predators have been poorly studied in upwelling systems. Although many carnivorous fish are opportunistic feeders, they can benefit from an increase in the abundance of small pelagics as shown by Hanson and Chouinard (2002). As predatory fish biomass increases, other less mobile and less productive prey could suffer extra mortality, being pushed towards, and maybe trapped, in a predator pit dynamic. In this sense, many studies have shown strong trophic interactions between gadiformes (cod-like fishes) and small pelagics, and between gadiformes and shrimp-like crustaceans (i.e., Beremboim et al., 2000; Hanson and Chouinard, 2002; Worm and Myers, 2003; Siegel et al., 2005; Bakun, 2006; Field et al., 2006). The emerging patterns indicate the likelihood of gadiforms' abundance being positively related to the abundance of small pelagics (bottom-up control) and shrimps' abundance being negatively affected by the abundance of gadiforms (top-down control).

The southern Humboldt exhibits characteristic features of upwelling ecosystems in terms of community structure and interactions among the main functional groups (Neira et al., 2004; Moloney et al., 2005). However, the degree of “wasp-waistedness” (sensu Jordan et al., 2005) and the relative impacts of bottom-up and top-down forces on this food web are still poorly understood. The lack of integrative analysis of diversity data for the southern Humboldt and the relative freshness of the wasp-waist concept in ecology might explain this poor understanding. However, some comprehensive assessments of the real magnitude of biological diversity in Chile are available (Simonetti et al., 1995), representing a good opportunity to identify patterns of biodiversity across important animal taxa.

On the other hand, the analyses of who eats whom in the southern Humboldt have consistently revealed that small pelagics and squat lobster are important prey in the diet of hake (Arancibia et al., 1998; Cubillos et al., 2003). During the 1990s and early 2000s the stocks of small pelagics and hake increased (Cubillos et al., 2002; Gatica and Cubillos, 2004) while the stock of squat lobster declined and its fishery has been banned since 2001 (Acuña et al., 2004). After 6 years of no-fishing the adult stock of squat lobster exhibits a lack of recovery, suggesting the presence of a *predator pit* induced by the relatively high biomass level of hake in the early 2000s. Observed dynamics of hake, small pelagics and squat lobster in the last decades agree with the hypothesis that the biomass of hake is positively affected by the abundance of small pelagic fish, while the abundance of squat lobster is negatively affected by predation by hake.

It is widely accepted that community changes in the marine environment, and in the study area in particular, are often related to changes in ocean temperature (and/or other physical factors) which may cause inter-annual to inter-decadal variability (Montecinos et al. 2003; Alheit and Ñiquen, 2004). Positive correlations between the abundance of hake and small pelagics could be forced by similar, but independent, responses to the same environmental condition. Conversely, a negative correlation between hake and squat lobster could result from opposite responses of these two populations to the same environmental condition.

It is also recognized that the worldwide decline in fish stocks is related to fishing, more than to any other environmental change (Hutchings, 2000; Myers and Worm, 2003). Since the early 1990s, the main fishery resources in central Chile are considered to be fully exploited, and the recent decline in many stocks has been attributed to overfishing (Cubillos et al., 1998; Quiñones et al., 2002; Arancibia and Neira, 2005a,b). Therefore strong correlations (positive or negative) between the analysed populations could be also induced by changes in the fishing pressure on these resources in recent decades.

Figure 4.1 summarizes hypothetical controls (trophic, fishing and environmental) and their interactions on the stocks of small pelagics, hake and squat lobster in the southern Humboldt system. Small pelagics may have responded to favourable environmental conditions during the 1990s and early 2000s and so could hake (because is bottom-up controlled by small pelagic fish, by environmental conditions or both). Squat lobster was not positively affected by these favourable environmental conditions, either because this species responds in the opposite way to this forcing or because of the top-down effect of predation by hake. These alternative explanations will be explored in more detail in this chapter.

The aims of this Chapter are i) to identify the wasp-waist taxon in the food web by analysing the pattern in the number of species across animal taxa, and ii) to analyse interactions among hake, squat lobster and small pelagic fish, fishing mortality and ocean temperature in order to identify controls operating on these stocks in the southern Humboldt current system off central Chile.

Methods

Identifying the "wasp-waist" taxon across animal taxa in the southern Humboldt

Cury et al. (2000) analysed the distribution of marine taxa in the southern Benguela ecosystem finding a wasp-waist pattern. For comparative purposes, the log of the number of species (log-N_i) across animal taxa inhabiting the southern Humboldt system off central Chile was analysed considering the same categories analysed by Cury et al. (2000): jellyfish, crustaceans, annelids/polychaetes, molluscs, fishes, seabirds and marine mammals. Fish species were divided into bony fishes and chondrichthyans.

Bony fishes were further divided into mesopelagic, small pelagic, other pelagic, and demersal fish. Considered taxa and the data sources are presented in Table 4.1. Distribution of the log of the biomass (log-B_i) and the log of the production (log-P_i) across these i was analysed using results of a mass-balanced model constructed by Neira and Arancibia (2004), representing the food web in the southern Humboldt system in 1992. The distribution of log-N_i, log-B_i and log-P_i across the trophic level (TL_i) of these same groups was also analysed. TLs were obtained from Neira and Arancibia (2004).

Identifying controls

Description of considered species

Chilean hake *Merluccius gayi gayi* (Guichenot, 1848) is a relatively large demersal fish that can reach over 80 cm in length, with the maximum age estimated to be 10.2 y for males and 18.8 y for females (Cubillos et al. 1999). This species is distributed from 23ºS to 47ºS on the shallow continental shelf to the upper continental slope (Aguayo, 1995). In central Chile hake is an opportunistic predator that migrates vertically to mid-waters at night. Hake diet is based on galatheid crustaceans (such as squat lobster), small pelagics (such as anchovy and Araucanian herring), euphausiids and cannibalism (Arancibia et al., 1998; Cubillos et al., 2003; Cubillos et al., 2007b). Small squat lobsters constitute most of the diet of young hake (<36 cm total length), while small pelagics are more important in the diet of adult hakes (>36 cm total length) (Arancibia et al., 1998).

The red squat lobster *Pleuroncodes monodon* (Milne Edwards, 1837) is a small crustacean (50 mm cephalotorax length; Roa 1993) distributed from Peru to central-south Chile, where it is one of the most representative species of the megabenthic community (Gallardo et al., 1994). Squat lobster inhabits the continental shelf over the upper continental slope (in depths of around 400 m), both in soft and hard sediments, feeding primarily on detritus.

Araucanian herring *Strangomera bentincki* (Norman, 1936) and anchovy *Engraulis ringens* (*Jenyns*, 1842) are the dominant small pelagic fish in the study area. They occur in schools near the surface (0-70 m) in coastal waters, reaching about 18 and 20 cm total length, respectively (Cubillos et al., 2001; 2002). These two species have similar biological characteristics of short lifespan, fast growth, high natural mortality, spawning time at the end of the austral winter, and catches that heavily rely on recruitment success (Cubillos et al., 2001; 2002). In the study area, these species are planktivores, with a diet based on phytoplankton and copepods (Arrizaga et al., 1993).

Description of the time series used in this study

To test the hypothesis of trophic controls operating among these species, time series of biomass for hake, squat lobster and small pelagics were collected. The main characteristics of these series are briefly presented below.

For all analyses, the biomass of small pelagics was assumed to be the sum of the individual biomass of Araucanian herring and anchovy. The rationale behind this assumption is that both species have the same prey (Arrizaga et al., 1993), similar predators (Neira and Arancibia, 2004) and are targeted by the same fleet (Cubillos et al., 2002). Therefore, they are considered here as a single functional group. Biomass time series analysed correspond to indirect estimates of biomass for these species between 1990 and 2004 (Canales et al., 2005). The assessment model used to estimate biomass in small pelagics (anchovy and Araucanian herring) corresponds to a catch-at-age statistical model using auxiliary information in the analysis, such as hydroacoustic biomass and catch per unit of effort (CPUE), to estimate fishing mortality (F).

For hake, direct biomass assessments are not conducted on a yearly basis. Therefore, indirect estimates of total biomass (individuals of 3+ years old) and spawning biomass (individuals 4+ years old) were used as well as an index of recruitment, which corresponds to an estimate of the abundance of the individuals in the age group 3 (pre-recruits). These are calculated using a catch-at-age statistical model with Bayesian inference which considers combined sex, a rate of natural mortality of 0.33 year^{-1}, and calibrated with biomass estimates obtained during acoustic surveys (SSP, 2004a).

Biomass time series for squat lobster were collected from Acuña et al. (2004) and correspond to indirect assessments of total biomass using the age-structured

COLERAINE model (Hilborn et al., 1999). This model is calibrated with catch, catch per unit effort, direct assessments using the swept area method, and length frequency data from surveys and the commercial fleet (Acuña et al., 2004).

Ocean temperature time series correspond to a time series of sea surface temperatures measured in a coastal meteorological station located in the port of Talcahuano (36°42’17’’S; 73°06’44’’W), close to Concepción city (see Fig. 1.1.), maintained by the National Centre for Hydrographic and Oceanographic Data of Chile (CENDHOC; www. www.shoa.cl/cendhoc/), for the period 1990-2004. It is considered that this area is roughly representative of sea surface temperature in the study area since it is located in its middle point (i.e., approximately at 36ºS), and it is the closer to the main upwelling centres in central Chile (Fig. 1.1).

Time series of fishing mortality (F) for hake, squat lobster and small pelagics were assembled by calculating: $F_i = \frac{Y_i}{B_i}$ where Y_i is the official landing of species i (hake, squat lobster and small pelagics) in each year of the series 1990 to 2004 (obtained from the yearbooks of the Chilean Fisheries Statistic Service; www.sernapesca.cl) and B_i is the biomass of the same species in the same years. In the case of small pelagics, Y_i corresponds to the sum of landings of Araucanian herring and anchovy.

Time series analysis I: Correlation analysis

Biomass time series described above were log transformed and correlated using r, the Pearson’s correlation coefficient.

Following Worm and Myers (2003), when correlating the biomass of hake versus prey no lags were considered under the assumption that predation has an immediate effect on the prey population. This assumption is supported by the observation that hake predates on all ages of squat lobster, small pelagics and it is a highly cannibalistic species (Arancibia et al., 2006b; Cubillos et al., 2007b).

Time series analysis II: Alternative hypotheses

A) Environmental forcing

To test the hypothesis that the environment (SST) affected the biomass of selected species, correlations between the biomass of hake, small pelagics and squat lobster and SST time series were analysed. Changes in temperature would be expected to affect larval processes and recruitment in particular. Under this assumption adult biomass will lag several years behind the temperature series. Therefore, considering recruitment ages for each species, time series of SST were correlated with log-biomass of hake (considering 0 to 4 year lags), log-biomass of small pelagics (0 year lags) and log-biomass of squat lobster (0 to 3 years lags).

B) Fishing forcing

To test the hypothesis that fishing influences the dynamics of analysed stocks, time series of log-biomass of hake, small pelagics and squat lobster were correlated with their corresponding F_i series. Under the assumption that fishing affects the studied populations instantaneously, no lags were considered while performing the correlations.

Correcting for autocorrelation

Significant autocorrelation is a major problem in many data sets, especially those dominated by low frequency variability (Bence, 1995; Pyper and Peterman, 1998). This problem is similar to spatial pseudoreplication because it violates the assumption of independence among observations (Hulbert, 1984). In general, this means that a correlation between two time series has fewer degrees of freedom than assumed by the significance test. If this is ignored the test will have a Type I error rate greater than the specified α and a significant correlation might be detected when none is present. Pyper and Peterman (1998) suggest a robust method ("modified Chelton" method) to adjust the degrees of freedom for the sample correlation. This method has the advantage of conserving both Type I and Type II error rates. This advantage is not shared by methods which remove autocorrelation from the data (e.g., "first differencing" and "pre-whitening" among others), but tend to inflate Type II errors rates and thus decrease the power of the hypothesis test (Pyper and Peterman, 1998).

Autocorrelation was tested by correlating log-transformed population biomasses in each year n with abundance in years n + 1,…, n+5 (i.e., lag-1 to lag-5). This analysis revealed moderate to high autocorrelation for small pelagics, hake, and squat lobster time series with correlation coefficients of 0.14, 0.78 and 0.9 at lag-1, respectively. Therefore the degrees of freedom for the correlation test were adjusted using the "modified Chelton" method described by Pyper and Peterman (1998).

Analysing interactions: trophic, environmental or fishing control?

To test the relative effect of trophic controls, SST and fishing mortality on the dynamics of the analysed species generalized linear models (GLMs; Hastie and Tibshirani 1990) were performed. GLMs are mathematical extensions of linear models that do not force data into unnatural scales, and therefore allow for non-linearity and non-constant variance structures in the data (Venables and Dichmont, 2004). Data may be assumed to be from several families of probability distributions, including the normal, binomial and Poisson, among others (Venables and Dichmont, 2004). GLMs are based on an assumed relationship (called a link function) between the mean of the response variable and the linear combination of the explanatory variables.

The purpose of the GLMs constructed here is to provide a mathematical basis to establish the strength of the statistical relationship between a response (i.e., the biomass of species i) and a set of candidate explanatory variables (biomass of prey or predator, fishing mortality, sea surface temperature). Performed GLMs are presented in Table 4.2.

In GLMs, the predictor variables X_j ($j = 1, ..., p$), where p is the number of predictors for each response variable, are combined to produce a linear predictor that is related to the expected value μ=E(Y) of the response variable Y through a link function $g()$, such that:

$$g(E(Y)) = LP = \alpha + X^T\beta \tag{4.1}$$

where Y denotes the response variable, α is a constant called the intercept, $X^T=(X_{i1}, X_{i2}, \ldots, X_{ip})$ is a vector of *p* predictable variables, and $\beta=(\beta_1, \beta_2,\ldots, \beta_p)^T$ is the vector of p regression coefficients (one for each predictor), T=transpose. This model represents generic variables *X* and *Y*. The corresponding equation for the *i*th observation in the sample is:

$$g(\mu_i) = \alpha + \beta 1 x_i 1 + \beta 2 x i2 + \ldots + \beta p x_i p \tag{4.2}$$

Because nonlinearity is an expected feature of the interactions between biological and ecological variables, a second analysis was conducted to explore nonlinear interactions between candidate explanatory variables and the response variables in Table 4.2. Generalized additive Models (GAMs, Hastie and Tibshirani, 1990) are a specific case of GLM allowing an extended form of linear predictors by including a “local smoother” term when fitting a relationship between variables. GAMs replace the coefficients found in parametric models with a “smoother” that transforms the trend of a response variable (Y) into an estimate of the trend that is less variable, i.e. smoother, than Y. The “smoothing” process uses a local averaging of the Y-values of observations having predictor values close to a target value. All GLMs and GAMs were implemented using the R package version 2.2.1(R Development core Team, 2005) assuming the identity link normal error family, since the generalizations are easy.

The goodness of fit of GLMs models was measured with the Akaike Information Criteria (AIC), which is a way to take into account model complexity against model capacity to fit the data by penalizing overparameterization and overfitting. The preferred model is the one with the lowest AIC value, i.e., the model that explains the data with minimum free parameters. AIC was estimated using R package version 2.2.1. In the case of GAMs, the Generalized Cross Validation (CGV) method was used as a proxy for the explanatory power of preformed models. CGV is analogous to AIC in that it aims at optimizing the trade-off between the number of parameters in a model and the goodness of fit of the model. A model with lower GCV has more explanatory power and is preferred. GCV was estimated using R package version 2.2.1.

Results

Identifying the wasp-waist taxon in the southern Humboldt

A wasp-waist pattern is found in the number of species across animal taxa, with small pelagic fish having the lowest number of species (Fig. 4.2a). In the southern Humboldt (off central Chile), only one order (Clupeiformes) and two families comprise the small pelagics. The family Clupeidae consists of 5 species, i.e., Pacific menhaden (*Ethmidium maculatum*), round herring (*Etrumeus teres*), South American pilchard (*Sardinops sagax*), Falkland sprat (*Sprattus fuegensis*) and Araucanian herring. Anchovy is the only representative of the family Engraulidae. However, in terms of abundance and landings, Araucanian herring and anchovy are by far the dominant clupeiformes in the southern Humboldt.

The wasp-waist pattern in the number of species is lost when biomass and production for the same taxa are considered. In this case, small pelagic fish are the second most abundant and productive taxa among those included in the analysis and instead of a wasp-waist, a rather "pot-belly" pattern seems to emerge from the data (Fig.4.2a).

The wasp-waist (in the number of species) and the "pot-belly" (in the biomass and production) patterns observed in the number of species across animal taxa are not evident when N_i, B_i, and P_i are analysed across trophic levels (Fig. 4.2b).

Identifying controls

No significant correlation between the biomass of small pelagics and the biomass of hake was found (Fig. 4.3). On the other hand, there is a significant negative correlation between the biomass of hake and the biomass of squat lobster, indicating a possible top-down control of the abundance of squat lobster by predation of hake (Fig. 4.3). The biomass of hake and the Recruitment index were significant only when correlating total biomass, i.e., no correlation was found between the spawner fraction and recruitment index (Fig. 4.3).

Alternative hypotheses: environmental and fishing controls

Fig. 4.4 presents correlations between the biomass of analysed stocks (hake, squat lobster and small pelagics) and sea surface temperature, and between the stock biomass and their corresponding fishing mortality. Total and spawner biomass of hake were significantly and negatively correlated with fishing mortality, but not with sea surface temperature. This could mean that fishing mortality was an important driver in hake biomass during the analysed period, while sea surface temperature did not play a significant role in hake dynamics. Squat lobster biomass was not significantly correlated with fishing mortality or sea surface temperature. This could mean that neither of these drivers was important in the dynamics of this species over the last 15 years. Small pelagics was neither correlated with fishing mortality nor sea surface temperature (Fig. 4.4).

Analysing interactions: trophic, environmental or fishing controls?

Results obtained from the GLMs constructed to test interactions among the biomass of considered populations, sea surface temperature and fishing mortality are presented in Table 4.3. In the case of hake, the GLM considering total hake biomass revealed that fishing mortality and the biomass of squat lobster were significant at a p-level of 0.05. SST, Recruitment index and biomass of small pelagic were not significant (Table 4.3). The removal of the SST and Recruitment index series (due to they low contribution to the model fit), revealed changes in the estimated parameters, and an increase in the significance of the contribution of small pelagics to the model fit, as revealed by a lower AIC value.

Considering that small pelagics are more important in the diet of adult hake, the same GLMs were run but considering Spawners biomass instead of total biomass. Again these models revealed no effect of SST and Recruitment time series. When the less significant variables were removed, a significant effect of small pelagics was observed. The model fit improved as indicated by a lower AIC value (Table 4.3).

As expected from the correlation analysis, the only significant explanatory variable found using GLM in the case of squat lobster is hake biomass (Table 4.3). Again, sea surface temperature and fishing mortality were not significant variables affecting the biomass of this group in the last 15 years (Table 4.3).

No significant effect of SST and F was found for small pelagics (Table 4.3).

Exploring nonlinearities

GAMs perfomed for hake (Table 4.3) indicated that adding a nonlinear term to the best fitted GLM for hake improved equally when the spline transformation is applied independently to small pelagics and to squat lobster (Table 4.3 and Fig. 4.5). However, the GCV value indicates that the model that considers a spline transformation in the biomass of small pelagic should be preferred over the model considering the spline transformation on squat lobsters.

Discussion

Wasp-waist and pot-belly patterns

The analysis of the number of species across animal taxa in the southern Humboldt system suggests a wasp-waist pattern; where a relatively high number of species occurs in the basal and apical trophic levels, while a low number of species (small pelagic fish) is found in intermediate to low trophic levels (Figs. 4.2a).

It is acknowledged that the number of species in taxonomic categories may be an important shortcoming in this analysis. Some categories are not fully studied in the southern Humboldt and, therefore, their composition in terms of the number of species could change in the future. For example, both terrestrial and marine vascular plants and vertebrates are the most studied groups in Chile, while the taxonomic status of non-vascular plants and most of the invertebrates is poorly known. Among vertebrates, bird diversity is the best known, while fish, regardless of their high economic importance, are the least studied group (Simonetti et al., 1996).

The number of species was first log-transformed in the present analysis to minimize the above limitation, i.e., in order to drastically affect the pattern found in this study, the number of species per taxa should vary in orders of magnitude. Therefore, it is considered that the wasp-waist pattern found in this study is rather robust to this limitation. In addition, the pattern found here for the southern Humboldt compares well with data described by Cury et al. (2000) for the southern Benguela Current system, supporting the likely wasp-waist nature of upwelling food webs. The wasp-waist pattern, however, may be affected by the way taxonomic categories are grouped, i.e., the "waist" is only revealed when fish are split in minor groups. Although the highly aggregated data on the other taxa prevents for the moment a more detailed analysis, future studies on this topic should be encouraged so as to support or unmask any artefact induced by the current data and/or selection of groups.

The analysis of biomass and production across animal taxa (and trophic levels) in the southern Humboldt system resembles the opposite to a waist, i.e., a rather dome shape or "pot-belly" pattern between biomass and production across the same animal taxa. This hypothetical *pot-belly* pattern is an expression of two main characteristics of wasp-waist populations and their food webs: i) wasp-waist populations are the main pathway through which primary production flows up the food web being ecologically adapted to efficiently capture the high productivity of their plankton prey in upwelling ecosystems, and therefore reach the high abundance (and biomass) that allows them to dominate their food webs; and, ii) wasp-waist populations need to be highly productive/abundant to control their even more productive prey and their dependent and opportunistic predators.

The wasp-waits and "*pot-belly"* patterns across animal taxa are not observed when N_i, B_i and P_i are plotted against TL. The TLs assigned to each taxonomic category could be biased since they correspond to the TL of one or few representative species in each category, rather than to an average TL for the whole category (see Neira and Arancibia, 2004).

Identifying controls in the southern Humboldt system

Results suggest that trophic controls may operate in the southern Humboldt off central Chile. Correlation analysis, GLMs and GAMs indicated a significant top-down effect of hake on squat lobster. On the other hand, the biomass of hake was not significantly correlated with SST and the biomass of small pelagic fish (absence of bottom-up control), but negatively and significantly affected by fishing mortality (top-down control by the fishery). In Chapter 3, a hypothetical forcing function acting on phytoplankton biomass was found to improve Ecosim model fit to available time series. This forcing function was found to be correlated with sea surface temperature (Fig 3.4), indicating potential bottom-up forcing in the food web. However, in this chapter no correlations are found between sea surface temperature and biomass trends. This may indicate that hypothetical physical forcing at the bottom does not necessarily cascade up the food web in a direct way. Rather, some groups (trophic levels) can be affected by bottom-up, top-down or wasp-waist manner that needs further analysis.

A GLM run for the interaction of the biomass of hake (adults) and sea surface temperature on the abundance of hake recruits (not shown in Table 4.2) showed that only adult hake biomass resulted significant. However, GLMs and GAMs models indicated that small pelagic could have a significant effect on the spawning fraction of the hake stock, which is in accordance with the knowledge that small pelagics are more important in the diet of adult hake than juvenile hake. Futhermore, GAMs revealed that this effect is likely nonlinear. The above results are in agreement with analyses relating abundances of species of gadiformes, small pelagic fish and shrimp-like crustaceans in various ecosystems (Beremboim et al., 2000; Hanson and Chuinard, 2002; Worm and Myers, 2002; Siegel et al., 2005; Bakun, 2006; Field et al., 2006).

Hake has been fully exploited during the analysed period (SSP, 2004a) and, therefore, the top-down effect of fishing mortality could have been expected to overcome any bottom-up control by prey (small pelagics, squat lobster and hake recruits). However, results from the correlation analysis and the GLM indicate that the interaction between hake and red squat lobster is likely top-down and small pelagic fish biomass could have a positive and significant effect on the adult stock (Table 4.3). This effect could be related to the opportunistic behaviour of hake as predators. In that way, as small pelagic abundance increases in the system, it is expected that hake strongly prey on small pelagics. This type of effect has been identified, in a different ecosystem, in the interaction between Atlantic cod (*Gadus morhua*) and herring (*Clupea harengus*), where predation on herring by cod increased following an increase in herring abundance (Hanson and Chouinard, 2002).

A possible mechanism explaining the nonlinearity in the interaction of small pelagics and hake relates to the energy content of small pelagics as prey compared with other prey such as squat lobster. Stable isotope (^{TM}13C) signatures suggest that small to medium sized Atlantic cod (40 to 60 cm LT) in Newfoundland (Canada) were more likely to spawn when feeding on pelagic (e.g., capelin *Mallotus villosus*) than benthic (e.g., shrimp *Pandalus borealis*) prey (Rideout and Rose, 2006). This leads to the hypothesis that periods of high abundance of small pelagic fish are beneficial for hake (and maybe other predators) since in addition to the higher abundance of the prey, the quality of food available increases reproductive success. This is particularly important as small pelagics are more important in the diet of adult hake (i.e., spawning individuals).

Although the likely top-down control of cod-like fish on shrimp-like crustaceans has been widely documented in shelf ecosystems (i.e., Worm and Myers, 2003; Parsons, 2005), this is the first time that this kind of top-down control has been documented in this kind of predator-prey relationship in the Chilean system, and, as far as the author knows, in an upwelling ecosystem. The evidence found in this study supported the likelihood of predation mortality (mainly exerted by hake) being one of the key factors regulating squat lobster population dynamics. The evidence also supports the hypothesis that the collapse and lack of recovery in the stock of squat lobster in recent years could have been induced by the high abundance (and consumption) of hake. Considering that total biomass of hake collapsed from more than 1 million tons in 2002 to less than 300 thousand tons in 2004, the prediction is that the recovery of squat lobster will be faster in the following years in the absence of strong predation by hake.

The wasp-waist control hypothesis establishes that small pelagic control their predators and prey, and because their weak trophic links do not experience strong top-down or bottom-up control (Rice, 1995). During the analysed period, small pelagics were not negatively affected by two strong top-down forces, namely biomass of hake, their main predator in terms of total consumption (Neira and Arancibia, 2004; Neira et al, 2004), and fishing mortality. Unfortunately, no time series are available for dependent predators of small pelagics (sea birds and sea lions, among other) where a more direct and significant bottom-up control by small pelagics is expected. Although suggestive, the positive effect of small pelagics on hake remains hypothetical and further research is needed. On the other hand, the lack of long time series for copepods and phytoplankton biomass in the study area (main prey for small pelagics) prevents statistical correlations with small pelagic biomass as to test that no bottom-up control occurs. However, SeaWiFS satellite data show no significant changes in *chlorophyll a* in the study area since 1997 (Herve Demarq, Institute pur le Développement, France pers. comm.), while copepods abundance has been decreased in one order of magnitude during the same period (Córdova et al., 2005, see Chapter 3, Fig. 3.2). The above information leads to the hypothesis that small pelagics are not top-down or bottom-up controlled in the southern Humboldt, but that they bottom-up control their predators and maybe top-down control their prey.

Alternative hypotheses

Among the interactions analysed, fishing mortality seems to have played a significant role only in the case of hake, while sea surface temperature was not significantly correlated with any variable (Fig. 4.5; Table 4.3). It can be argued that the effect of fishing mortality is underestimated in the stocks where no effect of fishing mortality was observed (squat lobster and small pelagics). In the case of squat lobster, the fishery was managed very conservatively during the 1990s to allow stock recovery after collapse in the mid 1980s, and the fishery has been closed since 2001 (data points when F=0 in Figure 4.4). A more detailed analysis could be conducted since without these points, there seems to be negative linear relationship between red squat lobster biomass and increasing fishing mortality. In turn, the stocks of small pelagics were subject to low fishing mortalities during the analysed period (Canales et al., 2005). Therefore it seems likely that fishing mortality did not play an important role in the dynamics of these populations in the period examined.

In the absence of direct data on (or a better proxy for) fishing mortality, it was assumed that catch/biomass (Y/B) is a good measure of fishing mortality, and thus high levels of Y/B should result in low levels of B. However, correlation analysis assumes correlated variables to be random, and thus there is a danger that Y/B and B may be autocorrelated since B is present in both axes. If this were the case, the power of the test may be reduced due to a reduction on the degrees of freedom. Even if Y/B were a good proxy for fishing mortality, as assumed here, a danger common to any correlation analysis still remains, i.e., correlation does not mean causation. In fact, the correlation between two variables may be caused by a third or “hidden” variable. Regardless this short comes, many cause-effects relationships are not subtle and they are often first learnt through correlations detected in observational data. Therefore, simple correlations are still useful tools to advance hypothesis on possible associations between variables. In addition, relating likely autocorrelated variables is a not too uncommon practice in fisheries science, i.e., effort as predictor variable and catch per unit effort as response variable in the Schaeffer’s surplus production model to estimate maximum sustainable yield (Sparre and Venema, 1998).

In terms of the environmental effect on studied populations, it can be argued that sea surface temperature might not be the best environmental proxy since climate does not affect populations through a single weather variable, but rather through a combination of weather features (Stenseth et al., 2004). However, it has been pointed out that proxies for the *overall* climate condition,-representing a ‘package of weather’, such as sea surface temperature, may provide a preliminary assessment of the ecological effects of climate fluctuations (Namias and Cayan, 1981). Therefore, temperature may be a “tracer” of other underlying processes rather than itself being the primary cause of population variation. In addition, there are several processes involved in the “triad” that correlate with temperature (Bakun, 1996). There is not much understanding on the early life history distribution of these species and their survival, and how this is linked to environmental variables. It is expected, however, that these species evolved reproductive strategies (spawning, recruitment, growth and maturity) to better perform in the seasonal upwelling system off central Chile. Future studies should explore the effect of other environmental variables that may become available with time (e.g., upwelling index at the time of first feeding, depth of thermocline, etc.).

Both hake and squat lobster have planktonic stages and it is expected that changes in sea surface temperature should affect their populations, albeit with some delay. Nevertheless, no significant correlations were found between sea surface temperature and the biomass of these stocks even when several lags were explored. However, the use of secondary (estimates using catch-at-age models) and not primary data (abundance or biomass) for covariates in the correlation analysis may have introduced additional variability not accounted for in the models. Therefore, it is far from surprising that a short, noisy abundance time series would not show any relationship to short, noisy environmental time series. In addition, although not the focus of this chapter, correlation of total biomass of these species with an environmental variable is not the best method to analyse the effect of environment on larval survival. Further analyses are encouraged since consecutive events of good/poor recruitment may influence biomass dynamics over time and space, then masking any strong correlation.

Concluding remarks

Evidence suggests that in the southern Humboldt upwelling system small pelagic fishes are likely to be the wasp-waist populations as they have the lowest number of species among considered animal taxa. Because of their high abundance and productivity, small pelagics are probably one of the main channels through which primary productivity flows up to predatory fish, other top predators and the fishery. Nothing can be conclusively said about the wasp-waist control hypothesis in this food web, i.e., wasp-waist populations controlling predators and prey, while being controlled by environmental variability. A strong negative correlation between hake and squat lobster was found likely implying a strong top-down control in this particular predator-prey interaction, as emerged from Chapter 3. Although not conclusive, the interaction between small pelagics and hake is suggestive of a positive nonlinear relationship worth to be further investigated as soon as more data are available. Although significant effect of fishing was found only in hake, precautionary management should be always the rule in the other fisheries. Although estimates of stock biomass did not significantly correlated with SST, it is expected that environmental changes must affect animal populations and therefore biological and fisheries oceanography must keep looking for stock-environment correlations.

It is expected that in the future more time series of biological and environmental variables will be available to complete the current understanding on controls in this productive food web (Fig. 4.6). However, future studies should be directed not only to answer who controls whom in this food web, but towards the analysis of what kind of control operates on exploited populations under determined environmental and fishing regimes, and what factors influence shifts from one control to other, and back, i.e., who controls whom, when and why? This may in turn shed light on the reversibility/irreversibility of ecosystem changes.

Table 4.1. Trophic level and number of species in selected animal taxa in the southern Humboldt system, with corresponding data sources. Key: TL=Trophic level; NS=number of species.

Animal Taxa	TL (*)	NS	Reference
Medusae	2.81	82	Moyano (1995)
Zooplankton Crustaceans	2.62	459	Báez (1995)
Annelids-polychaetes	2.01	606	Rozbaczylo and Carrasco (1995)
Molluscs	2.00	1187	Lozada and Osorio (1995)
Fish			Pequeño (1995)
Mesopelagic	3.84	78	
Small pelagic	2.10	6	
Other pelagic	4.08	329	
Demersal	3.74	50	
Chondrichthyans	3.00	78	
Seabirds	3.74	456	Araya and Bernal (1995)
Marine mammals	4.51	48	Contreras and Yáñez (1995)

[*] *Calculated using an Ecopath model constructed to represent the southern Humboldt ecosystem off central Chile (source Neira and Arancibia, 2004).*

Table 4.2. Generalised linear models performed to test interactions between trophic, fishing, and environmental drivers on exploited stocks in the southern Humboldt system off central Chile. Key: B_{hake}= Biomass of hake; $Recruits_{hake}$= Abundance of pre-recuits in hake; $B_{small\ pelagics}$= Biomass of small pelagic fish; $B_{squat\ lobster}$= biomass of squat lobster; F_{hake}= fishing mortality of hake; $F_{small\ pelagics}$= Fishing mortality of small pelagic fish; $F_{squat\ lobster}$= fishing mortality of squat lobster; s= spline transformation.

Code	Model
	Generalized linear models
GLM hake 1	$\log(B_{hake}) = \log(B_{small\ pelagics}) + \log(B_{squat\ lobster}) + \log(Recruits_{hake}) + SST + F_{hake}$
GLM hake 2	$\log(B_{hake}) = \log(B_{small\ pelagics}) + \log(B_{squat\ lobster}) + F_{hake}$
GLM hake 3	$\log(B_{hake\ spawners}) = \log(B_{small\ pelagics}) + \log(B_{squat\ lobster}) + \log(Recruits_{hake}) + SST + F_{hake}$
GLM hake 4	$\log(B_{hake\ Spawners}) = \log(B_{small\ pelagics}) + \log(B_{squat\ lobster}) + F_{hake}$
GLM small pelagics	$\log(B_{small\ pelagics}) = \log(B_{hake}) + SST + F_{small\ pelagics}$
GLM squat lobster	$\mathrm{Log}(B_{squat\ lobster}) = \log(B_{hake}) + SST + F_{squat\ lobster}$
	Generalized additive models
GAM hake 1	$\log(B_{hake}) = s(\log(B_{small\ pelagics})) + \log(B_{squat\ lobster}) + F_{hake}$
GAM hake 2	$\log(B_{hake}) = \log(B_{small\ pelagics}) + s(\log(B_{squat\ lobster})) + F_{hake}$

Table 4.3. Results of the generalised linear (GLM) and generalized additive (GAM) models testing the effects of trophic controls, fishing mortality and sea surface temperature as explanatory variables for the biomass of hake, squat lobster and small pelagic fishes. Key: df=degrees of freedom; AIC=Akaiki information content; edf=estimated degrees of freedom; GCV= Generalized Cross Validation. Significance codes: ***=p<0.001; **=p<0.01;*=p<0.05.

Model	Estimate	Standard error	t-value	Pr (>| t |)
GLM hake 1				
Intercept	13.15	5.06	2.598	0.029 *
Small pelagics biomass	0.49	0.27	1.187	0.108
Squat lobster biomass	-0.41	0.07	-5.870	<0.001***
Hake recruits	-0.039	0.11	-0.364	0.724
Sea surface temperature$_t$	-0.037	0.10	-0.353	0.732
Fishing mortality$_t$	-12.43	2.40	-5.173	<0.001***
Null deviance: 4.06 with 14 df	AIC: -5.71			
GLM hake 2				
Intercept	11.32	3.85	2.94	0.014*
Small pelagics biomass	0.51	0.25	2.01	0.069
Squat lobster biomass	-0.39	0.05	-7.54	<0.001***
Fishing mortality	-12.22	2.13	-5.73	<0.001***
Null deviance: 4.06 with 14 df	AIC: -8.99			
GLM hake 3				
Intercept	9.99	3.13	3.20	0.011*
Small pelagics biomass	0.55	0.18	3.10	0.013
Squat lobster biomass	-0.40	0.05	-7.67	<0.001***
Hake recruits	-0.01	0.08	-0.10	0.919
Sea surface temperature	0.01	0.07	0.18	0.856
Fishing mortality	-5.27	0.52	-10.12	<0.001***
Null deviance: 4.15 with 14 df	AIC: -16.68			
GLM hake4				
Intercept	10.07	2.42	4.15	0.002**
Small pelagics biomass	0.54	0.16	3.47	0.005**
Squat lobster biomass	-0.40	0.03	-12.07	<0.001***
Fishing mortality	-5.27	0.40	-13.02	<0.001***
Null deviance: 4.14 with 14 df	AIC: -20.62			

Table 4.3. Continuation.

Model	Estimate	Standard error	t-value	Pr (>| t |)
GLM small pelagics				
Intercept	14.14	1.64	8.61	<0.001***
Hake biomass	0.13	0.08	1.56	0.147
SST	-0.05	0.09	-0.53	0.607
F	-0.83	0.56	-1.49	0.165
Null deviance: 0.45 with 14 df	AIC:-5.54			
GLM squat lobster biomass				
Intercept	30.62	5.15	5.90	<0.001***
Hake biomass	-1.10	0.29	-3.76	0.003**
SST	-0.36	0.31	-1.18	0.262
F	-0.41	0.85	-0.48	0.638
Null deviance: 9.47 with 14 df	AIC: 29.65			
GAM hake 1				
Intercept	18.28	0.26	68.39	<0.001***
Squat lobster biomass	-0.41	0.02	-16.18	<0.001***
Fishing mortality	-4.96	0.29	-16.95	<0.001***
Approximate significance of smoother	Edf	Est. rank	F	p-value
s(small pelagics biomass)	5.24	9.00	6.735	0.01*
R-square adjusted =0.98	Dev. Exp: 99%	GCV=0.008	n=15	
GAM hake 2				
Intercept	7.97	2.41	3.307	0.008**
Small pelagics biomass	0.39	0.16	2.51	0.03*
Fishing mortality	-5.61	0.38	-15.25	<0.001***
Approximate significance of smoother	Edf:	Est. rank	F	p-value
s(squat lobster biomass)	2.591	8	27.80	<0.001***
R-square adjusted =0.98	Dev. Exp:98.4%	GCV=0.011	n=15	

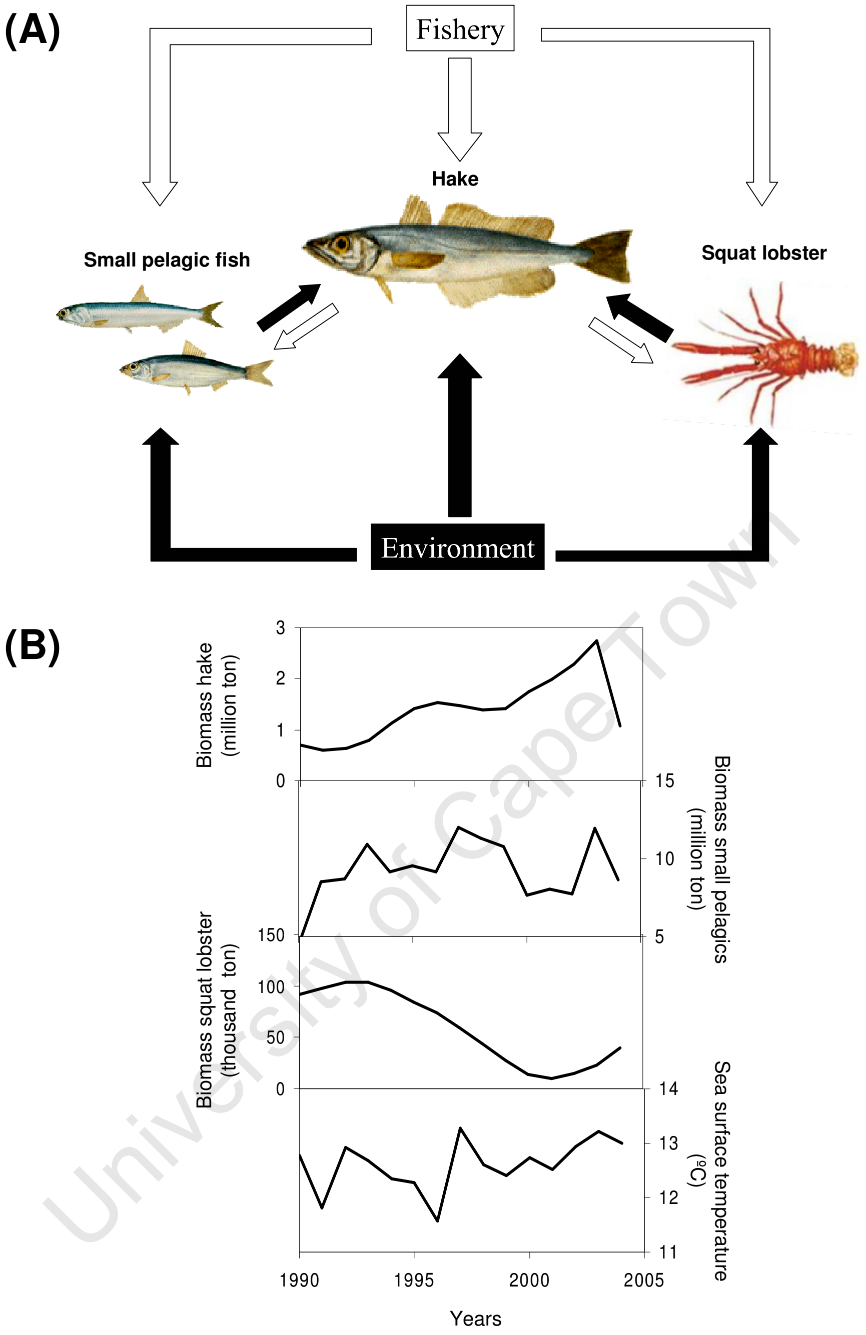


Figure 4.1. (A) Main hypothetical interactions between trophic, fishing and environmental factors on three exploited stocks in the southern Humboldt system off central Chile. Key: solid arrows indicate bottom-up control; empty arrows indicate top-down control. (B) Time series used in the analyses.

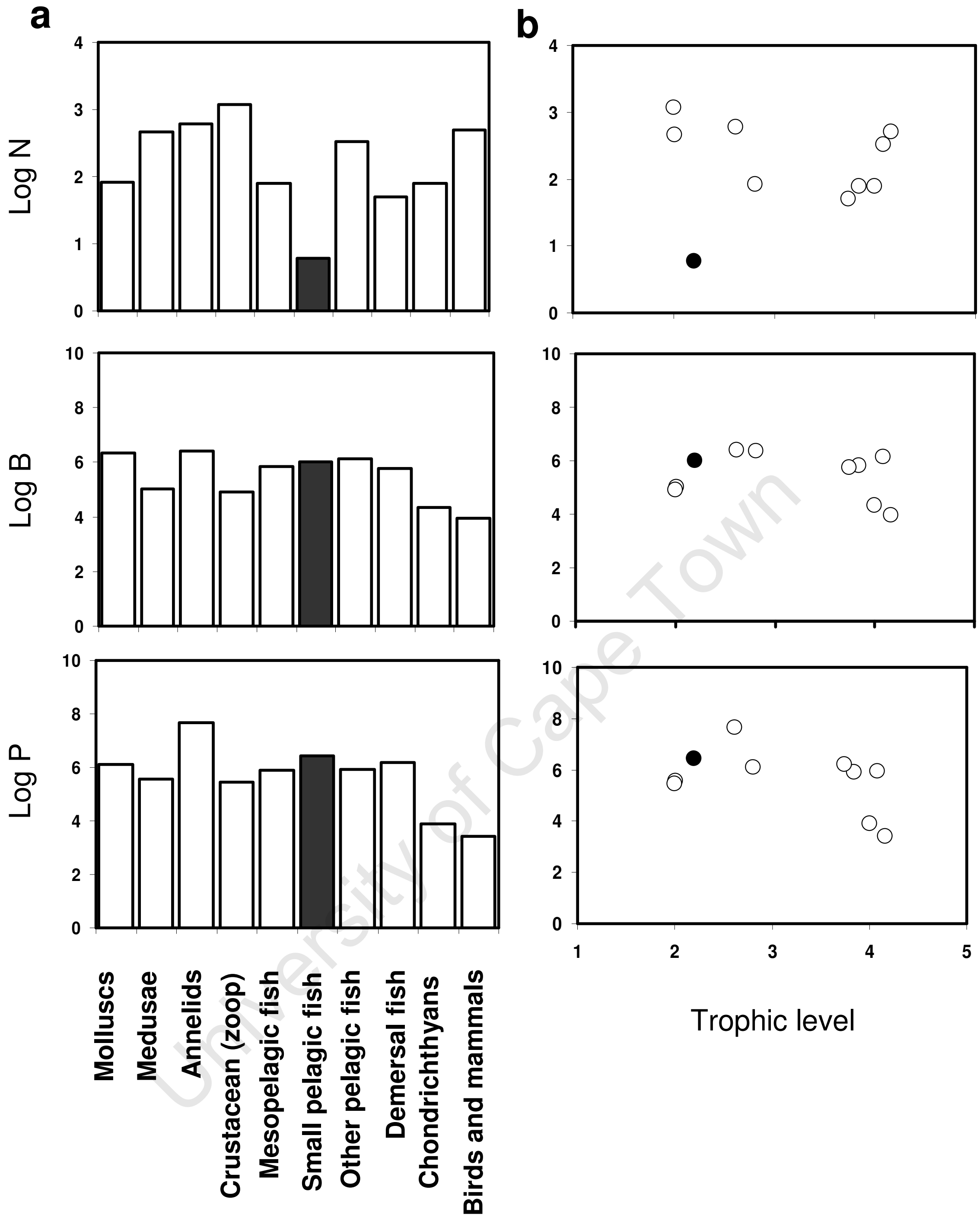


Figure 4.2. Number of species (N), biomass (B) and production (P) across (a) animal taxa and (b) trophic level in the central southern Humboldt system off central Chile. Small pelagic fish are highlighted.

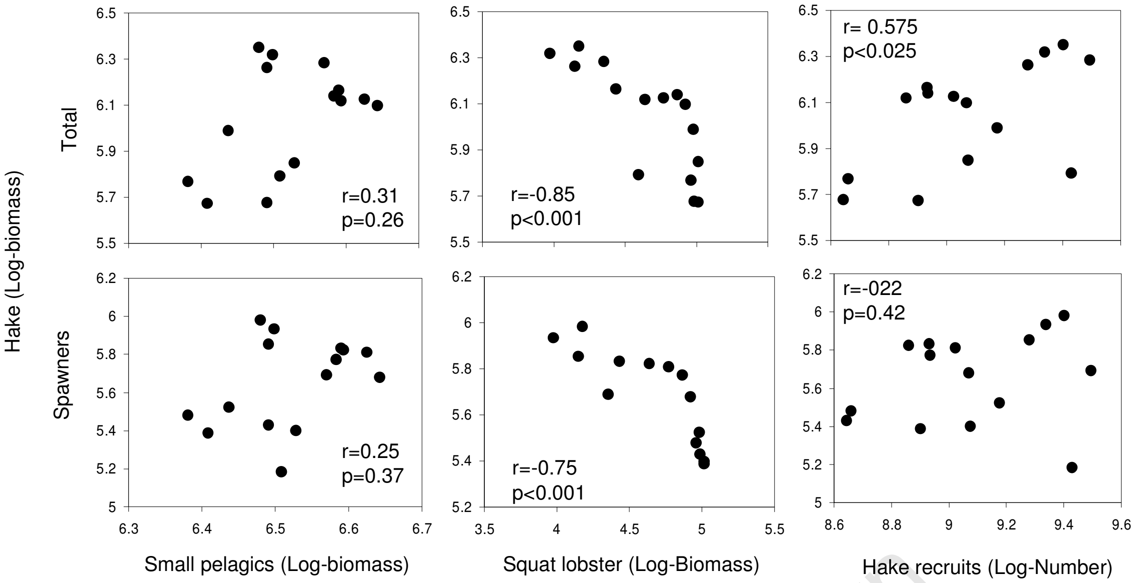


Figure 4.3. Correlation analysis between the log-transformed biomass of hake (total and spawners) and small pelagics, between hake and squat lobster, and hake and recruits in the Southern Humboldt system off central Chile from 1990-2004.

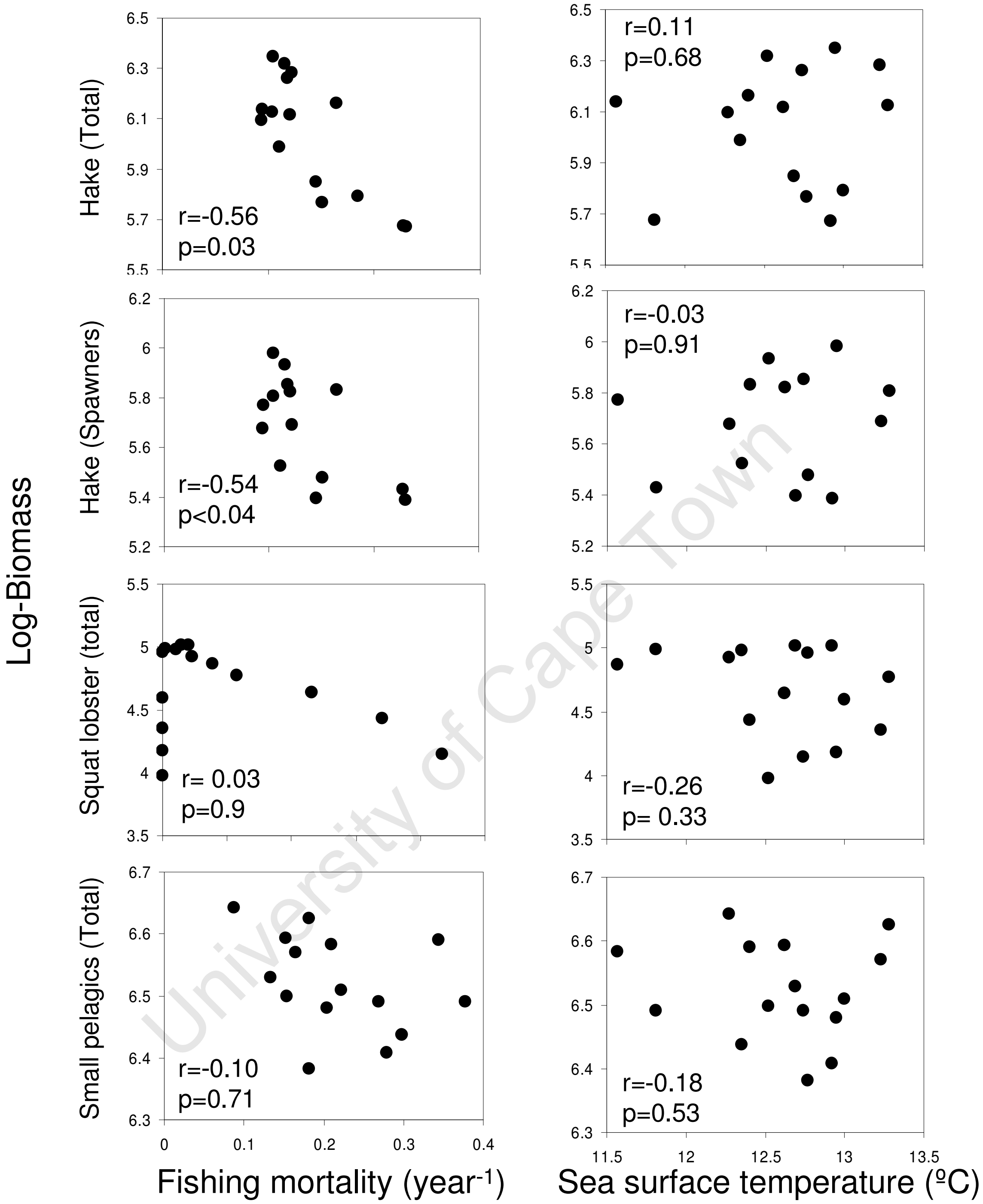


Figure 4.4. Correlation analysis between the log-transformed biomass of hake, squat lobster and small pelagics versus fishing mortality and sea surface temperature.

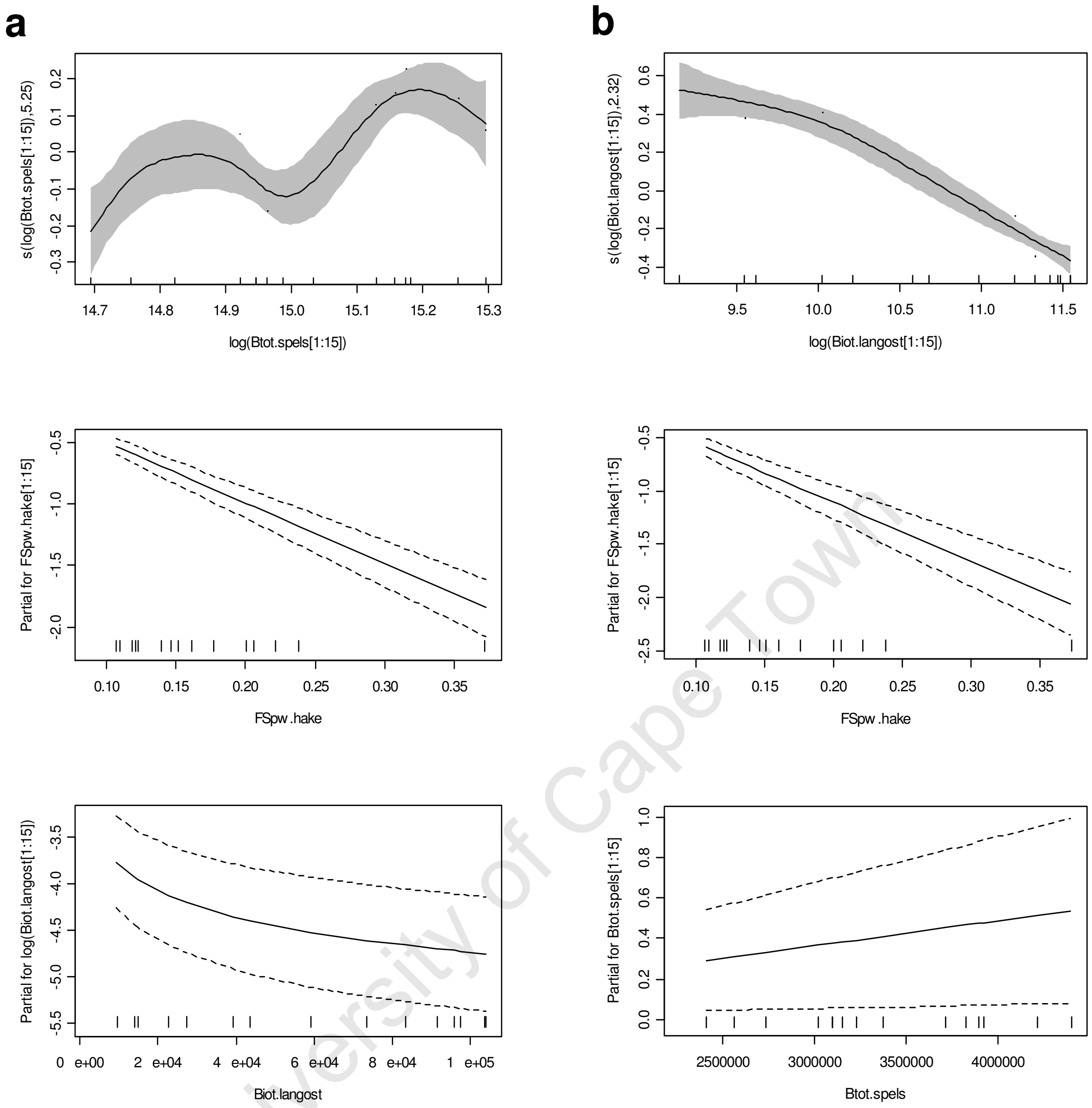


Fig. 4.5. Generalized additive models (GAMs) performed to analyse nonlinear combinations between the biomass of hake (spawners, 4+ years old) and small pelagics, squat lobster and fishing mortality. a) GAM considering nonlinear effect only between the biomass of small pelagic fish and hake; b) GAM considering a nonlinear effect only between the biomass of squat lobster and hake.

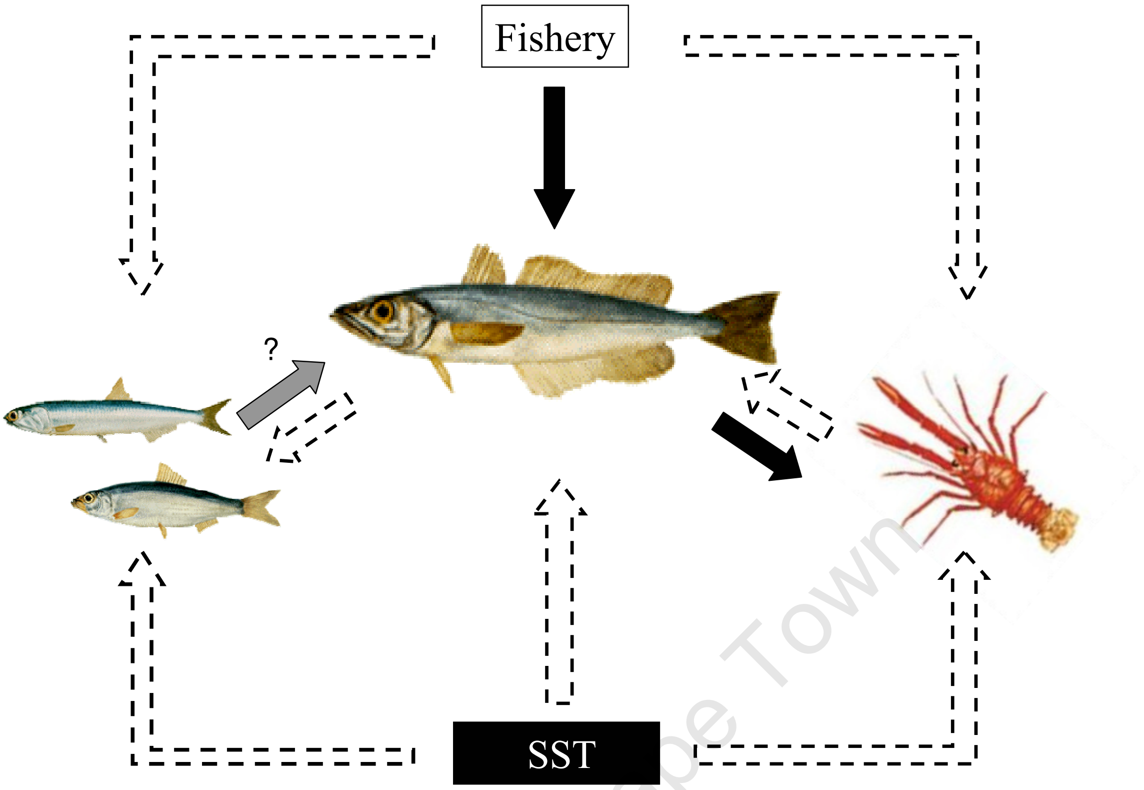


Figure 4.6. Schematic representation of controls operating on stocks in the southern Humboldt system according to results obtained in this study. Sea surface temperature does not directly affect the dynamics of analyzed populations. Small pelagics may have a positive (bottom-up) effect on hake, which in turn have a negative (top-down) effect on the abundance of squat lobster. Hake is also affected by the fishery. Key: solid arrows=significant effects; empty arrows=non significant effects; grey arrow=hypothetical nonlinear effect.

CHAPTER 5

IDENTIFYING AND UNDERSTANDING ECOSYSTEM CHANGES IN THE SOUTHERN HUMBOLDT CURRENT SYSTEM USING ECOSYSTEM INDICATORS

Abstract

Due to their multivariate nature, ecosystems need to be analyzed using a battery of indicators that reflect different processes, interactions, states and levels of exploitation. A set of indicators is calculated to analyze the southern Humboldt system off central Chile over the past five decades. For the main fleets/stocks, the number of vessels, landings, fishing mortality, biomass, average size, size and age of maturity, trophic level and network properties are collected and analyzed. Community indicators are calculated by combining some of these data with time series of landings. High levels of exploitation were concentrated in the 1990s, with a series of sequential stock collapses: horse mackerel (1997), red squat lobster (2000) and hake (2004). In the case of the fleet targeting small pelagics, the high levels of exploitation during the 1990s continued into the early 2000s, but have decreased since then. Decadal fluctuations in abundance and catch of important stocks are observed. The biomass and landings of small pelagics are variable, and an outbreak of jumbo squid has been recorded in the past few years. The mean length of horse mackerel, hake and anchovy has decreased over the past few decades. The mean trophic level of the community has decreased, and this is accompanied by a decrease in the length and age at maturity in the fish community, in number and length of pathways in the food web, and information content. These changes indicate i) an increase in the turnover rate of the exploited community (currently dominated by species with small body size, short life span, and low trophic level) and ii) that ecosystem maturity and stability may be less developed than at the onset of industrial fisheries. Changes observed at the community level may not have resulted in increasing system variability, with the rate of change in variance of the landings of important groups/stocks decreasing over time (except for horse mackerel where they are increasing). In summary, even though some indicators seem to be affected by environmental variability, the observed trends are in accordance with what is expected from the theory of fishing on ecosystems.

Keywords: ecosystem changes, fishing pressure, environmental variability, ecosystem indicators, Southern Humboldt, central Chile.

Introduction

Fishery-induced impacts on living and non-living components of ecosystems are documented and quantified worldwide. Fishing directly decreases the abundance and size of target and non-target species, and non-friendly gear disrupts physical/chemical characteristics of marine habitats. Indirectly, fishing alters predator-prey interactions and nutrient cycling resulting in deleterious changes in community structure, species diversity and ecosystem resilience (Botsford et al., 1997; Goñi, 1998; Jennings and Kaiser, 1998; Pauly et al., 1998a; Frank et al., 2005; Worm et al., 2006; Myers et al., 2007). Overfishing is perceived as a serious threat to marine ecosystems (Hutchings, 2000; Jackson et al., 2001; Worm et al., 2006) and stakeholders increasingly request the integration of traditional single-species management with more holistic ecosystem management. The ecosystem approach to fisheries (EAF) aims to address these shortcomings and ensure sustainable fisheries without jeopardizing the marine environment (FAO, 2003).

As in any management system, EAF requires quantitative indicators that reflect the exploitation and the state of marine ecosystems. Garcia et al. (2003) and Cury and Christensen (2005) define indicators as variables, pointers or indices of a phenomenon. In this case, the positions and trends in ecosystem indicators (EIs) inform us about ecosystem state and dynamics relative to desired objectives (Dengbol and Jarre, 2004), and they are important in linking observations and management. EIs improve our understanding of the "ecology of ecosystems" by representing ecosystem components and their interactions. In addition, EIs could improve management by promoting ecosystem research linked to traditional fisheries advice, and defining management objectives at the ecosystem level (Cury and Christensen, 2005).

Since complexity increases from individuals and populations to communities and ecosystems, no single indicator can capture and integrate all aspects of ecosystem variation. Rather, a battery of suitable EIs covering different data, groups and processes is needed (Cury and Christensen, 2005; ICES, 2005; Rice and Rochet, 2005). Concerted efforts are being made to develop and select quantitative EIs resulting in several measures of ecosystem attributes being tested for their use in EAF (i.e., see Daan et al., 2005a). This chapter deals with i) calculation of some EIs in the southern Humboldt, and ii) understanding possible ecosystem changes by synthesising trends in these indicators and introducing four hypothesis of ecosystem change.

Synecology, in contrast to autecology, focuses more on the interactions among populations that constitute an ecosystem than on the abundance of the organisms that comprise those populations (Odum, 1969). These feeding interactions are often represented as food webs or ecological networks in which species interactions are quantified as flows of matter/energy and summarised in terms of other network properties (Ulanowicz, 2001).

Food webs are a fundamental aspect of ecology and provide a useful basis to analyze ecosystem changes (Elton, 1927; Lindeman, 1942; MacArthur, 1955; May, 1973; Odum, 1971; Paine, 1980; Martinez, 1994; Williams et al., 2002; Montoya et al., 2006).

Trophic structure, the allocation of biomass to trophic levels, is a major characteristic of food webs and probably the most obvious aspect of community structure related to the transfer of energy in feeding interactions (Elton, 1927; Lindeman, 1942). Fishing markets and gear selectivity tend to favour the removal first of large fish, which normally have high trophic level (Pauly et al., 1998b). As the abundances of these species decrease, fisheries sequentially target species located at lower trophic levels, resulting in an overall decrease in the trophic level of the catch. This process, known as "fishing down the food web" (FDFW; Pauly et al., 1998a), is hypothesized to affect ecosystem structure worldwide (Pauly et al., 1998a; 2002). In addition to FDFW, cascading effects can be observed after a decrease in the abundance of fish and/or other marine organisms at high trophic levels (e.g., Pace et al., 1999; Cury et al., 2005b; Frank et al., 2005).

Marine food webs seem to have a shorter average path length than terrestrial ones with species being, on average, two links apart (Williams et al., 2002). Although there is no general agreement in the debate of stability being conferred by complexity -but see Worm et al. (2006) for evidence supporting this view- the diversity or number of pathways has attracted the attention of ecologists for decades (Paine, 1980). Fishing can reduce the abundance of target populations to the point of near-extinction (Hutchings, 2000; Myers et al., 2003; Worm et al., 2006). During this process, the relative importance of some trophic pathways can be drastically altered, while others could even disappear. Under fishing pressure in the Southern Humboldt, it is hypothesized that FDFW should be accompanied by a decrease in both average path length and the number of pathways in the food web.

The principles of ecological succession have important bearing on the relationships between man and nature (Odum, 1969). Ecological succession in terrestrial ecosystems leads to a stabilized ecosystem where maximum biomass (or high information content, IC) is maintained per unit of available energy flow (Odum, 1969). Pauly et al. (1998a) predict that FDFW should decrease, in the long term, the landings (and ultimately the abundance) of both predators and prey. A second hypothesis tested here is that FDFW in the southern Humboldt should be accompanied by a decrease in IC of the exploited community.

By disturbing the structure and functioning of marine ecosystems, fishing tends to result in communities dominated by small bodied and rapidly reproducing species. Odum (1985) hypothesized that, in stressed ecosystems, a decrease in K-selected species will be followed by an increase in opportunistic r-selected species. This is consistent with the observation that overfishing of fish located at high trophic levels does not always lead to an increase in abundance of species situated at lower trophic levels, but rather an increase in species with shorter life spans (sometimes having high trophic levels), such as octopus in north and west Africa (Caddy and Rodhouse, 1998) or jumbo squid in the Humboldt Current System (Arancibia et al., 2006a). Therefore, the third hypothesis to be tested is that even if fishing of top predators is reduced or stopped (in heavily impacted ecosystems), the turnover rate of the community should increase because cascading effects should benefit groups with short turnover times (even if they have high TLs).

Predation, especially when linked to omnivory, is considered a stabilizing factor in ecosystems (Murdoch, 1969; Fagan, 1997; Hudson and Bjornstad, 2003). By targeting a range of prey, generalist predators can feed more heavily on the most abundant species. As these particular species decline in abundance under predation, predators can shift to other relatively more abundant prey. In this way, no prey is drastically reduced nor is any prey allowed to become very abundant (Murdoch, 1969). Therefore, by reducing the abundance of predators, overfishing should result in destabilized food webs, leading to increased variability in prey species abundance.

In marine ecosystems, it can be difficult to discern sources of fish stock variability, e.g., environment versus fishing. For example, Halley and Stergiou (2005) found that in many stocks the variability of landings is not constant, but increases with the length of time over which it is calculated. In contrast, Carpenter and Brook (2006) propose that increasing variance could be an indicator of an impending ecological transition (a regime shift).

Food web dynamics in upwelling ecosystems are hypothesized to be wasp-waist controlled, with the dominating wasp-waist populations not strongly influenced by predation and prey availability, but driven by environmental factors (Rice, 1995; Bakun, 1996; Cury et al., 2000). Therefore, even if the abundance of predators is reduced by fishing, this may not necessarily result in increasing variability in the dominant prey (small pelagics) and, by extension, in food web dynamics. Upwelling systems are strongly influenced by decadal scale changes (Lluch-Belda et al., 1989) and the hypothesis is that stock dynamics, and their variability, should be strongly affected by these changes (Rothschild and Shannon, 2004).

In the southern Humboldt system off central Chile, ecosystem changes induced by fishing and/or other forcing factors remain poorly understood. In terms of fishing effects, Arancibia and Neira (2005a) found a significant decrease in the TLm in this system in the past two decades, likely as a result of fishery-induced changes, since bottom-up ENSO events do not seem to have had a significant effect on this trend as proposed by Caddy and Garibaldi (2000). Inter-annual and inter-decadal environmental variability in the system are associated with ENSO events and global forcing, respectively (Strub et al., 1998; Montecinos et al., 2003). Alheit and Ñiquen (2005) propose that a regime shift affected the Humboldt Current System in the mid 1980s. In this chapter, I use available data and model outputs in the southern Humboldt system to examine the hypothesis that the increase in fishing effort/catch led to i) a decrease in the trophic level of the catch (TLm), ii) a decrease in the magnitudes of network properties, and iii) an increase in the turnover rate of the community. However, iv) these changes have not affected system variability, property primarily driven by decadal changes in the environment.

Methods

Selection of indicators

Integrative community/ecosystem indicators are still being tested in many ecosystems. Ecological indicators tend to be conservative, so it is reasonable to complement them with a selection of population indicators, including, when possible, target and non-target species (Hall and Mainprize, 2004; Fulton et al., 2005). Consequently, the assessment of ecosystem changes in the Southern Humboldt is approached from two levels: population and community. The indicators considered are described below according to three broad categories.

A. Exploitation

Indicator series relative to fishing pressure were collected for the main target species and fleets in the study area. The following target species were considered: horse mackerel (*Trachurus symmetricus*), Chilean hake (*Merluccius gayi*), Araucanian herring (*Strangomera bentincki*), anchovy (*Engraulis ringens*) and red squat lobster (*Pleuroncodes monodon*). The analyzed fleets correspond to the industrial purse seine, industrial demersal trawlers and small scale purse seine fisheries. Analyzed data represent i) the number of fishing vessels per fleet operating from 1980 to 2004, and ii) the exploitation rate on the above stocks. The catch rate was calculated as the landing/biomass ratio, since no estimates of discard are available. Data on fishing vessels per fleet were obtained from SSP (2004a,b), I. Payá (unpublished data in www.subpesca.cl) and IFOP (http://www.ifop.cl/caracteristicas_merluza.html). Data to calculate catch rate for each stock are described in Chapter 3.

B. Population/species based indicators

The following indicators at the population level were analyzed: landings, biomass and/or catch per unit of effort. The stocks analyzed were horse mackerel, hake, Araucanian herring, anchovy, jumbo squid (*Dosidicus gigas*) and red squat lobster. The mean length of the catch was also collected for horse mackerel, hake, anchovy and Araucanian herring.

C. Aggregated indicators

In the absence of long time series of abundance for all exploited stocks, aggregated indicators were calculated using the landings data for all groups as detailed in Table 5.1. Landings cover the period 1950-2003 and were obtained from FishStat (FAO, 2000) and the Chilean Fisheries Statistic Service (www.sernapesca.cl).

By the late 1970s, horse mackerel became the most important fishery resource off Central Chile due to the development and later westward expansion of an important offshore fishery, mainly composed of an industrial purse-seine fleet. Consequently, landings of horse mackerel have strongly influenced total landings in central Chile in the last three decades By being a highly migratory and relatively high trophic level species (TL=3.99), horse mackerel access the production of the coastal upwelling off central Chile but also open ocean waters, where an important part of horse mackerel catches are originated. Therefore, the high landings of horse mackerel during the 1980s and 1990s also masked the process of FDFW from being detected in the exploited community inhabiting the continental shelf (Arancibia and Neira, 2005)., the indicators are presented here i) including and ii) excluding landings of horse mackerel.

Following the methods used in calculating the mean trophic level of the catch (Pauly et al., 1998a), in this study some indicators have been weighted, i.e., the indicator has been calculated as the contribution of individual groups (Table 5.1) weighted by their contribution to total landings in each year. The generic formulation is:

$$MT_j = \sum_{i=1}^{n} M_{ij} \left(\frac{Y_{ij}}{Y_{Tj}} \right) \tag{5.1}$$

where MT_j is the metric of interest in year j, M_i is the value of the metric for each stock/group i (Table 5.1), Y_{ij} is the landing of i in year j, and Y_{Tj} is total landing in the same year, i.e., $\sum_{i=1}^{n} Y_{ij}$. The values of M_i correspond to those obtained from Neira and Arancibia (2004) and, in the absence of more data, extrapolated to the whole time series weighted by the Y_{ij} as indicated in Eq. 5.1. Although the weighting is based on landings not biomass, in the long run, higher landings indirectly indicate more abundant species, i.e., horse mackerel and small pelagics have higher landings of central Chile because they are more abundant in the system.

The underlying assumption is that this simple weighting system can reflect changes in ecosystem functioning and material flow over time. Although questionable (i.e., this assumption does not take compensation into account), it is expected that these weighted metrics are informative of gross changes at the system level, just like the mean trophic level of the catch can reflect changes in system trophodynamics elsewhere.

To estimate M_{ij} without horse mackerel, both $M_{\text{horse mackerel}}$ and $Y_{\text{horse mackerel}}$ are not included in Eq 5.1. This step did not imply a new balance of the model without horse mackerel.

Total landings and landing composition

Composition of the landings was analyzed by considering the following functional groups: mammals, cephalopods, crustaceans, and molluscs. Fish species were split into pelagic and demersal according to the habitat in which they feed.

Landings of trophic guilds is an indicator of changes in structure and function of the exploited community (Caddy and Garibaldi, 2000; Heath, 2005). Consequently, landings were split into pelagic and demersal fish species in order to calculate the pelagic/demersal ratio. The landings of pelagic fish species were subsequently split into piscivores and planktivores, and the landings of demersal fish species into pelagic feeders and benthic feeders. The trends for each of these trophic guilds was analysed, as well as the ratios of piscivores/planktivores and benthic feeders/pelagic feeders. The classification of fish species into the above categories was based on their vertical distribution and diet composition data.

Weighted length/age of maturity of a community

Trippel (1995) proposed age at maturity as a promising indicator of population size. In the absence of long time series of age at maturity (AM_i) and length at maturity (LM_i) for each exploited stock i, the weighted length at maturity (LM) and the weighted age at maturity (AM) were calculated for the exploited community by combining landing series and estimates of AM_i and LM_i (see Table 5.1). When AM_i was not available from the literature, it was calculated by solving the growth equation of von Bertalanffy for t_m (i.e., age at maturity). The equation is:

$$t_m = t_0 - \left(\frac{1}{K}\right)\left[\ln\left(1-\left(\frac{LM}{L_\infty}\right)\right)\right] \qquad (5.2)$$

where t_0 is the mean theoretical age at which length is zero, K is the growth constant, LM is the length at maturity (Table 5.1), and L_∞ is the length designating the end point of the asymptote of the growth curve. The von Bertalanffy growth parameters for each group i pertaining to the investigation period are listed in Table 5.1.

Trophodynamics

The primary production required to sustain landings (PPR) was proposed by Pauly and Christensen (1995) as an indicator of the potential net primary production used directly or indirectly by fishing activities. PPR in each year j was calculated as follows:

$$PPR_j = \sum_{i=1}^{n}(Y_{ij} \times 10^{(TL_i^{-1})}) \qquad (5.3)$$

Following Pauly et al. (1998a), the mean trophic level of landings (TLm) was calculated by combining landings (Y_{ij}) and trophic levels (TL_i) of species as given in

Table 5.1. Essington et al. (2006) criticize the concept of FDFW since the decrease in TLm could result from "*fishing through the food webs*", i.e., new species with low TL being added to fisheries' catches more than declining catches of fish with higher TL. Therefore, I use a $_{\text{cutoff}}$TLm, where 'cutoff' refers to the TL below which species or groups are excluded from the analysis, thereby emphasizing changes in the relative abundance of the fish with high TLs. Following Pauly and Watson (2005), a cut off value of 3.25 was used to eliminate the potential masking effect of variable and abundant species located in low TLs such as small pelagic fishes.

The Fisheries-in-Balance index (FiB, Pauly et al., 2000) was calculated here to assess whether the fishing is ecologically sustainable or whether landings and ecosystem productivity are impaired, i.e., catches are smaller than theoretically predicted from fishing at more productive, lower TLs.

$$FiB = \log\left(Y_i\left(1/TTE\right)^{TLm_i}\right) - \log\left(Y_0\left(1/TTE\right)^{TLm_0}\right) \qquad (5.4)$$

where Y is catch, TLm is the mean trophic level in the catch, TTE is trophic transfer efficiency, and 0 refers to any year used as baseline (Pauly et al., 2000).

Food web/network analysis (based on network properties estimated for 1992)

For each group in Table 5.1, theoretical food web/network indicators were calculated using an Ecopath model representing the Chilean system in 1992 (Neira and Arancibia, 2004) and routines of network analysis included in the Ecopath with Ecosim software version 5.1 (Christensen and Pauly, 1992; Walters et al., 1997).

If the location of a unit of energy in the food web is known, the uncertainty about where it will next flow to is reduced by an amount known as the 'average mutual information' (I) (Ulanowicz and Norden, 1990), which is calculated as:

$$I = \sum_{i=1,\, j=1}^{n} f_{ij} Q_i \log\left(\frac{f_{ij}}{\sum_{k=1}^{n} f_{kj} Q_j}\right) \qquad (5.5)$$

where f_{ij} is the fraction of the total flow from j to i, and Q_i is the probability that a unit of energy passes through i estimated by Ecopath with Ecosim based in the model that represents the upwelling system off central Chile in 1992 (Neira and Arancibia, 2004). I_i values were combined with landing data series to calculate the weighted mutual information of the exploited community (MI).

The number of pathways in which each group in a food web model participates (NP_i) is calculated in Ecopath by listing all pathways leading from all groups on Trophic Level I (primary producers and detritus) to any selected consumer. For each consumer in the system, the program searches through the diet compositions, and lists all the pathways from primary producers to the specified consumer. NP_i values were combined with landing data series to calculate the weighted number of pathways of the exploited community (NP).

The mean length of the pathways for each group (MLP_i) is calculated as the total number of trophic links divided by the number of pathways. MLP_i values were combined with landing data series to calculate the weighted length of pathways (MLP) of the exploited community.

Increasing variability in landings of main functional groups and stocks

The following levels of groups were considered in the analysis: cetaceans, squids, crustaceans and fish. Among fish, the following groups were analyzed: demersal, small pelagic and medium size pelagic fish. Four fish species were selected among the previous categories: hake (demersal), Araucanian herring and anchovy (small pelagic), and horse mackerel (medium pelagic). The first step was to log-transform the landings data for the above groups. The Hurst exponent (H) was then calculated. H is an indicator of the rate of increase in the variance in each time series as a function of the length of the time series (Hurst et al., 1965). For each log-transformed time series, the average variance $\bar{v}_k$ was calculated for all time windows of size k ($3<k<n$) as a function of k. Following Inchausti and Halley (2002) and Halley and Stergiou (2005), I calculated $\bar{v}_k$ considering the following *k*: 3, 6, 12, 24 and 48. These window sizes were chosen because the variance usually increases linearly with

the logarithm of the sequence-length so they are evenly spaced on a logarithmic scale (Inchausti and Halley, 2002). H is obtained as the regression slope in a log-log scale between the average variance $\bar{v}_k$ and the sequence length *k*. Considering that for many processes the variance growths with time interval Δt as $v \approx |\Delta t|^{2H}$, one thus then need to estimate 2H using the following equation:

$$\log(\bar{v}_k) = 2H + \log(k) + c \tag{5.6}$$

Therefore, H embodies all time windows of length *k*. If H=0, then we have a stationary time series (variance does not grow); H=0.5 implies a situation of random walk (variance increases with the length of the series); 0<H<0.5 means the variance increases with time but at a decelerating rate; H>0.5 means the variance of the time series grows at an accelerating rate.

To analyse whether variance in landings increased before the proposed regime shift in the mid 1980s (Alheit and Ñiquen, 2004), the average variance of five-year time windows was analysed for the following stocks: anchovy, Araucanian herring, hake and horse mackerel. A time series of sea surface temperature (SST) for the period 1950-2004 was analyzed to assess the behaviour of the variance of this environmental signal. The time series of SST was recorded in a coastal meteorological station located in the port of Talcahuano (36°42’17’’S; 73°06’44’’W) and which is maintained by the Centre for Hydrographic and Oceanographic Data of Chile (CENDHOC; www.shoa.cl/cendhoc).

Results

Pressure indicators

Available indicators of fishing pressure are presented in Fig. 5.1. The number of fishing vessels in the fishery of Chilean hake (industrial trawlers) and horse mackerel (industrial purse-seiners) increased consistently during the 1980s until the mid 1990s. In the case of the fishery targeting small pelagics (small-scale purse-seiners), the number of vessels increased from the mid 1990s to the present (Fig 5.1a).

The fishing mortality (Y/B) of important stocks is presented in Fig. 5.1b. For Chilean hake, three periods of high F were observed at the beginning of the 1980s, 1990s and 2000s. The F values in the last two years are the highest of the time series (Fig. 5.1b). Small pelagic fish experienced large F during the early and late 1990s, with reduced levels in the 2000s. For horse mackerel, F steadily increased from 1980 until the mid 1990s (maximum in 1996), but decreased right after the stock collapse in 1997-98. In the case of the red squat lobster, F increased strongly during the 1990s (maximum in 1999). In the early 2000s, the stock was considered collapsed and the fishery has been banned since then.

Population-based indicators

The trends in abundance (biomass, catch per unit effort), landings and average length of important stocks in the system are shown in Fig 5.2. Wide fluctuations in both biomass and landings are observed (Fig. 5.2a), including sequential collapses in horse mackerel (1997), red squat lobster (2000), and hake (2004). Small pelagic fish (anchovy and Araucanian herring) show high inter-annual variability in both landings and biomass. The trends in both landings and relative abundance of jumbo squid indicate an outbreak of this species since the early 2000s.

The average length of the main fish stocks is presented in Fig. 5.2b. In the case of horse mackerel, the average length decreased from about 40 cm fork length in 1975 to nearly 30 cm in 2004. In Chilean hake the average length decreased from about 45 cm total length in 1980 to about 23 cm in 2004. In the case of small pelagics, the average length shows a decreasing trend since the mid 1990s. As indicated by a Spearman rank correlation, these trends were significant, with the exemption of Araucanian herring (Fig. 5.2b)

Aggregated indicators

Total landings and landing composition in the SH are presented in Fig. 5.3. Total landings, including and excluding landings of horse mackerel, have been decreasing since the mid 1990s and the mid 1980s, respectively. The composition of landings has changed from a previously demersal fish-dominated state (with some marine mammals) towards a state where more than 80% of the landings are of pelagic fish species, demersal fish species represent a small percentage and marine mammals have disappeared from the landings because exploitation was banned in the early 1980s based on their low abundances (Fig. 5.3). The pelagic/demersal ratio (with and without horse mackerel) strongly increased during the time series reaching a maximum in the late 1980s. After this maximum, the pelagic/demersal ratio has been steadily decreasing, but it is still higher than it was in years previous to 1970s.

The landing by trophic guilds is shown in Fig 5.4a. In terms of pelagic fish, there is a clear decrease in the landings of piscivores from the late 1960s until mid the 1980s and an increase towards the 1990s, while planktivores increased until the mid 1990s and then decreased. In the demersal fish community, the landings of the benthic feeders increased until the end of the 1980s, strongly decreased until the mid 1990s, and show high variability in more recent years. The landings of pelagic feeders were high during the 1950s and 1960s, decreased during the 1970s and 1980s, and increased again during the late 1980s.

The ratios of piscivores/planktivores and benthic feeders/pelagic feeders are shown in Fig. 5.4b. The piscivores/planktivores ratio strongly declined during the first decade and remained low during the rest of the time series, implying a strong change in the pelagic community at the beginning of the time series, with domination by planktivorous species since the 1960s. The benthic feeders/pelagic feeders ratio indicates a community dominated by pelagic-feeding species for all of the time series except during some years in the mid 1980s. The increase in the ratio from the 1970s through the mid 1980s is mainly due to a strong decrease in the landings of pelagic feeders, but also to an increase in the landings of benthic feeders (Fig. 5.4a).

The trends in the weighted age at maturity and the weighted length at maturity of the exploited community are presented in Fig. 5.5. The age at maturity follows a different trend depending on whether landings of horse mackerel are included in the analysis. When the landings of horse mackerel are included, the age at maturity decreased until the early 1970s and then increased up to values similar to those at the beginning of the series. However, when horse mackerel is excluded from the calculation of the indicator, the age at maturity showed a decreasing trend with an increase only in the last three years of the time series. The weighted length at maturity (LM) shows a decreasing trend regardless of the inclusion of horse mackerel in the calculation of the indicator.

Trophodynamic and network indicators are presented in Fig. 5.6. The primary production required to sustain the landings follows the same trend as the landings (with and without horse mackerel, Fig. 5.3). This could mean that the fisheries were consistently removing increasing relative amounts of PP from the system until the mid 1990s (with horse mackerel) and mid 1980s (without horse mackerel).

The trophic level of the landings (TLm) including horse mackerel decreased until the early 1970s, then increased until the late 1970s (due to the development of the fishery targeting horse mackerel), and remained at relatively high and constant values until the early 2000s. TLm without horse mackerel follows the same trajectory as TLm with horse mackerel until the 1970s. However, after an increase during the early 1970s, it decreased during the 1980s and 1990s showing an increase only in the last three years. The $_{\text{cut-off}}$TLm indicates that TLm calculated considering groups with TL>3.25 increased until the late 1970s and decreased after that, but with a slower rate when horse mackerel is considered in the calculation of $_{\text{cut-off}}$TLm.

The fisheries-in-balance index (FiB) with and without horse mackerel increased until the late 1970s. From the early 1980s the indicator followed two different trends depending on the inclusion or exclusion of horse mackerel in its calculation. A further increase until the mid 1990s and a decrease during 1995-2000 (with horse mackerel), and an increase until the mid 1980s and a decrease until 2000s (without horse mackerel). In the most recent years, both trends have been increasing.

Indicators derived from network properties in 1992 are presented in Fig. 5.6b. The landings of horse mackerel did not influence the weighted number of pathways, which strongly decreased in the first few decades (presumably in direct response to the onset of fishing) and stayed low for the rest of the time series. The mean path length exhibited a similar trend to that of number of pathways, but with a slow increase of the indicator when landings of horse mackerel are included. The weighted mutual information indicator exhibited a decreasing trend which is more pronounced when horse mackerel is included in the calculation of the indicator.

Variance growth as indicator of ecosystem change

Fig. 5.7 shows the Hurst exponent (H) calculated for different functional groups and exploited stocks in the southern Humboldt system. The only major taxonomic group for which variance is accelerating (i.e., H>0.5) is fish (H=0.6). Mammals, cephalopods and crustaceans show decelerating variances (0<H<0.5). However, when fish are split into functional groups (i.e., medium size pelagics, demersals and small pelagics), all showed characteristics close to a random walk. When the landings of anchovy, Araucanian herring, Chilean hake and horse mackerel are analyzed, only landings of horse mackerel showed accelerating variance.

Fig. 5.8 presents the five-year average variance ($\bar{v}$) of the landings of anchovy, Araucanian herring, Chilean hake, horse mackerel and sea surface temperature off Talcahuano. The $\bar{v}$ values for landings of Araucanian herring and horse mackerel increased from the 1960s until 1975-1980, i.e., well before the proposed regime shift in the southern Humboldt in mid 1980s (Alheit and Ñiquen, 2004). However, for landings of anchovy and Chilean hake, $\bar{v}$ increased until 1981-1985 and 1971-1975, respectively. Some time series exhibited secondary peaks in $\bar{v}$ after mid 1980s. In horse mackerel the secondary peak (and the highest $\bar{v}$ in the series) occurred in the period 1996-2000, while in hake it occurred in the period 1986-1990. In Araucanian herring and SST two extra peaks are observed in 1986-1990 and 1996-2000.

Discussion

The ecosystem approach to fisheries (EAF) is an evolutionary rather than a revolutionary process in current fisheries management (Garcia et al., 2003). EAF implies an incremental use of indicators from single-species towards multi-species-, food web- and, at a later stage, the whole ecosystem- analyses (Pickitch et al., 2004). The definition of a set of ecosystem indicators to monitor important parts/relationships indicating general ecosystem state is a crucial step in this evolution.

This study constitutes the first analysis of ecosystem changes in the Southern Humboldt System (SH) using multiple indicators. The selection of indicators resulted from a trade-off between a minimum number of indicators that could be reliably calculated and those needed to reach an overall view of the ecosystem. EIs analyzed here fulfil the criteria of clarity, sensitivity, exclusiveness and measurability (Rice and Rochet, 2005). In fact, many of them are included in the recommendations of the SCOR Working Group 119 on quantitative ecosystem indicators for fisheries management (Cury and Christensen, 2005), and collated on the basis of detecting and predicting long-term ecosystem changes in the Benguela Current System (Jarre et al., 2006). This set of ecosystem indicators could allow future inter-system comparisons.

Because of limitations in data and models, the analysis of indicators is based on observed trends rather than absolute values of those indicators. In the absence of time series of abundance for all exploited populations in the SH, many indicators analyzed assumed that there is a correspondence between fish landings and fish population abundance. This assumption is debatable since changes in market demand, discards, size/species selectivity of fishing gear and uncertainties in landing statistics, among other factors, affect this desirable correspondence (Caddy et al., 1998). However, some correspondence between relative abundance in the landings and in the ecosystems from which these landings are extracted can be expected. The globalization of both markets and fisheries, and the horizontal and vertical expansion of fisheries result in species being exploited wherever they occur (Watson and Pauly, 2001). In addition, most of the landings time series analyzed here reflects, at least to some extent, population abundance levels for the main stocks, especially in hake (see Fig. 5.2a). From 1990 onwards, landings reflect global quotas set by the Chilean authority based on forecasted population abundance levels obtained in yearly surveys.

On the other hand, trophodynamic indicators and network analysis strongly rely on the quality of input data. Diet composition is an important input since is the base for analysing trophic interactions and calculating the trophic level of each functional group. However, diet composition data is often highly variable in time and space. In addition, marine species normally exhibit ontogenetic changes in their diet. Thus, assuming a constant diet composition for this analysis might have an impact on results that needs to be considered in future studies.

Trends in exploitation

Exploitation indicators analyzed here (Fig. 5.1) show that fishing pressure increased in the most important fleets from the 1980s until 1997. It is not possible to extrapolate this pattern to earlier decades (<1980s) since most of the Chilean fisheries were open access until the First Fishing Law was passed in the early 1990s. Therefore, it is possible that the number of fishing vessels and the levels of F were lower or similar to those found in the early 1980s or fishing power and technology were similar, at least in the fleets and stocks analyzed. Since the available data on exploitation are fleet- and stock-specific, it is also difficult to extrapolate observed trends to the whole food web. However, considering that the analyzed stocks are the dominant populations in their corresponding communities (Neira and Arancibia, 2004; Neira et al., 2004), the indicators of fishing pressure analyzed here are assumed to be reliable proxies of fishing pressure at the level of the food web.

Considering this, it is possible to conclude that high levels of exploitation in the system were concentrated in the 1990s. By the end of this period, the system experienced sequential collapses of horse mackerel (1997), red squat lobster (2000) and hake (2004). In the case of the fleet targeting small pelagics, the high levels of exploitation during the 1990s continued to the early 2000s, but have decreased in recent years.

Population indicators

The species-based indicators revealed long-term fluctuations in abundance and landing of target species (Fig. 5.2a). For the stocks analysed, these fluctuations seem to be influenced by a combination of fishing pressure, environmental variability and trophic interactions (see Chapter 3) at least for the period 1979-2004. The origin of the recent jumbo squid outbreak in the system is not yet clear, but it is hypothesized to be related to environmental conditions (i.e., la Niña conditions after the strong El Niño event in 1998-1997), food supply and the low abundance of predators (Arancibia et al., 2006a).

Despite these fluctuations, the mean length of the main target fish species has steadily declined in the last few decades (Fig. 5.2b). Although this is considered a typical effect of fishing, it can also be caused by periods of good recruitment. However, for the stocks analyzed here, there are no signs of good recruitment in recent years (C. Gatica, Instituto de Investigacion Pesquera, Talcahuano, Chile, pers. com.).

Aggregated indicators

The analysis of aggregated indicators revealed that most of them are influenced by the landing of horse mackerel. Following Arancibia and Neira (2005), this work supports the view that the ecosystem indicators in the southern Humboldt should be analysed with and without landings of horse mackerel.

The maximum catch was reached in the mid 1990s (with horse mackerel) and mid 1980s (without horse mackerel). The composition of the landings showed a clear dominance of pelagic species, which is typical of upwelling systems. However, the pelagic/demersal ratio has been decreasing since the mid 1980s, which can be interpreted as overfishing of pelagic stocks (Shannon et al., in press.). Alternatively, this could indicate a change in the primary productivity of the system. For example, de Leiva Moreno et al., (2000) found that the pelagic/demersal ratio is a good proxy for the differential impact of nutrients on pelagic and benthic systems from 14 semi-enclosed marine areas around Europe. The benthic/demersal components are negatively affected by hypoxia resulting from excess primary production, which has fewer negative effects (or may even be positive) for pelagic fish. In fact, a positive correlation between the pelagic/demersal ratio and the mean Chl-*a* was found in the same study (de Leiva Moreno et al., 2000). The lack of time series of primary productivity in the southern Humboldt prevents, for the moment, a formal testing of these two hypotheses: overexploitation of pelagic stocks or decreases in PP have caused the recent decreases in the pelagic/demersal ratio.

It is clear that a change in landing composition of pelagic and demersal fish species could have been influenced by different processes (Fig. 5.4). The pelagic landings have been dominated by planktivorous species since the early 1960s, while a clear change occurred in the demersal fish community during the 1980s as indicated by the strong increase in the benthic/pelagics feeders. These results could indicate important changes in production and consumption in the demersal community before and after the 1980s as also observed by Heath (2005) in the North Sea food web.

The length at maturity did not show a noticeable change in its trend when horse mackerel was excluded form the analysis (Fig, 5.5). However, the age at maturity did show a discrepancy in its trend with and without including horse mackerel. This must be related to the fact that the age of maturity of horse mackerel is about 8-10 times higher than the age of maturity of other abundant fish species in landings (anchovy and Araucanian herring, see Table 5.1). On the other hand, the size of maturity of horse mackerel is only two times higher compared to the same species (see Table 5.1.).

The aggregated nature of weighted indicators and the uncertainty associated with their parameters could have biased observed trends. However, in fish many features are length dependent (e.g., trophic level, sexual maturity, longevity, growth, etc.) and the mean length of important stocks has not been constant, but has decreased during the last few decades (Fig. 5.2b). Therefore, using a fixed value (of trophic level, age at maturity, length at maturity, etc.) for each stock/functional group in the calculations of the weighted indicators could have resulted in changes that are underestimated at the end of the time series.

At the stock level, reproductive capacity is critical for stock dynamics, especially during rebuilding. Stocks that have a mix of mature age classes produce more and better eggs than stocks consisting primarily of young fish (Trippel, 1995). At the community level, the decrease in size and age at maturity could mean an increase in production and consumption in the system, i.e., an increase in the community turnover rate.

Trophodynamic indicators (Fig. 5.6a) exhibited increasing trends to maximum values and then decreased, suggesting that some ecological thresholds could have been reached (and maybe even exceeded). PPR increased to maximum values in the mid 1990s (with horse mackerel) and the mid 1980s (without horse mackerel). Again the lack of time series of PP makes it difficult to assess whether this increase meant that the fisheries extracted comparatively more PP from the system during these periods.

However, some information can be obtained by cross analyzing the other trophodynamic indicators. For example, Caddy et al. (1998) criticize the phenomenon of FDFW because, among other factors, the decrease in TLm could result from bottom-up processes in addition to fishing. In this sense, the increase in total catch during the 1980s and 1990s was explained by an expansion of the fisheries towards more productive pelagic fish such as horse mackerel and small pelagics, but also Chilean hake (Figs. 5.2a and 5.3). This expansion was matched with a decrease in the TLm and an increase in the FiB index. Therefore, the fisheries were ecologically balanced during this period, i.e., the decrease in TLm resulted in an increase in landings, and the fisheries were fishing through, rather than down, the food webs (Essington et al., 2006). However, the FiB increased only until the mid 1990s (with horse mackerel) and mid 1980s (without horse mackerel). This indicates that the expansion of the fishery towards more productive pelagic fish may have reached a limit during these periods, i.e., the decrease in TLm (and $_{\text{cut-off}}$TLm) was not matched with an increase in landings. Therefore, fishing down the food webs in the southern Humboldt seems to have been occurring only since the mid 1990s (with horse mackerel) and mid 1980s (without horse mackerel).

Although network indicators are theoretical, results obtained in this study are interesting in the light of recent global studies. Linkages between biodiversity and productivity, stability and robustness to overexploitation have been informed in marine ecosystems (Worm et al., 2006). In addition, food web modelling indicates that ecosystem structure can affect the extinction risk of species (Jonsson et al. (2006). Therefore, the hypothetical decrease in the number (diversity) of pathways and mutual information found in this study may have an effect on the extinction risk and resistance to exploitation in the southern Humboldt food web. This is relevant considering that current catastrophic predictions, e.g., the debatable global collapse of all currently exploited taxa by 2048 (Worm et al., 2006), do not consider this kind of fishing-induced change at the food web level.

In terms of the length of food chains, food web modelling conducted by Sterner et al. (1997) indicated that community stability should tend to lengthen, not shorten, food chains. Therefore, decreasing the length of the food chains (expressed here as mean path length) in the SH could lead to an even less stable food webs and to a wider impact of external changes in the system. This is supported by Williams et al. (2002) who indicate that the dynamics of species within ecosystems may be highly interconnected and, therefore, external and internal forcing (i.e., biodiversity loss, invasions, fishing, and global warming) may affect more species than previously thought.

Changes observed at the community level may have not resulted in increasing system variability. As observed in Fig. 5.7, the rate of increase in variance of landings was only accelerating in fish (among functional group) and horse mackerel (among fish stocks).

The analysis of the five-year average variance ($\bar{v}_5$) in the time series of landing and sea surface temperature indicated that in some time series $\bar{v}_5$ increased from the early 1960s to the late 1970s (Fig. 5.8). The high $\bar{v}_5$ prior to the 1960s in some time series could be mainly related to the fact that the most of the fisheries developed quickly during the 1950s. These results support the hypothesis that system variability increases before a regime shift, e.g. in the mid 1980s (Alheit and Ñiquen, 2004) which is also observed in the SST series.

Unexpectedly, secondary peaks in $\bar{v}_5$ were observed in some time series. Specifically, the period 1986-1990 strongly affected Chilean hake and Araucanian herring (the highest value in the series). In these species, $\bar{v}_5$ could have been influenced by the pass of the Fisheries Law in 1990, which introduced uncertainty in the stakeholders in both the previous and following years (Aliaga et al., 2000), but also by the 1987-ENSO event affecting the study area. Therefore, both environmental events and socio-economic objectives need to be considered when interpreting indicators. In the period 1996-2000 $\bar{v}_5$ showed a secondary peak in horse mackerel (the highest value in this series) and a tertiary peak in Araucanian herring. The high $\bar{v}_5$ in horse mackerel landings is likely caused by a combination of heavy fishing and the ENSO 1997-98 event, which could have affected Araucanian herring too.

Concluding remarks

The simple analysis of total catch and stock status could be enough to conclude that fisheries in Chile are not sustainable. However, using a variety of indicators allowed a more holistic picture of likely ecosystem changes in the southern Humboldt. As pointed out by Link (2005), ecosystem effects of fishing - and other forcing factors - are multivariate. Many indicators are sensitive to fishing, but not all of them are specific (Rochet and Trenkel, 2005; Travers et al., 2006), varying (with different sensitivity) in response to different environmental factors. In this sense, environmental fluctuations are the rule in the Pacific Ocean and southern Humboldt system: the inter-annual cycle of El Niño and La Niña seems to be replicated in an inter-decadal cycle known as El Viejo and La Vieja (Chávez et al., 2003). Although some indicators seem to be affected by a proposed regime shift in the system during the mid 1980s and by ENSO events, at the longer time scale the observed trends are in accordance with what is expected from the theory of fishing on ecosystems.

In the absence of a quantitative definition for ecosystem overexploitation (Murawski, 2000), the cross analysis of indicators leads to the following conclusions regarding the hypothesis laid out in the introduction. Results indicate a decline in the trophic level of the catch (confirmation of hypothesis 1) and that the system could have reached or even exceeded some ecological thresholds, i.e., landings are ecologically inconsistent with system productivity. The reduction in components of and connections in the food web could have negatively affected ecosystem maturity and stability, decreasing the magnitude of network properties (hypothesis 2). The exploited community is dominated by species with small body size, short life span and low trophic level, indicating an increase in community turnover rate (hypothesis 3). The variance of the landings of important stocks is not constant, but is decelerating (except in horse mackerel where it is accelerating), with the short term average variance (5 years) of important stocks likely influenced by decadal environmental changes, but also by ENSO events and overfishing (hypothesis 4).

Table 5.1. Data used to calculate aggregated indicators for the exploited community in the Southern Humboldt system off central Chile (33º-39ºS). Key: TL=Trophic level; MPL= mean path length; MI=mutual information; NP number of paths; $L_{infinitum}$ (cm), K ($year^{-1}$) and t_0 (years) are parameters in the von Bertalanffy growth equation. TL, MPL, MI and NP (obtained from Neira and Arancibia, 2004).

Taxa		**Habitat**	**Feeding traits**	**Common name**	**Scientific name**	**TL**	**MPL**	**MI**	**NP**	**Length (cm)**	**Age (year-1)**	**$L_{infinitum}$ (cm)**	**K**	**t_0 (year)**	**References**
Fish	Bony fish	Pelagic	Planktivores	Araucanian herring	*Strangomera bentincki*	2.50	2.17	3.73	6	10.5	0.69	18.00	0.67	-0.62	Fishbase (Froese and Pauly, 2007)
				Anchovy	*Engraulis ringens*	2.50	2.17	3.81	6	12.0	0.45	19.50	0.57	-1.23	Fishbase (Froese and Pauly, 2007)
				horse mackerel	*Trachurus murphy*	3.70	3.60	1.18	15	25.0	4.46	70.80	0.09	-0.90	Kuroiwa (1997)
				Mackerel	*Scomber japonicus*	3.70	3.60	1.18	15	26.0	4.43	70.80	0.09	-0.90	Pardo and Oliva (1992)
				Pacific pomfret	*Brahma australis*	3.70	3.60	1.18	15	38.0	3.18	58.92	0.28	-0.37	Leal and Oyarzun (2003)
				Hoki	*Merluccius magellanicus*	3.70	4.16	0.95	37	55.5	4.00	115.90	0.11	-1.81	Fishbase (Froese and Pauly, 2007)
			Piscivores	Snoek	*Thyrsites atun*	4.12	4.78	0.97	78	55.0	1.96	91.00	0.42	-0.25	Fishbase (Froese and Pauly, 2007)
				Sword fish	*Xiphias gladius*	4.12	4.78	0.97	78	155.0	2.61	282.00	0.29	-0.11	Fishbase (Froese and Pauly, 2007)
		Demersal	Pelagic feeders	Hake	*Merluccius gayi*	3.55	4.21	4.63	71	39.0	3.36	57.40	0.29	-0.23	Alarcon and Arancibia (1993)
				Southern whiting	*Merluccius australis*	3.55	4.21	4.63	71	69.4	9.53	110.00	0.10	-0.85	Balbontin and Bravo (1993)
			Benthic feeders	Congers	*Genypterus spp.*	3.89	4.59	5.57	71	69.4	7.67	136.00	0.10	0.00	Ruiz and Chong (1998)
				Flatfishes	*Hipoglissina macrops*	3.89	4.59	5.57	11	25.0	1.90	41.50	0.28	-0.41	Andrade (1999)
				Cardinal fish	*Epigonus crassidcaudus*	4.12	3.73	5.59	11	26.0	7.67	45.20	0.11	-0.78	Pino and Cubillos (2002)
				Pacific sand perch	*Prolatilus jugularis*	4.12	3.73	5.59	11	25.0	7.70				Fishbase
	Chondrychthyans	Demersal	Benthic feeders	Raja	*Raja spp*	3.00	2.00	9.72	1	96.0	14.00	128.30	0.11	0.51	Licandeo and Lamilla (2006)
				Elephant fish	*Collorhyncus callorhyncus*	3.20	2.00	9.72	1	50.0	5.00				Fishbase (Froese and Pauly, 2007)
			Pelagic feeders	Sharks	*(Isurus oxyrhyncus)*	3.20	2.00	9.72	1	237.5	20.00				Bishop et al. (2006); Fishbase
Molluscs	Cephalopods	Pelagic	Planktivores	Squid	*Loligo gahi*	3.78	3.35	3.53	26	15.0	0.67	37.00	0.34	-0.28	Cephbase* Cubillos et al (2004)
			Piscivores	Jumbo squid	*Dosidicus gigas*	3.78	3.35	3.53	26	35.5	0.58				Markaida et al. (2004)
				Octopus	*Octopus mimus*	3.78	3.35	3.53	26	35.5	1.19				Cephbase
Crustaceans		Benthic	Detritivores	Red squat lobster	*Pleuroncodes monodon*	2.00	1.00	0.11	1	2.7	4.75	5.05	0.20	-0.51	Roa (1993)
				Yellow squat lobster	*Cervimunida johni*	2.00	1.00	0.11	1	2.7	4.75	0.00			Roa (1993)
				Pink shrimp	*Heterocarpus reedi*	2.00	1.00	0.11	1	?	4.75	4.83	0.17	-0.51	Roa and Ernst (1996)
				Crabs	*Cancer spp.*	2.00	1.00	0.11	1	2.7	5.00				Weber (1994)
Mammals	Cetaceans	Whales				4.51	5.45	1.75	197	2000.0	6.50				Lockyer (1972)
	Sea lions		Piscivores	Austral sea lion	*Otaria flavescens*	4.23	5.06	1.54	345	100.0	4.75	254.40	0.31	-1.60	Rosas et al. (1993)

*www.cephbase.utmb.edu

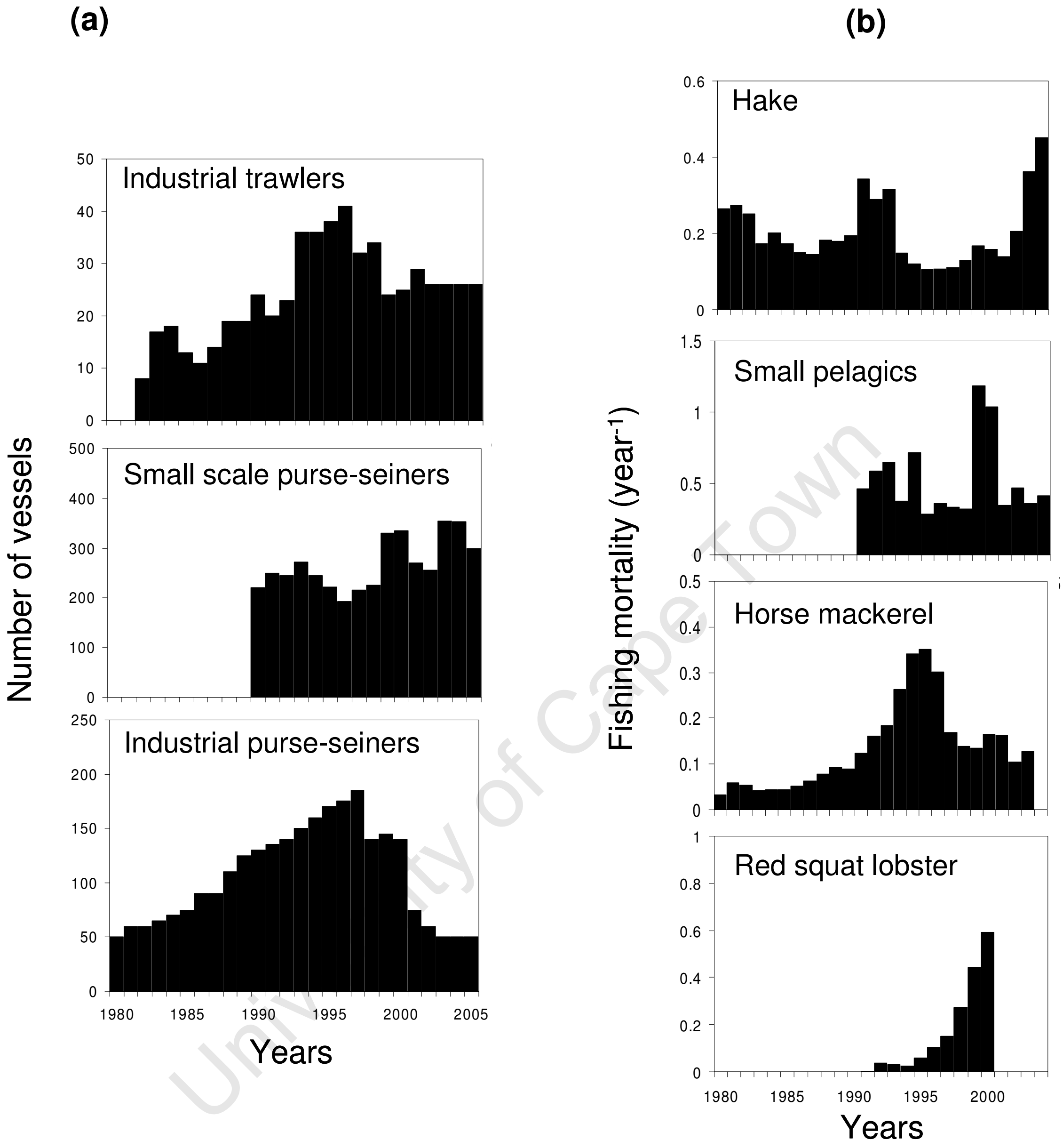


Figure 5.1. Indicators of exploitation in the southern Humboldt system off central Chile (33-39ºS). a) Number of ships in the most important fisheries. b) Estimated fishing mortality (Y/B) for important stocks.

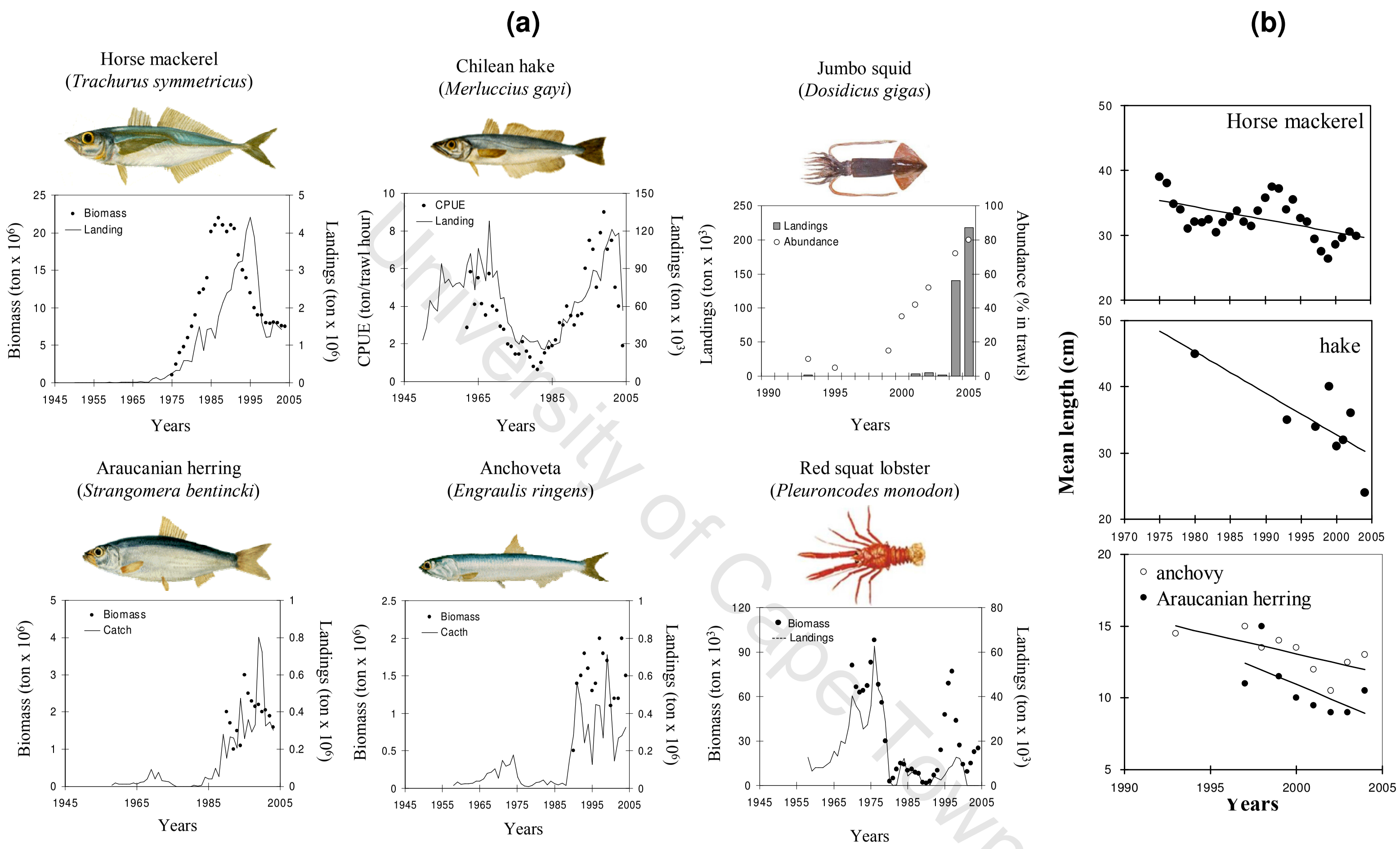


Figure 5.2. Changes over time in species based indicators in the southern Humboldt system off central Chile (33-39ºS). a) Abundance and landings; b) mean length. Spearman rank correlation testing significant decrease in the mean length over time: horse mackerel (r=-0.54, p<0.01); hake (r=-0.77, p=0.025), anchovy (r=-0.68, p=0.04), Araucanian herring (r=-0.61, p=0.10).

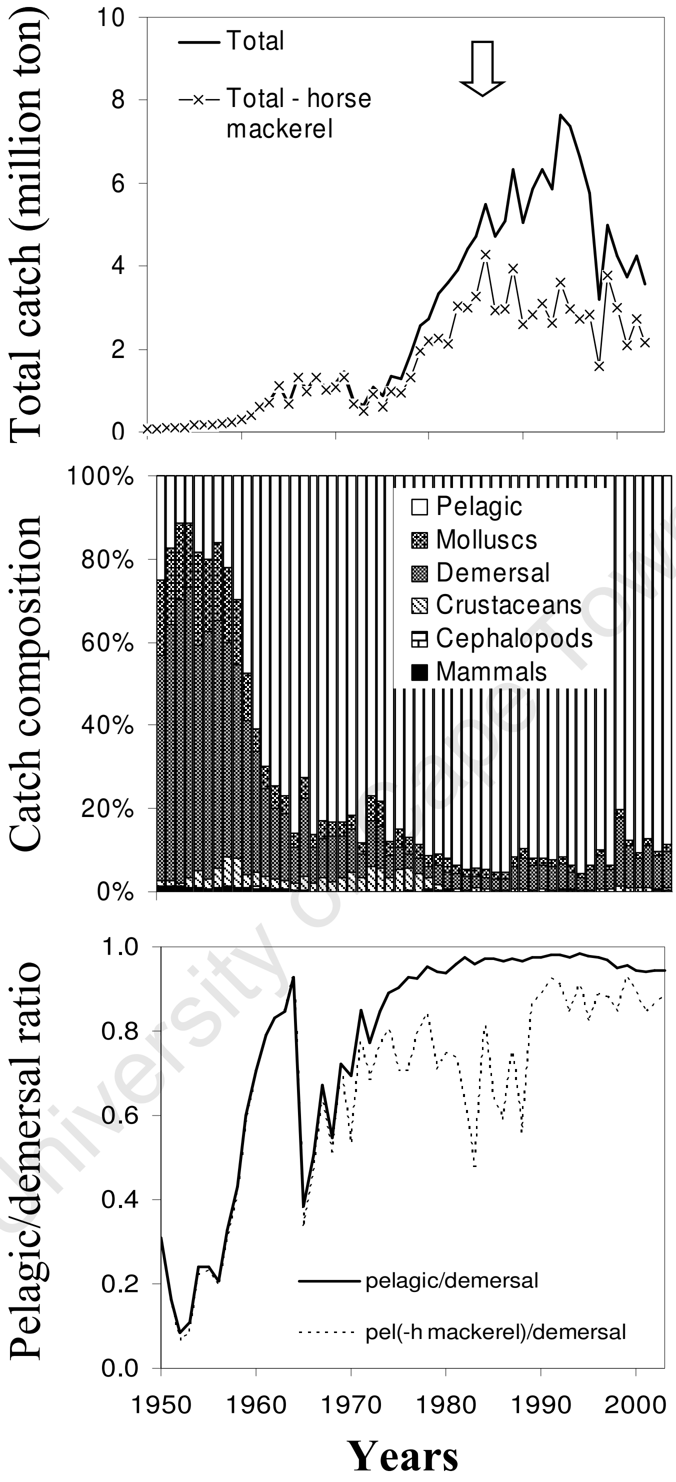


Figure 5.3. Observed trends in total landing, landing compositions and the ratio of pelagic: demersal fish from the southern Humboldt system off central Chile (33-39ºS). The arrow indicates proposed regime shift in the Humboldt system in the mid 1980s (Alheit and Ñiquen, 2004).

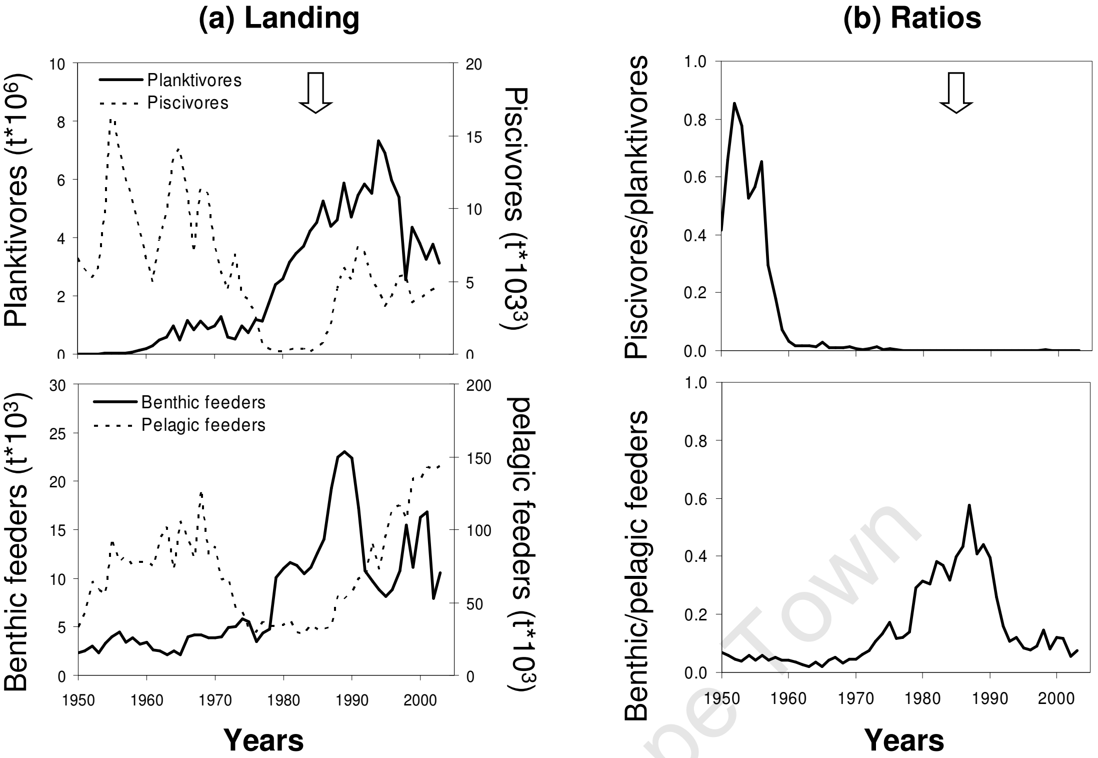


Figure 5.4. Changes in the landings of different trophic guilds in the southern Humboldt system off central Chile (33-39ºS). a) Reported landings per trophic guild; b) ratios between trophic guilds. The arrows indicate proposed regime shift in the Humboldt system in the mid 1980s (Alheit and Ñiquen, 2004).

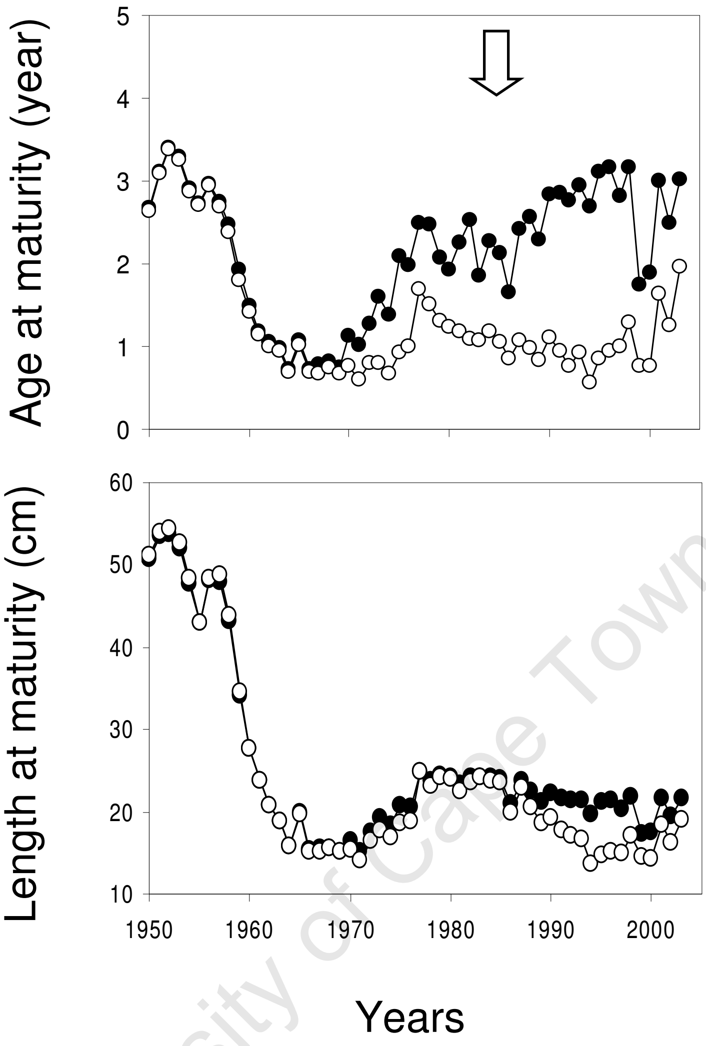


Figure 5.5. Changes over time in weighted age and length at maturity in the exploited fish community of the southern Humboldt system off central Chile (33-39ºS). The arrow indicates proposed regime shift in the Humboldt system in the mid 1980s (Alheit and Ñiquen, 2004). Symbols: black dots include landings of horse mackerel; white dots exclude landings of horse mackerel.

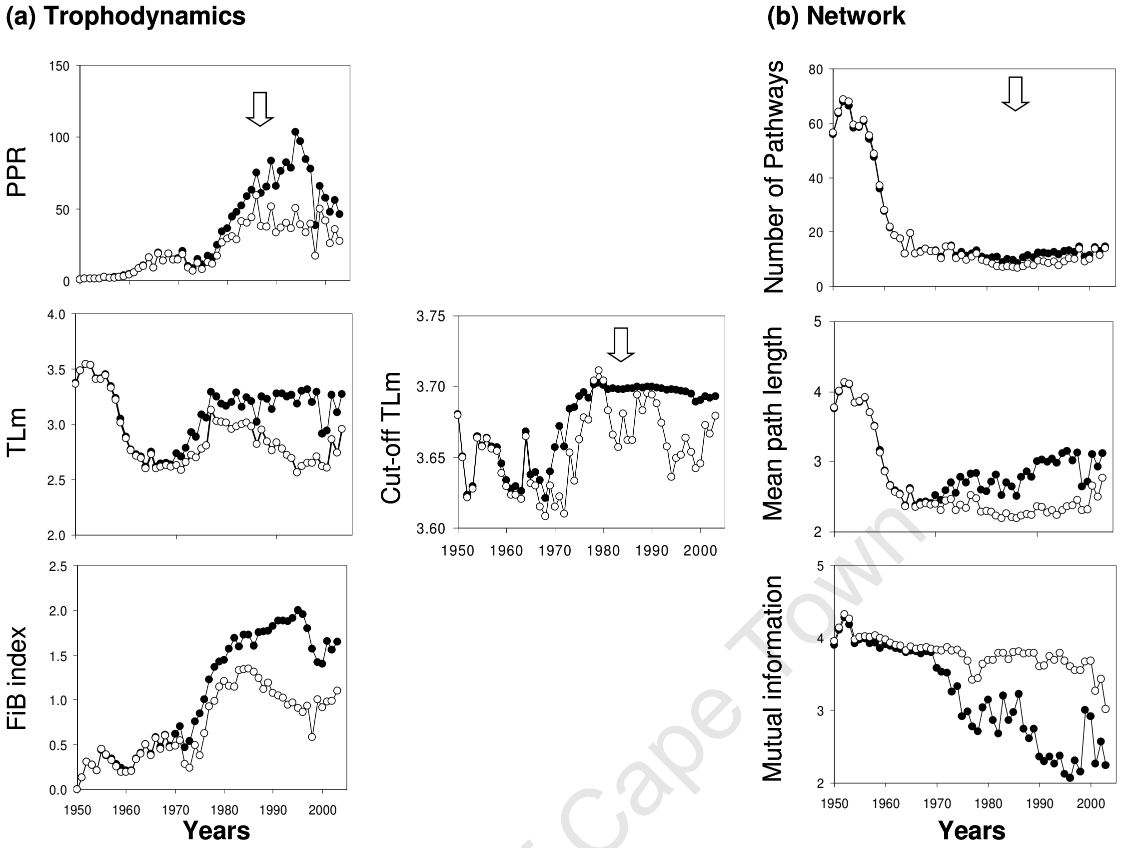


Figure 5.6. Changes over time in trophodynamic- and network-based indicators of the exploited community in the southern Humboldt system off central Chile (33-39ºS). The arrows indicate proposed regime shift in the Humboldt system in the mid 1980s (Alheit and Ñiquen, 2004). Symbols: full dots indicators including landings of horse mackerel; empty circles indicators calculated excluding landings of horse mackerel.

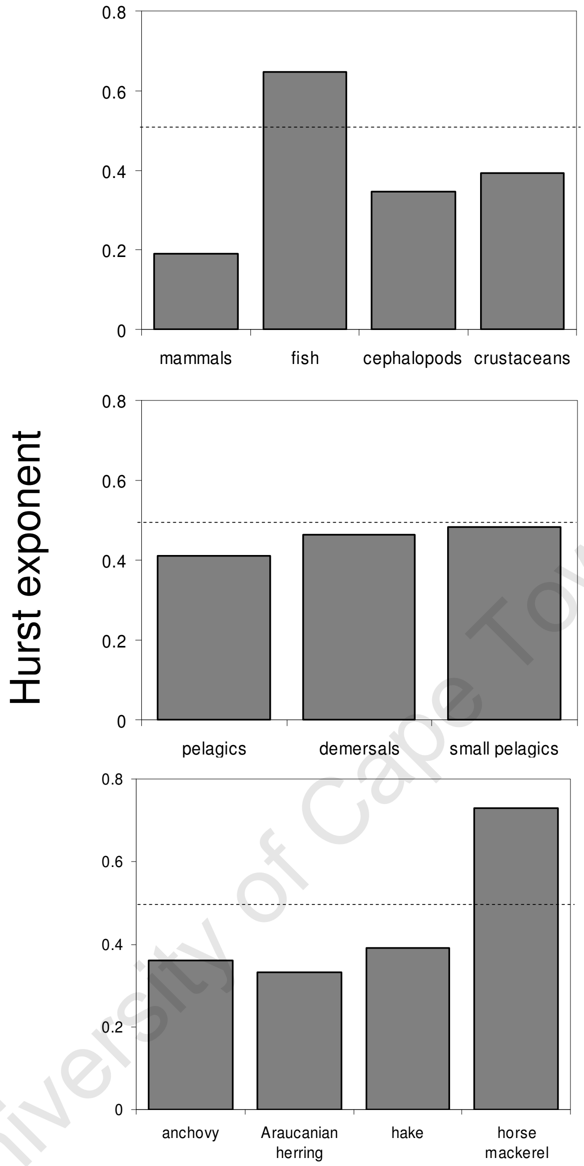


Figure 5.7. The Hurst exponent calculated from the average variance shown in time series of different lengths for landings of functional groups and stocks in the southern Humboldt system off central Chile (33-39ºS). Dotted lines correspond to H=0.5 and indicate a random walk or a variance that increases with the length of the series. Note that H>0.5 indicates accelerating variance, and H<0.5 indicates decelerating variance.

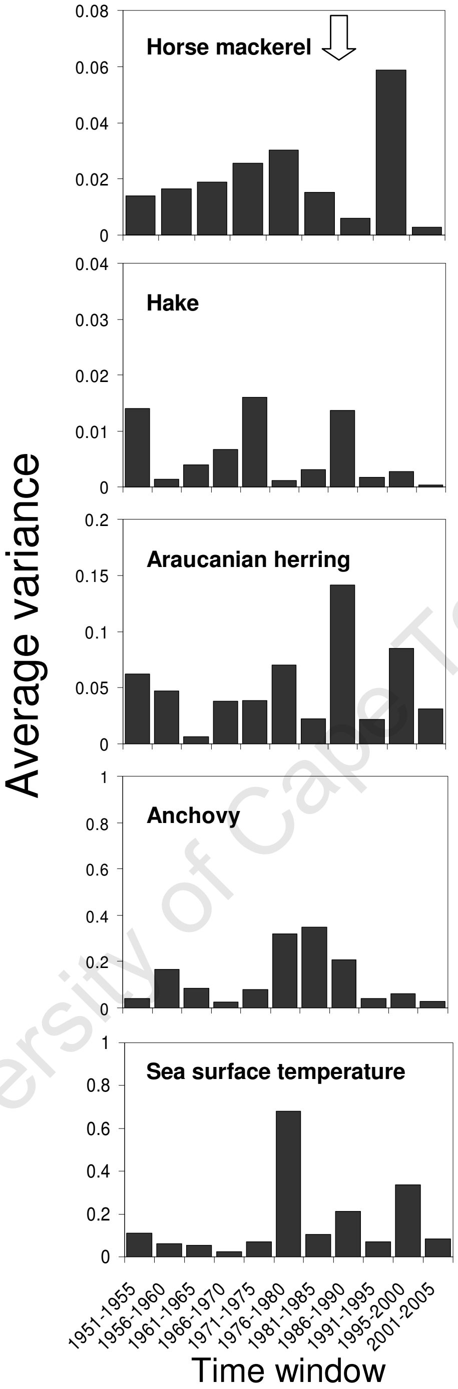


Figure 5.8. Five-year average variance for time series of landings of different stocks and sea surface temperature in the southern Humboldt system off central Chile (33-39ºS). The arrow indicates proposed regime shift in the Humboldt system in the mid 1980s (Alheit and Ñiquen, 2004).

CHAPTER 6

ECOSYSTEM-BASED OBJECTIVES, INDICATORS AND REFERENCE POINTS FOR FISHERIES MANAGEMENT IN UPWELLING ECOSYSTEMS

Abstract

The global call for an ecosystem approach to fisheries (EAF) has forced fishery science to consider whole-ecosystem properties in addition to the status of particular species as motivation for management decisions. The definition of ecosystem-based objectives, ecosystem indicators (EIs) and ecosystem reference points (ERPs) plays a key role in this process. Previous work had proposed and evaluated a series of EIs in the most important upwelling ecosystems in the southern hemisphere (the Benguela Current System and the Humboldt Current System). However, the definition of ERPs has not been fully evaluated, with limit reference points (ecological thresholds) remaining unknown or poorly understood. In this chapter, literature, empirical data and model results concerning marine ecosystems -with emphasis on upwelling systems in the southern Hemisphere- are used to review and propose ecosystem-based objectives and reference points for available EIs. Considering that in most cases there is no agreement on specific target reference points, two categories of ERPs are explored: i) Baseline reference points (BRPs), describing the values of the corresponding EIs in a pristine ecosystem, and ii) limit reference points (LRPs), not acceptable values for EIs. BRPs and LRPs are proposed from previously constructed food web models of the SH system that represent the pristine and pre-industrial fishing periods. The chapter finishes by discussing ecosystem-based control rules triggered when limit reference points are exceeded, i.e., when EAF objectives are not met.

Keywords: ecosystem approach to fisheries, management objectives, indicators, reference points, upwelling ecosystems, southern Humboldt.

Introduction

The ecosystem approach to fisheries needs to consider whole-ecosystem considerations in addition to the status of target species as motivation for management decisions (FAO, 2003). Before being included in the decision making process, however, ecosystem considerations need to be set on an operational basis, i.e., a framework linking objectives, indicators, reference points and control rules. For example, management rule systems implemented in single-species fisheries have a very simple principle: when a limit reference point value is exceeded (i.e., the management objective is not met) a control rule is triggered to restore the exploited population to a safer condition (Caddy and Mahon, 1995).

The COMFIE-type rule (ICES, 1997) uses two categories of reference points based on the biomass and the fishing mortality of a determined stock. The first pair of reference points are the precautionary biomass (B_{pa}) and the precautionary fishing mortality (F_{pa}). The second category includes the limit reference points, i.e., the minimum acceptable biomass (B_{Lim}) and the maximum acceptable fishing mortality (F_{Lim}). The above reference points delimit three regions in a bi-dimensional plot: i) a safe zone that is the aim of fisheries management in the long term ($B>B_{pa}$; $F<F_{pa}$), ii) a precautionary zone which should be avoided as far as possible ($B_{pa}>B>B_{Lim}$; $F_{pa}<F<F_{Lim}$) and iii) a high-risk zone in which there is either overfishing (i.e. $F>F_{Lim}$) or the stock has been overfished and is at risk of serious or irreversible harm (i.e. $B<B_{Lim}$).

Although important international research efforts have been directed at developing and testing quantitative ecosystem indicators for fisheries management (see Daan et al., 2005a), management rule systems for EAF are still in their infancy (Babcock and Pikitch, 2004; Pikitch et al., 2004). To be useful in management, these indicators need to be closely linked to i) clear objectives (i.e., what is to be achieved, or what definitely needs to be avoided), ii) reference points (measures of management performance) and ii) control rules (actions required when management does not meet objectives) (FAO, 2003; Cury et al., 2005a).

Ecosystem-based objectives, reference points and control rules have been difficult to set mainly because of limitations in the understanding of ecological complexity, uncertainties in data quality and model behaviour, and difficulties in balancing multiple stakeholders' interests (Cury et al., 2005c). The first two shortcomings limit the reliability of projections on the response of stocks and communities to management and climate forcing. The multiple and conflicting stakeholders' interests (e.g., maximize economic and social benefits vs. conserve stocks and ecosystems) limit management capacity to set agreed targets for the use of ecosystem goods and services.

Pervasive negative effects of overfishing on marine ecosystems provide a basis to agree on ecosystem states that should be avoided by cautious ecosystem-based management (FAO, 2003, Cury et al., 2005c). Once these states are identified, reliable ecological indicators can be monitored to follow management success. Historical or theoretical patterns can be used to define references points for those indicators (Rochet and Trenkel, 2003). Measurable management actions (controls) that favour conditions under which ecosystems are likely to persist as sources of goods and services then can be easier to agree and establish.

The definition of high and low risk zones delimited by ecological indicators and their reference points is an area of growing interest in fisheries science. The focus is avoiding potential high-risk consequences of exceeding ecological thresholds that could lead to unwanted and non-reversible ecosystem states (Groffman et al., 2006).

Regime shifts are well known changes in ecosystem states in the ocean. A well documented shift occurred in the North Pacific Ocean between 1976 and 1980 when physical and, especially, biological variables showed marked and rapid changes from one ‘‘regime’’ to another (Wooster and Zhang, 2004). Similar shifts have been documented in several systems including the eastern South Pacific Ocean (Alheit and Ñiquen, 2004) and the northern Atlantic (Reid et al., 2001; Beaugrand, 2004). Observed patterns allow concluding that regime shifts result from changes in the environmental forcing reverberating though the whole ecosystem facilitated by the physical–biological coupling (Steele, 2004).

In addition to bottom-up physical trends, top-down effects of overfishing affect whole ecosystems. Overfishing can trigger changes in particular or multiple prey-predator links resulting in trophic role reversals such as cultivation effects (Walters and Kitchell, 2001) and whole food web cascades (Frank et al., 2005; Daskalov et al., 2007). These changes can reorganize the entire food web into a 'quasi-permanent' regime featuring fundamental differences in structure and function from the preceding one (Cury and Shannon, 2004; Frank et al., 2005; 2006; Daskalov et al., 2007).

The slow recovery of overexploited stocks after strong reductions in abundance in recent decades (Hutchings, 2000) could indicate that, in some ecosystems, ecological thresholds beyond single species collapses and environmental cycles are being exceeded. Identifying and anticipating these ecological limits should be key aspects of the ecosystem approach to fisheries.

Ground fish populations have been reduced to less than 10% of their pristine abundance (Myers and Worm, 2003; Christensen et al., 2003). Theoretical studies show that because of that, pristine food webs could have been very different from presents ones (i.e., Odum, 1969; Christensen and Pauly, 1998; Chapter 2). This led to the argument that rebuilding food webs and not the sustainability of individual stocks should be a proper goal for ecosystem-based fisheries management (see Pitcher and Pauly, 1998). Many comparisons of ecosystem states before and after the rising of industrial fisheries have been conducted (e.g., Pauly et al., 1998c; Pitcher et al., 2002; Watermeyer et al., in rev.). On Chapter 2, for instance, we have seen that the marine food web off central Chile could have supported more biomass of long-living and high-trophic level species in the pre-industrial model compared to the present state model. The value of ecosystem indicators calculated from "pristine states" is that they are base-line reference points helpful in evaluating current ecosystem state and potential guidelines for future recovery plans.

In the absence of controlled experiments, the comparison of food web models representing upwelling systems in the southern Hemisphere can yield insights on the range of values of some ecological indicators (Moloney et al., 2005). Available Ecopath models for the SH (i.e., Moloney and Jarre, 2003; Chapter 2) describe ecosystem states for, pre-industrial fishing, onset of industrial fisheries, full at exploitation, and following heavy exploitation. All these models have been inter-calibrated and have standard structures, which makes them suitable for comparing indicators and for assessing base line and limit reference points.

This chapter reviews available literature and data from empirical and modelling studies of the main upwelling systems in the southern Hemisphere (Humboldt and Benguela), with emphasis on the Chilean system. The aims are i) to develop broad and fishery-specific objectives for EAF, and ii) to propose reference points (base line and limit) for a set of ecological indicators. Control rules are discussed that can be triggered if management objective are not met.

The methods followed in this chapter consisted of:

a) A literature review with emphasis on the objectives that should guide the ecosystem approach to fisheries. This review targeted two layers: broad objectives related to the ecosystem approach to fisheries, and fisheries-specific objectives based on results of ecosystem risk assessment (Fletcher, 2005) conducted in South African (Shannon et al., 2006) and Chilean fisheries (Neira and Arancibia, in prep.).

b) Based on the above review of management objectives, limit and base-line reference points were derived for a set of indicators currently agreed as measures of performance. Reference points are proposed on the basis of a literature review and comparative analyses of food web models representing the Humboldt system off central Chile and the important upwelling systems in the southern Hemisphere (Table 6.1).

Models in Table 6.1 were selected because, unlike other models published for some of these sub-systems (i.e., Heymans et al., 2004; Neira et al., 2004; Shannon et al., 2003), they have been inter-calibrated (in terms of similar species groups and broad functional groups, as well as input parameters) then constructed following a common upwelling ecosystem model. Although models can never be identical (the composition of functional groups can be considerably different in terms of the contributing components and the quality of data available in each system), models in Table 6.1 represent the best standard structure that is suitable for comparative analyses (see Moloney and Jarre, 2003; Moloney et al., 2005; as well as Chapter 2 in this thesis).

Results

A. Reviewing objectives for an ecosystem approach to fisheries

Human exploitation of marine ecosystems has revealed some important lessons: i) although renewable, natural resources are limited, ii) populations are highly connected to their surrounding ecosystem directly and indirectly, and this interaction network affects their productivity, iii) biomass removal of one species has direct and indirect effects on other target and non-target species as well as on the physical habitat, affecting related or dependent species, and iv) single-species management approaches have performed poorly, as witnessed by the degraded state of many fisheries and their ecosystems.

An ecosystem approach to management has gained acceptance among stakeholders (Grumbine, 1994; Garcia et al., 2003). Since the 1980s, the call for integrating ecosystem considerations into fisheries management in both international and national policy statements has increased notably, e.g., the International Law of the Sea (1982), the Earth Summit in Rio (1992), the Convention on Biological Diversity (1996) and the World Summit on Sustainable Development (2003). However, the operational bases for the ecosystem approach to fisheries remain a big challenge for fisheries science (Hempel and Pauly, 2002). Stanley (1995) identifies conflicting views in the core of ecosystem management approaches. The first is "biocentric" and considers human use of resources to be constrained by the primary goal of maintaining ecological integrity. The second view is anthropocentric and retains the importance of human use of resources, but it includes ecological and social considerations. Basically the debate is whether ecosystems should be protected and conserved because of their intrinsic value or because their utility to human societies. The challenge is to mediate, articulate and balance these differences in perspective (Hilborn, 2007). Current trends such objectives that value less disturbed ecosystems and allocations that improve the fisheries' economic efficiency can result in more congruent objectives and less conflict (Hilborn, 2007).

When it comes to policy statements, vocabulary is another source of disagreement.

Some widely used concepts (e.g., ecosystem health, ecosystem integrity and ecosystem sustainability, among others) have been criticized for having diverse and sometimes misleading interpretations. Most importantly, they are not objective and quantifiable properties of an ecosystem, and lack support by either empirical evidence or ecological theory (Sutter, 1993; Wicklum and Davies, 1995, Alverson, 2004). On the other hand, statements such as “taking into account the biological constraints with due respect to marine ecosystem” (e.g., EU Common Fisheries Policy, 1993) and “maintain ecosystem health and sustainability” (e.g., Ecosystem Principle Advisory Panel US, 1999) are not clear since they reflect different management priorities.

Despite these shortcomings, there is an increasing agreement that the ecosystem approach to fisheries should explicitly recognize and harmonize the existence and interdependence of two main aspects: human wellbeing (all members of the society determine and meet their needs from a large range of choices) and ecosystem wellbeing (the ecosystem maintains its diversity, quality and capacity to adapt to changes) (Prescott-Allen, 2001; Ward et al., 2002; Garcia et al., 2003).

Therefore, the very broad objective of an ecosystem approach to fisheries should be to ensure (or improve if conditions are not met) and maintain both human and ecosystem wellbeing. Ecosystem-based fisheries management implies the conservation of ecosystem structure, processes and interactions through sustainable use. This means considering and balancing a range of frequently conflicting objectives, and the realization that consensus may not be achievable without equitable distribution of benefits among present and future generations of stake holders (Laffoley et al., 2004).

Analysing human wellbeing (including equity among stake holders and the capacity to achieve good governance) requires socio-economic and political approaches that are beyond the objectives of this review (see Prescott-Allen, 2001). This chapter only explores objectives, indicators and reference points related to ecological wellbeing.

A series of objectives for ecosystem management in general and the ecosystem approach to fisheries in particular have been proposed (see Table 6.2). It is considered that those proposed by FAO (2003) are the most specific and quantifiable, and these are explored further here.

1. Avoid overfishing

This objective acknowledges that living resources and their production are limited. As a consequence, stocks can only sustain certain levels of fishing pressure (limited fishing mortality) beyond which ecological productivity and abundance decrease as well as the capacity to support people and future opportunities. As mechanisms behind stock recovery are not yet well understood (see objective 2), the first objective for management is to avoid overfishing and maintain long-term (re)productive capacity of target species. This is normally done by applying the fishing mortality estimated to maintain the spawning biomass present in the sea at a target productivity level.

What should this target level be?

Although criticized (May et al., 1973), buried (Larking, 1977) and re-defined (Mace, 2001), the concept of maximum sustainable yield (MSY) has survived as a target reference point in the international fishing agenda, e.g., the provisions in the UN Convention on the Law of the Sea (1982), the principle of Chapter 17 of Agenda 21 from the UN Conference on Environment and Development (1992), and the Implementation Plan adopted at the World Summit on Sustainable Development (2002). In its Section 31, the later plan calls specifically for actions to *maintain or restore stocks to levels that can produce the maximum sustainable yield with the aim of achieving these goals for depleted stocks on an urgent basis and where possible not later than 2015.*

However, MSY is often regarded as a limit rather than a target reference point (Mace, 2001). Although in their infancy, concepts such as “ecologically sustainable yield”, the yield an ecosystem can sustain without changing state (Zabel et al., 2003), and “multi-species sustainable yield” (Walters et al., 2005) are more appealing as target reference points and are candidates to replace MSY.

In Chile, recruitment overfishing was identified as a high-risk issue for the fishery of Chilean hake (Neira and Arancibia, in prep.). In South Africa, where fish stocks have been more conservatively managed, overfishing was not identified as a risky issue in any of the fisheries analyzed with ERA, e.g., small pelagics, demersal and rock lobster (Shannon et al., 2006).

Specific objectives under and ecosystem approach to avoid overfishing are:

- Set F_{limit} for all exploited species.
- Enforce $F<F_{limit}$ for all exploited species.
- Improve estimates of underreported catch and discards.

It must be noted that some conceptual and technical difficulties may arise when calculating fishing mortality reference points in the multi-species context, as opposed to reference points based in fishing mortality of single-species. A potential avenue worth to explore is perhaps setting effort reference points for each functional fishing fleet operating in the ecosystem.

2. Ensure reversibility of impacts and facilitate rebuilding

The state of world fisheries (FAO, 2005) indicates that about 17% of all fish stocks have been overexploited, 7% are depleted, and only 1% is recovering from depletion. The low occurrence of depensation in exploited stocks suggested that the effects of overfishing were still reversible by the mid 1990s (Myers et al., 1995). A few years later, however, the resilience of fish to large population reductions was demonstrated to be lower than expected. After reviewing 96 fish stocks, Hutchings (2000) found little evidence of rapid stock recovery (especially in gadoids and non clupeid species) after prolonged declines (45-99% reductions in reproductive biomass). Therefore, stock rebuilding is regarded as an imperative in both international (FAO, 2003; Caddy and Agnew, 2004) and national strategies (e.g., UN Fish Stock Agreement, Safina et al., 2005). Delaying rebuilding will perpetuate overfishing, which in turn decreases stock resilience and compromises recovery. Therefore, the broad objective is that retained species in which biomass has dropped below the limit reference point ($B<B_{Lim}$) should be managed as to increase the probability of recovery (at least) to levels that can produce the maximum sustainable yield. However, stock levels higher than those producing MSY should be preferred.

How long should these recovery periods be?

Safina et al. (2005) argue that ten years is a reasonable and beneficial rebuilding period because, according to population dynamics experts, it is roughly twice the time that most depleted fish populations in the US need for rebuilding to target levels under zero fishing. Ten years is also a manageable period to ensure that managers actually instigate rebuilding, thus increasing chances of success and minimizing future ecological, social and economic costs (Safina et al., 2005).

Specific objectives to ensure rebuilding are:

- Set B_{limit} for all exploited species.
- Set recovery periods for all exploited species (or use a ten-year period as a default).

3. Minimize fishing impacts

Avoiding overfishing and allowing stock rebuilding are key steps to accomplish sustainable fisheries and are likely to have positive effects on overall ecosystem state. However, ecosystem effects of fishing extend well beyond retained species, and even sustainable fishing (i.e., $B>B_{Limit}$ and $F<F_{Limit}$ for all exploited species in the ecosystem) can have negative ecosystem-wide side effects (e.g., by-catch mortality, alteration of bottom habitat and biota, reduced forage biomass for dependent predators, and threats to the conservation of rare species and high-quality habitats, among others).

Therefore, the broad objective is to keep fishing impacts on ecosystems at the lowest possible level. Minimizing fishing impacts is also regarded as an effective way to ensure ecosystem potential to recover and to promote the reversibility of fishing-induced changes both at the stock and ecosystem level.

Specific objectives to minimize fishing impacts are:

- Prevent that the abundance of non-exploited species from falling below limit levels, e.g., conservation criteria of the International Union for the Conservation of Nature and Natural Resources (IUCN), that assesses species as critically endangered, endangered and vulnerable.

- Minimize by-catch.
- Aim for the World Summit for Sustainable Development target of protecting at least 20% of each habitat type by 2010.
- Eliminate and or restrict the use of destructive gears (reduce impacts on the sea bed).
- Minimize discards to avoid wasting fishery resources and unbalanced increase of scavenger populations.

4. Consider (maintain) species interactions

Several decades of trophodynamic studies (e.g., who eats and controls whom?) have revealed that “no fish is an island” (see www.ecopath.org), i.e., marine populations are part of complex and intricate webs of interactions. Because predation is believed to be the most important ecological interaction in marine ecosystems (Bax, 1991; 1998), the alteration of predator-prey relationships caused by overfishing is regarded as a potential cause of regime shifts and an antagonistic force preventing stock and ecosystem recovery.

Cury and Shannon (2004) reviewed regime shifts and species replacements in both the southern and the northern Benguela ecosystems, and concluded that bottom-up control could initiate and sustain regime shifts in both ecosystems. However, in the northern Benguela, overfishing appears to have initiated and maintained a regime shift characterized by very low biomass levels of small pelagic fish, reduced efficiency of energy transfer, and an increased biomass of horse mackerel and jellyfish (Cury and Shannon, 2004; Moloney et al., 2005). By contrast, the alternation between sardine and anchovy observed in the southern Benguela over the last two decades, when stocks were more conservatively exploited, appears not to have had major effects on the overall functioning of the ecosystem (Shannon et al., 2004b). In the North Atlantic, overfishing has led to alternative ecosystem states with slow/no recovery of collapsed populations of cod (*Gadus morhua*) (Pace et al., 1999; Choi et al., 2004;

Hutchings and Reynolds, 2004; Shelton et al., 2005). More recently, two major shifts in the Black Sea food web have been triggered by overfishing, resulting in food web cascades related to the depletion of marine predators and an outburst of the invasive comb jelly (*Mnemiopsis leidyi*) (Daskalov et al., 2007).

These examples highlight how overfishing at different trophic levels can result in system-wide trophic cascades (Daskalov et al., 2007; Frank et al., 2007). They also indicate that “natural” trophic or environmental controls may have been altered by overfishing.

Considering this, maintaining species interactions objective is defined as to identify, quantify, acknowledge and maintain ecological relationships between harvested, dependent and related species.

In the upwelling system off South Africa, the dependence of many predator species on small pelagic fish was highlighted and considered by stakeholders to be of extreme and moderate risk respectively for marine birds and other predators (i.e., seals and cetaceans) (Shannon et al., 2006). Implications of strong trophic interactions between lobsters, abalone and urchins were also considered to be of extreme risk. In the fishery of Chilean hake off central Chile, the dependence of hake on prey and the effects of outbreaks of opportunistic predators such as jumbo squid (*Dosidicus gigas*) were considered of moderate risk (Neira and Arancibia, in prep.).

Specific objectives for maintaining species interactions are:

- Allow a certain production of prey/forage fish to remain in the sea to avoid compromising populations of dependent predators.
- Avoid threshold levels of pelagic fish below which the implications for seabirds (and other dependent predators) are detrimental.
- Avoid thresholds beyond which the ecological function of a species is reduced such that their "ecosystem function" is diminished and/or the biological productivity of the entire system is adversely affected (although those features are not yet well defined or readily measurable).

However, since fishing management is fish focussed, the trophic role and the importance of other ecosystem components (that are not normally monitored because they lack commercial value) in maintaining interactions is often poorly known. Therefore, an additional and important objective should be to monitor the abundance of, for example, benthic fauna and other components in a routinely basis.

5. Apply precautionary approach

Although research conducted in the oceans in recent decades has resulted in an increasing understanding of the physical, chemical and biological factors affecting the dynamics of marine populations, marine ecosystems are still only partially known (Field et al., 2002). Ecosystems are open, interconnected, complex and dynamic. They vary at all scales, e.g., from hours to centuries and centimetres to kilometres and are affected by environmental conditions and human activities, i.e., fishing, aquaculture, etc. (Jackson et al., 2001). As a result, ecosystem resilience and the extent and reversibility of human impacts are not only difficult to anticipate, but are hard to disentangle from environmental changes. Therefore, wild marine populations must be managed in a way that recognizes inherent uncertainties (e.g., the incompleteness of knowledge about the state or processes of nature).

Within the framework outlined in Article 15 of the UNCED Rio Declaration, the precautionary approach to fisheries recognises that changes in fisheries systems are only slowly reversible, difficult to control, not well understood, and subject to changing environment and human values. Therefore, the precautionary approach to fisheries calls for the application of prudent foresight, taking into account of the uncertainties in fisheries systems and the need to take action with incomplete knowledge (FAO, 1995). The implementation of this objective requires, inter alia: consideration of the needs of future generations, identification of undesirable outcomes and measures to avoid and/or correct them promptly, prioritize conserving the productive capacity of the stock when the likely impact of a use is uncertain, among others.

General actions related to the precautionary approach to fisheries normally found in the literature are: (1) improve research to advance understanding of ecosystems; (2)

take measures to account for complexity and dynamics, and that are robust to uncertainty, and (3) give attention to transboundary impacts. These objectives are encapsulated in the Precautionary Approach and will not be treated further here (for details see FAO, 1995).

In South Africa, the recent change in distribution patterns of fish populations (sardine in particular) was classified as being of high risk (Shannon et al., 2006). Poor understanding of low frequency, decade-scale variability in productivity, population size and species dominance (regime shifts) was considered to be of high to moderate risk. Detrimental effects on lobsters of increased frequency and magnitude of harmful algal blooms, low oxygen events and corresponding lobster walkouts were listed as moderate risks to the coast rock lobster fishery. In the fishery of Chilean hake, uncertainties on the assessment method (acoustic), discard mortality, recruitment variability and the magnitude of natural mortality (predation and cannibalism) where considered of high risk (Neira and Arancibia, in prep.).

Specific objectives for implementing the precautionary approach are:

- Improve estimates of recruitment, survival after discard and misreporting of catch, among other sources of uncertainty.
- Evaluate the likely effects of regime shifts on stock productivity and mortality rates.
- Consider spatial management in fisheries with known geographical shifts or involving spatially important predator/prey interactions.
- Consider fishing mortality rates appropriate to the state/regime in which the ecosystem occurs.
- Quantify predation mortality and evaluate the performance of models when this parameter is maintained constant or allowed to vary over time.

One of the principles of the ecosystem approach to fisheries recognizes that there are uncertainties in managing fisheries for the benefit of ecosystems. Conservation measures should contain elements of “learning by doing” and incorporating feedback from research. Management systems should be adaptive (Walters, 1986).

6. Maintaining ecosystem integrity

Ecosystem integrity is often stated as one of the goals of ecosystem management (Grumbine, 1994; FAO, 2003). Although no agreed definition exists, ecosystem integrity normally refers to the maintenance of two fundamental and interconnected ecosystem properties: structure (e.g., biodiversity at the levels of the biological community, habitat, species and genes), and function (e.g., ecological processes that support both biodiversity and resource productivity). Management must take into account that ecosystems are dynamic and their attributes and boundaries are constantly changing. Interactions with human users are also dynamic (Ward et al., 2002), and management should try to maintain the evolutionary potential of species and ecosystems (Grumbine, 1994).

No specific issues arose on this item from ERAs in South Africa or Chile. However, some extra objectives for maintaining ecosystem integrity that have not yet been mentioned are:

- Do not introduce (and eradicate if already introduced) alien species.
- Control/reduce/eliminate pollution.

These six broad objectives are harmonized in the main goal of the framework for the development of ecologically sustainable fisheries (Fletcher et al., 2002): '*using, conserving and enhancing the community's resources so that ecological processes, on which life depends, are maintained, and the total quality of life, now and in the future, can be increased*'.

B. Indicators and reference points to support EAF objectives

This section reviews indicators that can translate the above management objectives into quantitative measures of performance to assess the effects of management actions. For each indicator, a base-line and a limit reference point are proposed based on available literature and the comparative analysis of results from available food web models (Table 6.1).

B.1. Indicators derived from biomass and catches/landings

B.1.1. Biomass

Biomass (B) corresponds to the weight of a fish stock, or some defined portion of it (Ricker, 1974). B is calculated using standard stock assessment techniques and corresponds to the number of individuals present in a determined area multiplied by their average weight. Because marine populations are selectively exploited, species composition can change markedly and thus the biomass of as many species as possible should be monitored. In this way, spurious conclusions from changes observed in the biomass of just one species can be minimized, since patterns seen across a range of taxa are better indicators of changes at the ecosystem level. In addition, aggregate biomass estimates can be used with unambiguous thresholds (Link 2005).

Biomass of individual species

The biomass of all retained and surveyed (target and by-catch) species should be monitored. Whenever possible, non-retained species should be monitored as well.

Biomass ratios

Ratios between biomasses of groups representing different feeding traits are a complementary measure to individual biomasses that are used as indicators of changes in both ecosystem structure and function (Heath, 2005; Shannon et al., in press). The following are some of the most common ratios analyzed in the literature: pelagic fish:demersal fish, pelagic fish:top predators, small pelagic fish:demersal fish, small pelagic fish:top predators, benthic-feeding fish:pelagic-feeding fish, and planktivores:piscivores.

Candidate reference points for indicators based on biomass

Based on observed stock collapses, for retained species, early limit reference points included minimum spawning biomass, and 20% of the biomass reached in the absence of fishing or in the pristine state (FAO, 1996). Alternatively, B_{Lim}=$B_{MSY.}$

For non-retained species the categories of threatened species of the International Union for Conservation of the Nature (IUCN), based on the UICN red list of threatened species, should be followed. This list provides taxonomic, conservation status and distribution information on taxa that have been globally evaluated using the IUCN red list categories and criteria (see IUCN, 2001). This system is designed to determine the relative risk of extinction, and the main purpose of the IUCN Red List is to catalogue and highlight those taxa that are facing a higher risk of global extinction. The categories are: not evaluated (when the taxa has not been yet evaluated against the criteria); data deficient (taxa for which inadequate information is available for direct/indirect assessment of its risk of extinction); least concern (taxa that do not qualify as critically endangered, endangered, vulnerable or near threatened); near threatened (taxa do not qualify as critically endangered, endangered or vulnerable, but likely to qualify in on of this categories in the near future); vulnerable (taxa meets the criteria to be considered to be facing high risk of extinction in the wild); endangered (taxa meets the criteria to be considering to be facing very high risk of extinction in the wild); critically endangered (taxa in extremely high risk of extinction); extinct in the wild and extinct.

In terms of ratios among feeding guilds, plots from models introduced in Table 6.1 indicate that high values of rates for the pelagic fish:demersal fish and pelagic fish:top predators are characteristic of heavy exploitation. In the Chilean case, the small pelagic:demersal and small pelagic:top predator ratios increased by factors of 7 and 150 respectively from the “pristine” to the “present” model (Fig 6.1). Similar figures are observed in terms of the pelagic/demersal fish and pelagic/top predator ratios (Fig. 6.1). The same figure shows that pelagic:demersal and pelagic:top predators ratios increase in the most altered models in the Chilean system. When the same ratios are compared among the Peruvian, Namibian and South African systems, they suggest that high pelagic:demersal ratios are characteristic of heavy exploited ecosystems (Fig. 6.2).

Following Link (2005), a limit for the biomass ratios is proposed as 50% of the highest observed value since it implies an important imbalance in the proportion of prey:predator

B.1.2. Catches

Although easier and cheaper to collect compared with estimates of biomass, information derived from landings/catches does not necessarily reflect population dynamics, because catches depend on fishing effort and the catchability of the fishing gears, which are seldom constant. Fish behaviour (e.g., schooling) can also affect catchability. In general, the same categories of indicators based on biomass can be analyzed using catches, with the exception of those involving groups that are not retained by fishing gear, e.g., top predators, jellies, etc. In addition, two other indicators can be considered:

Centre of gravity of the catches

The centre of gravity of the catches can be regarded as a spatial mean (a centroid), representing the weighted mean position of all catches for a specific time period, with minor and major axes given by the variance of those catches or their spatial dispersion (Bez and Rivoirard, 2000). The centre of gravity of the catch has been shown to be useful in the southern Benguela system for assessing the distribution of purse seine fishing effort, and could be used by managers and operators to determine the relative cost (in terms of fuel, distance to factories, etc.) of harvesting the sardine resource (Fairweather et al., 2006).

Discards:landings ratio

By-catch and discarding are major components of the impact of fisheries on marine ecosystems (Alverson et al., 1994). Discards, are a portion of the catch returned to the sea as a result of economic, legal, or personal considerations (Alverson et al., 1994) and they are a measure of ecological waste in a fishery. Harrington et al. (2005) reported an overall discards:landings ratio of 0.28 for the USA and stated that this is one of the highest in the world. However, the authors reported that some regional fisheries can reach even higher discard:landing ratios, e.g., southeast USA (0.59), highly migratory species fisheries USA (0.52) and the northeast USA fisheries (0.49).

On the other hand, the Alaskan and west coast USA fisheries had lowest ratios of 0.12 and 0.15, respectively. Shrimp fisheries in the southeast USA were major contributors to the high discard rate in that region, with discard ratios of 4.56 (Gulf of Mexico) and 2.95 (south Atlantic).

Reference points for indicators based on catches

Rather than relying only on reference points, trends in indicators based on catches should provide early warnings of changes in the system that can be corroborated using indicators based on biomass. The centre of gravity of the catches could help in identifying the need for spatial management, while the discards:landings ratio would indicate success in reducing waste and by-catch.

B.2. Indicators based on mortality

Mortality is one of the main factors influencing the dynamics of a population (Ricker, 1974). Total mortality (Z) is normally split into natural (M) and fishing mortality (F). M includes deaths caused by predation (M2) and "other mortalities" (M0) such as diseases, senescence, etc. In unexploited populations Z equals M, whereas retained species (target and by-catch) are additionally affected by F.

Total mortality (Z)

Die and Caddy (1997) suggest that Z is a robust indicator of exploited populations since it has a clear meaning and the effects of fishing on it are predictable (Rochet and Trenkel, 2003). Although reference points for Z can be set, which is another positive aspect for this indicator, changes in Z are not exclusive of fishing impacts. A suitable estimate of Z can be obtained using the expression developed by Beverton and Holt (1957).

$$Z = \frac{\left(L_\infty - \overline{L}\right)K}{\overline{L} - L_c} \tag{6.1}$$

where K and L_∞ are the von Bertalanffy parameters of the species, $\overline{L}$ is the average length of fish in the catch, and L_c is the size at first capture.

Fishing mortality (F)

Management is generally based on reference points for F, e.g., the F value necessary to keep the spawning stock biomass at a particular level of productivity. Some of these are F_{MSY} that produces the maximum sustainable yield (MSY), $F_{10\%epr}$ that produces 10% of the eggs that a non-fished population will produce, and F_{MEY} that produces the maximum economic yield.

Natural and predation mortality (M and M2)

Understanding the patterns of natural mortality is essential to improve models of population dynamics and stock assessment procedures. A large part of the variability in year-class strength can be associated with variable natural mortality rates during the juvenile stages (deBarros and Toresen, 1998). Although M2 has been demonstrated to be a significant, if not the most important, cause of mortality in many populations (Bax, 1992; 1998), stock models normally assume that its impact is less important than fishing mortality (Sissenwine and Daan, 1991), probably because M0 and M2 are not accurately known. Some whole ecosystem (Ecopath with Ecosim), multiespecies (multispecies virtual population analysis), minimum realistic models and extended single-species analysis are able to estimate values for M2. Some of them have been brought as input in single-species models, see Plagányi (2007) for a review of methods.

Exploitation rate (E=F/Z)

To avoid overfishing, management aims to maintain spawning stock biomass at levels that do not compromise long-term productive capacity (Patterson, 1992; Trenkel and Rochet, 2003). The exploitation rate is defined as the proportion of total mortality caused by fishing, e.g., F/Z (Baranov, 1918). Therefore, E is a measure of fishing intensity and maintaining E in a range of appropriate values is useful in securing a stable spawner-stock biomass (Patterson, 1992).

Limit reference points for indicators based on mortalities

Die and Caddy (1997) propose a limit reference point based on Z defined by the following inequality or limit:

$$Z_{Lim} < K\left[\frac{(L_{\infty} - Lm)}{(Lm - Lc)}\right] \tag{6.2}$$

where L_{∞} and K are parameters of the von Bertalanffy growth equation, Lm is the mean length at maturity and Lc is the mean length at first catch. This limit reference point seeks to ensure individuals a 50% chance of spawning at least once in their lifetime.

Long-term management targets are inappropriate for small pelagic fish because they do not take into account potential stock collapses due to a impaired stock-recruit relationship at low biomasses (i.e, based on MSY, F_{max} or $F_{0.1}$) or they are too demanding on data (F_{med} and F_{high}) (Patterson, 1992). The latter author used a simple model approach fitting fisheries models to medium-length time series of exploited small pelagic fisheries (28 stocks and 11 species). It related changes in stock biomass to exploitation rate, and used this to estimate likelihoods of stock decreases at different exploitation rates (Patterson, 1992). The pelagic stocks included in the model appeared to reach equilibrium at an exploitation rate E=0.4, which can be used as an appropriate target reference point for the sustainable exploitation of (pelagic) fish stocks. Among modelled pelagic stocks, three are typical of upwelling ecosystems, i.e., Pacific sardine (*Sardinops sagax*), anchovy (*Engraulis encrassicolus*) and Peruvian anchovy (*E. ringens*). Therefore, this estimate of exploitation rate is suitable for upwelling systems.

Alverson and Pereyra (1969) proposed a value of E=0.5 as a target reference point, on the basis of production models approaching F_{MSY}. Clark (1991) found that in most of the cases where F_{MSY} was estimated, the target E based on life history parameters tended to be close to M.

Mertz and Myers (1998) discuss some patterns in E of fish stocks from different taxonomic groups and geographic regions. Piscivorous fish species exhibited E ≈ 0.8, while planktivorous prey species (with characteristically high natural mortality rates) had E ≈ 0.5. Although no mention is giving about the status of analyzed pelagic species, ground fish stocks were considered overexploited (Mertz and Myers, 1998).

The less conservative value of E = 0.5 identified by Mertz and Myers (1998) and supported by Trenkel and Rochet (2003) can be considered as default limit reference point for all fish in general.

Fig. 6.3 shows the exploitation rate for important fish stocks calculated from mass-balanced models representing the southern Benguela, the northern Benguela and the southern Humboldt off central Chile for different periods of time. In the southern Benguela, E has been far below the limit E=0.5 (Shannon et al in press; Fairweather et al., 2006). In general, the highest E in the different stocks was found in the model representing the 1980s and the lowest in the most recent model. In the northern Benguela, although E was high in all stocks during the 1980s and after 1995, E never exceeded the limit reference point of 0.5. In the southern Humboldt, E values were high during 1992 and 1980 for all stocks. The exception was hake in which E was largest during 2004. E exceeded the target reference point of 0.4 and even the limit reference point of 0.5 in anchovy (1992), hake (1992 and 2004) and horse mackerel (1992).

B.3. Trophodynamics

Trophodynamic indicators reflect many food web characteristics and ecological processes, e.g., community structure, pathways of energy flow and trophic transfer efficiency, among others. In addition, they quantify the strength of predator-prey interactions as well as potential competitive interactions. Most importantly, they can track how fishing alters these processes (Cury et al., 2005a).

Consumption of predators (or the sum of removal by all predators) compared to fishing removal

The amount of biomass removed of a target species reflects how energy is re-distributed in a food web, particularly when compared to how much of the same species is consumed within the system (Overholz et al., 2000). Link (2005) pointed out that the indicator of total fish biomass consumed by all species within the food web ($B_{\text{sum consumers}}$) relative to total biomass removals (all species) by fisheries (landings, by-catch, discards, etc.; B_{removed}) should provide a useful assessment of how much energy is being used within the system relative to how much is being sequestered by fishing.

Following Link (2005) the LRP is set at $B_{\text{removed}}=B_{\text{sum consumers}}$. The rational of this limit reference point is that if fishing sequesters more biomass than the totality of consumers, then populations of dependent predators may be at risk.

Mean trophic level of the catch (TLm)

This indicator tracks the process known as fishing down the food web (Pauly et al., 1998a). No base-line value for this indicator can be identified since in the absence of fishing (pristine state) the indicator is not defined (division by zero). It has been suggested that a threshold of decrease should be 25% below the mean in the time series, with a limit reference point of 50% of the mean in the time series (Link, 2005). Cury and Shannon (2004) and Tudela et al. (2005) pointed out that high trophic levels of the catch is not necessarily “healthy” since they could represent the starting point of the fishery, when the catch is dominated by species with high trophic level, or a highly disturbed system where small pelagics have collapsed. Therefore, it is proposed here that TLm should exhibit also a limit reference point of TLm=50% above the mean TLm in the time series.

From the time series of TLm in Chile (Fig. 6.4) it was found that the average TLm was 3.1 (and 2.89 when horse mackerel was not included in the calculation). Data from Shannon et al (in press), indicate that the average TLm was 3.61 for the southern Benguela and 3.39 for the northern Benguela (Fig. 6.4).

Fisheries-in-balance index (FiB)

The FiB (Pauly et al., 2000) indicates whether changes in landings are consistent with the productivity of the species being fished according to their trophic level. A shortcoming of this indicator is that it depends on trophic level and the catch in a reference year. This indicator: a) remains constant (FiB=0) if TLm changes are matched by "ecologically correct" changes in catches, b) increases (FiB>0) if either bottom-up effect or a geographic expansion of the fisheries occur, and c) decreases (FiB<0) if the fisheries withdraw less biomass than expected from more productive lower trophic levels. Therefore, the limit reference point for this indicator is $\text{FiB}_{\text{Limit}} < 0$. In Chile, the FiB index has been in steep decline since the mid-1990 (all landed species) and the mid 1980s (without horse mackerel). However, the limit reference point has not being exceeded (Chapter 5, Fig. 5.6)

Primary production required to sustain the catch and consumers

These indicators assume that primary production values (PP) are available (either from remote sensing and/or in situ measurements). Pauly and Christensen (1995) estimated the global average primary production required to sustain the catches (PPR_C) to be 8%. The average PPR in upwelling systems is higher than the global, i.e., 25.1%, ranging from 17.8% to 47.9%. Following the criteria for the biomass of exploited stocks compared to the biomass removed by predators, the following reference point is proposed:

The limit reference point for this indicator could be set as $\text{PPR}_{\text{lim}} = \text{PPR}_C = \text{PPR}_Q$.

Where PPR_C corresponds to the primary production required to sustain the landings and PPP_Q corresponds to the primary production required to sustain the consumption by predators. In Chapter 5 we have seen that the PPR_C in central Chile increased strongly from early 1980s to mid 1990s decreasing in more recent years (Fig. 5.6). Future research should analyse changes in PPR_Q during the same period.

B.4. Size-based spectra

In the ocean, many processes are size-dependent, e.g., consumption, production, turnover rate and predation, among others. Size-based indicators have been widely proposed as population/ecosystem indicators and the evidence indicates that increasing fishing pressure will generally result in a population dominated by smaller individuals (Shin et al., 2005).

Population level: Length-at-50% of maturity

The mean length of the catch ($\bar{L}$) is a precise indicator with good statistical power and, therefore, an accurate indicator of change in population structure (Trenkel and Rochet, 2003). Although the change in $\bar{L}$ might be due to environmental effects it would still provide insight into the population structure (Patterson, 1992). Trenkel and Rochet (2003) suggest that length-at-50% maturity (L_{50}) in a catch/survey should be a target reference point, ensuring that at least half the individuals will have the chance to contribute to reproduction. Caddy and Mahon (1995) also suggest $\bar{L} > L_{50}$ as threshold reference point, but add the requirement of relating it to a target percentage spawning stock biomass which would depend on natural mortality. Jennings and Dulvy (2005) suggest reference points that could be adjusted annually, because fluctuations in the environment will influence the size composition of an exploited population.

As fish populations respond to increasing fishing mortality by growing faster, maturing earlier and increasing their fecundity (Ware, 1985; Rijnsdorp, 1994; Trippel, 1995; Rochet, 1998, Rochet, 2000), the length at 50% maturity (L_{50}) (normally defined as the length-class at which 50% of female fish sampled are sexually mature), is a good indicator. In Chapter 5 we have seen how the mean size of main target species (horse mackerel, Chilean hake, anchovy and Araucanian herring) has decreased in the last decade (Fig. 5. 2).

Fairweather et al (2006) found a positive correlation between population size and L_{50} for sardine in the Southern Benguela System. The authors concluded that if L_{50} is decreasing, population size is decreasing and thus the population's viability might be negatively affected and fishing effort and catches might need to be reduced.

Community level

In terms of the community size spectrum, modelling results have been shown that the slope and height are responsive to fishing while the intercept is responsive to system productivity (Maury et al., 2007). Link (2005) proposed a limit reference point to be an increase in the slope of 10% per year (which corresponds to the maximum slope observed after a period of intense fishing in the Northeast U.S.A. large marine ecosystem, Methratta and Link, 2006).

B.5. Biomass of gelatinous zooplankton

Although this indicator falls within the indicators for biomass discussed previously, it is treated separately here because changes (particularly increases) in gelatinous zooplankton can indicate trophic cascades and regime shifts induced by fishing. It has been shown that fishery-induced regime shift, such as those documented in the northern Benguela (Cury and Shannon, 2004) and the Black Sea (Daskalov, 2002; Daskalov et al., 2007), were characterized by a decrease in small pelagics and associated with an increase in the biomass of local or invasive species of gelatinous zooplankton. In support to these observations, trophic modelling exercises conducted by Shannon et al. (in press) indicate that overexploiting small pelagic fish in different food web models may lead to increases of different magnitudes in gelatinous zooplankton biomass.

Limit Reference point

The LRP for this indicator can be set in 200% increase relative to average jellyfish biomass or volume in a time series (Link, 2005). This is based in that jellyfish blooms are associated with ecosystem perturbations such as overfishing, eutrophication and climate change. As a result, jellyfish blooms can affect fish populations for long periods. All these perturbations noticeably alter ecosystem structure. The biomass of jellyfishes and the ratio jellyfish:zooplankton in several Ecopath models in Table 6.1

are shown in Fig. 6.5. The Namibia model has the greatest values of the jellies biomass and jellies: zooplankton ratio. Compared to Namibia, the Chilean, Peruvian and South African systems seem to have lower biomass of jellyfish. However, it must be pointed out that this are Ecopath outputs rather than observations and more detailed data are needed to further intra- and inter-system comparisons.

Discussion

The advantages and disadvantages of each objective, indicator and reference point are given in the previous sections. Some indicators and their corresponding limit reference point are summarized in Table 6.3. It can be seen that many limit reference points (both at the population and community) have been exceeded in the upwelling system of central Chile.

In terms of biomass indicators, the limit reference point has been exceeded in horse mackerel, Chilean hake and red squat lobster. The conservation status of many species is poorly known and research should be directed to evaluate how many populations are at risk, vulnerable of endangered and whether these categories are increasing. The biomass ratio among feeding guilds may have exceeded the limit since they present in the current state the highest values for the periods considered (Fig. 6.1). In terms of mortality indicators, the exploitation rate E was exceeded in the main stocks in the system during the1990s. Currently $E > E_{Lim} = 0.5$ only in Chilean hake and rebuilding management actions are needed in this stock.

Regarding the situation of trophodynamic indicators, fishing is likely removing more than overall predator consumption and management action should be directed to allow more biomass of fish in the sea to be available to predators, i.e., forage species management. TLm and FiB have not being exceeded but are decreasing.

Size based indicators (L_{50} and the slope of the size spectrum) have not being evaluated. However, in Chapter 5 we have seen that the mean size of horse mackerel, hake and anchovy have been decreasing in the last decade (Fig. 5.1b). Furthermore, the weighted length at maturity has also decreased (Fig. 5.5), suggesting that the size spectrum of the exploited community may have been affected, i.e., an increase in its slope.

The biomass of jellyfish in central Chile is lower than the extreme values found in the Namibian system. However, as already mentioned, these are model outputs and observations are needed before arriving to meaningful comparisons.

Overall, many limit reference points might have been exceeded in the system and a more holistic management seems to be needed to secure stock and ecosystem sustainability, rising concern on i) the possibility that the system is approaching a fishing-induced regime shift and ii) the reversibility of such a change.

Indicators and reference points in a strategic ecosystem approach to fisheries management.

Any management plan requires the definition of what is expected to be accomplished or what needs to be avoided. The broad objective of improving/maintaining both ecosystem and human wellbeing demonstrate that the ecosystem approach to fisheries is not about managing or manipulating ecosystem processes, which is clearly beyond current, and maybe future, human capacity. Instead, ecosystem-based management is concerned with ensuring that fishery management decisions do not adversely affect ecosystem function and productivity. Thus, harvesting of target stocks and resultant economic and social benefits should be sustainable in the long-term (Garcia et al., 2003).

Traditional systems of fisheries management have not, and may never, meet long-term sustainability objectives since they are intrinsically “target resource oriented” (Garcia et al., 2003). This “myopic” approach (Walters and Martell, 2004) has contributed to a situation of pervasive degraded fisheries worldwide, which is threatening current and future human and ecosystem wellbeing (Jackson et al., 2001; Worm et al., 2006).

The goal of sustainable fisheries is different from, and in some cases incompatible with, the goal of maintaining natural marine communities (Zabel et al., 2003). It is well known that sustainable fishing will inevitably decrease the abundance of target populations well below their pristine levels. The ecosystem consideration comes into play when these changes lead to community shifts in systems where exploited populations have strong influences on the population dynamics of their prey, predators or both, such as occurs in cod (top-down) or small pelagic fish (wasp-waist) dominated systems, such as ecosystems off the east coast of Canada and the upwelling system off Namibia, respectively, and maybe central Chile (see Chapters 3 and 4).

The ecosystem approach to fisheries must avoid unsustainable fishing and environmentally unfriendly practices leading to irreversible shifts towards less productive ecosystems. In this sense, the ecosystem risk assessment methodology (Fletcher, 2005) is an important step towards identifying problems or issues pertaining to each fishery operating in the study area, proposing ways in which these issues can be addressed, and seeking some degree of consensus among stakeholders in the process (Shannon et al., 2006).

The present review supports the point made by Frid et al. (2006) that the required scientific inputs to implement the ecosystem approach to fisheries are much wider than those of traditional fishery science. Ecosystem-based objectives are needed in fisheries management because the increasing impacts of fishing on ecosystems indicates that the cost of mismanaging a community might be far greater than the cost of mismanaging a single fishery. As already discussed, despite the fact that no strong depensation effect has been found yet in overexploited stocks (e.g., evidence supporting reversibility of overfishing), recovery after overfishing is low or nonexistent even in the absence of fishing. Therefore, rebuilding communities from changed states can be complex, expensive and not necessarily successful. Such potential impacts are rarely considered in cost-benefit or risk analyses.

Jennings and Dulvy (2005) and Trenkel et al. (2007) argue that knowledge of the direction of trends in ecological indicators (specifically in size-based indicators) can be sufficient to support the management decision-making process. This means that there may be no absolute need to identify reference points for the same indicators (Jennings and Dulvy, 2005). However, as mentioned before, in some indicators both increasing and decreasing trends can mean undesirable states. For example, if we consider the traditional interpretation of the mean trophic level of the catch, a decrease should be regarded as a deteriorating ecosystem condition, while an increase is regarded as improving ecosystem condition. However, as seen in the Namibian system, an increase in TLm indicates a changed system where small pelagic fish are overexploited (Cury et al., 2005a; Shannon et al., in press). The fact that TLm can have this ambiguous interpretation does not necessarily discard it as suitable indicator. By the contrary, it may well mean that a more comprehensive understanding of the changes in the system trophodynamics is needed. On the other hand, ecosystem processes are slow, and it is possible that, due to pressures from different stakeholders, reversing a trend may be difficult unless stakeholders know how far/close the system is from a limit reference point.

The structure of exploited fish communities in many ecosystems is currently driven by fishing intensities that have reduced a number of target populations to levels below sustainability (FAO, 2003). Giving the later and in the light of the shifting baselines syndrome in fisheries (Pauly, 1995), analysing current trends may not be the best reference since it ignores the fact that ecosystems have been long exploited; a base line is needed.

In this chapter, a set of general principles and conceptual objectives for an ecosystem approach to fisheries have been discussed. They are derived basically from high-level policy agreements (albeit not always compulsory) which can be regarded as a basis from which to develop more specific national policies. We have seen also how they can be translated into more operational objectives for which specific indicators and reference points are already developed or can be elaborated. It can be argued that some ecosystem-based objectives analyzed here (avoiding overfishing and ensure reversibility) are not different from single-species management objectives, although it can equally be argued that any similarity between the two approaches requires similar definitions of “overfishing” and “reversibility”. It must be noted that the ecosystem approach to fisheries is not about replacing single-species with ecosystem/multiespecies objectives, but combining tactical year-to-year management and strategic long-term management. Therefore, conservative single-species objectives are and will continue to be important parts of the ecosystem approach to fisheries. This framework is important and necessary to develop a strong link between the selected objectives and a formal and continuous assessment of the performance achieved (Sainsbury and Sumaila, 2003). Operational objectives related to ecosystem wellbeing must therefore be set in relation to the elements that, jointly, will contribute to maintain the ecosystem function and productivity, then securing sustainability of ecosystem goods (e.g. food) and services.

Control rules: Can we invoke something else besides effort reduction?

This chapter concludes by briefly discussing alternative ecosystem-based control rules triggered when limit reference points are exceeded. However, as they are not fully developed and specific, they could be also regarded as management guidelines. Basically the question is: Is decreasing fishing effort everything?

Link (2005) proposed a series of ecosystem-based rules related to exceeding limit reference points in some indicators. However, they all point to the same response: decrease fishing effort. Frid et al. (2006) discuss fishing effects on physical habitat, proposing that the damaging activity should be removed from the sensitive area. Basically this is done by creating marine protected areas. Under the arguments of how much area should be protected, the IUCN guidelines suggest 20-30% of each habitat type to be strictly protected. There are disagreements about the size and number of protected areas, but the basic idea is that the set area must be large enough to maintain viable populations at all trophic levels.

Effort reduction is an effective measure against overfishing, but it cannot protect all ecosystem attributes that are in jeopardy. Although objectives, indicators, and reference points presented in this chapter are related to the effects of fishing on ecosystems, especially in systems like the Humboldt upwelling system where environmental drivers are important in determining ecosystem dynamics, ecosystem management and control rules need to be analyzed in three main dimensions: stocks, “ecosystems” and the climate.

This is used as a framework to discuss control rules in the dimensions in which they should be applied (Fig. 6.6). Possible scenarios are shown in which the three main dimensions (stocks, ecosystems, and environment) are split into favorable (improving, represented by +), status quo (represented by 0), and unfavorable (deteriorating, represented by -). A simple scale of colors is also used to illustrate favorable (green) to unfavorable conditions (red) combinations of scenarios. Cells are colored differently to highlight that the overall situation is less favorable as we move rightward and downward.

The first three rows indicate healthy conditions for exploited stocks under various levels of ecosystem status and environmental conditions. As can be seen, the situations range from an ideal state for stocks and the ecosystem in favorable environmental conditions (cell + + +) to situations of decreasing ecosystem status and unfavorable environmental conditions (cell + - -). In these cells, single species objectives are met, but cautions should be exercised for ecosystem objectives and recovery objectives should be directed to improving the deteriorating state of other ecosystem components (allow reversibility of changes and maintain ecosystem structure) in a framework of constant monitoring of environmental conditions.

The following three rows represent situations in which exploited stocks are in *status quo* and ecosystem status and environmental conditions vary as in the previous example. Ecosystem indicators show an improvement in general ecosystem status in a steady environment. In these combinations of scenarios, management should aim at avoiding overfishing in stocks and reducing deterioration of other ecosystem components. These combinations are more than early warning and management should aim allow recovery and secure reversibility of fishing impacts.

The last three rows represent deteriorating state of exploited stocks with different levels of ecosystem status and environmental conditions. The combinations range from a situation where stocks are deteriorating, but ecosystem status is improving with favorable environmental conditions (- + +) to deteriorated stocks and ecosystem in a non-favorable environment (- - -). All this combinations represent a red alarm for management and decreasing fishing pressure on deteriorating stocks, setting recovery periods for stocks and conservation objectives set on other ecosystem components. The last cell (- - -) represents the worst combination and both single-species and ecosystem considerations have failed. As precautionary approach is one of the objectives of the overall system, action should take place before this cell is reached. Alternative control rules should be to stop fishing by banning the fisheries, establishing marine protected areas and/or a combination of them.

The time scales on which assessments of target populations and their communities are conducted should be consistent with the statistical power of the surveys to provide information on trends. Managers risk squandering credibility and resources if they respond to noise rather than to signal. The main goals for single species management are to i) secure sustainability and ii) avoid overfishing. Likewise, it is possible to argue that the main goals of EAF are i) maintain and/or rebuild ecosystems and ii) avoid irreversible changes to ecosystems. Provided that EAF goals are met, then potential trade-offs between different ecosystem configurations that meet both ecosystem wellbeing as well as human wellbeing should be defined as to be used in a decision analysis process.

Table 6.1. Trophic models used to compare trophodynamic indicators in upwelling systems.

Upwelling system	**Period represented**	**Reference**
Southern Humboldt (central Chile)	<1900: Close to pristine conditions before industrial fishing. 22 compartments.	See Chapter 2
	1992: Fully exploited condition. 22 compartments.	Neira and Arancibia (2004)
	>2000: A period following several stock collapses. 22 compartments.	See Chapter 2
Northern Humboldt (Peru)	1973-1981: a period following the collapse of the huge anchoveta (*Engraulis ringens*) fishery and during which the biomass of sardine (*Sardinops sagax*) was increasing. The period did not include major El Niño events. The model considers 27 compartments.	Moloney et al. (2005) based on Jarre et al. (1998)
Southern Benguela (South Africa)	1980s: a period with anchovy (*Engraulis encrasicolus*) dominating over sardine (*Sardinops sagax*). This is a period when many of the directed ecological studies were conducted in the southern Benguela, so data quality is high. The model considers 27 compartments.	Moloney et al. (2005) based on Shannon et al. (2003)
Northern Benguela (Namibia)	1995-2000: a period in which the system was dominated by pelagic gobies (*Sufflogobius bibarbatus*), jelly fish and horse mackerel (*Trachurus trachurus campensis*). The model considers 27 compartments.	Moloney et al. (2005) based on Roux (unpublished data)

Table 6.2. Different objectives for ecosystem-based management.

Grumbine (1994)	Slocombe (1998)	Ward et al. (2002)	FAO (2003)
Maintain viable populations of all native species in situ	Develop consensus	Monitor the "natural" structure and function of ecosystems including the biodiversity and production of natural systems and identified important species, is the focus of management	Avoid overfishing
Represent, within protected areas, all native ecosystems types across their natural range of variation	Develop understanding of the ecosystem	Consider human use and values of ecosystems are central to establishing objectives for use and management of natural resources	Ensure reversibility of impacts and rebuild
Maintain evolutionary and ecological processes (i.e., disturbance regimes, hydrological processes, nutrient cycles, etc.)	Implement a framework for planning and management	Acknowledge that ecosystems are dynamic; their attributes and boundaries are constantly changing and consequently interactions with human uses are also dynamic	Minimize fishing impacts
Manage over periods of time long enough to maintain the evolutionary potential of species and ecosystems	Make a difference	Manage natural resources are best within a management system that is based on a shared vision and a set of objectives developed among stakeholders	Consider (maintain) species interactions
			Apply precautionary approach
Accommodate human use and occupancy within this constraints		Use adaptive management based on scientific knowledge, continued learning and monitoring processes	Maintain ecosystem integrity

Table 6.3. State of Chilean system based on indicators and limit reference points discussed in Chapter 5 and Chapter 6. Key: $\sum Q_{Predators}$=sum of predator consumption; $\sum Q_{Fisheries}$=sum of fisheries removal; TLm=mean trophic level of the catch; FiB=Fisheries-in-balance indicator; PPR_C= Primary production required to sustain fisheries; PPR_Q=Primary production required to sustain consumption of predators; L_{50} =Length-at-50% of maturity; $B_{jellies}$=Biomass of gelatinous zooplankton.

Indicator	Limit reference point	Situation in Central Chile	Comments
Biomass (B)			
a. B target species	20% of stock biomass in the absence of fishing or in the pristine stage	Exceeded in some species	Hake, horse mackerel, red squat lobster (see Chapter 5, Fig. 5.2)
b. B non-target species	IUCN categories	Not yet evaluated	No assessments of the conservation status
c. B feeding guilds	50% of the highest observed value	Likely exceeded	The highest value observed for small pelagic:demersal, pelagic:demersal, small pelagic:top predators and pelagic to predators are observed in the more recent models (this chapter, Fig. 6.1)
Mortalities			
Exploitation rate	0.5 (default all fish species)	Exceeded in the 1990s	Currently exceeded only in Chilean hake (this chapter, Fig. 6.3)
Trophodynamics			
$\sum Q_{Predators}$ vs $\sum Q_{Fisheries}$	$\sum Q_{Predators} = \sum Q_{Fisheries}$	Likely exceeded	The fisheries are removing the most of the production of the main stocks (see Chapter 2; Fig. 2.4)
TLm	+/- 50% of the mean in a time series	Not exceeded	But decreasing (see Chapter 5; Fig. 5.6)
FiB	FiB<0	Not exceeded	But declining (see Chapter 5; Fig. 5.6)
Size-based			
L_{50}	$\overline{L} = L_{50}$	Not evaluated	However, the average size of important stocks have decreased in last decades (see Chapter 5, Fig. 5.2b)
Slope of size spectrum	Increase in the slope in 10%	Not evaluated	The weighted Length-at-maturity has of the exploited community decreased (see Chapter 5, Fig. 5.5)
$B_{jellies}$ and $V_{jellies}$	50% increase in average $B_{jellies}$ or $V_{jellies}$	Not exceeded	However, this is Ecopath output.

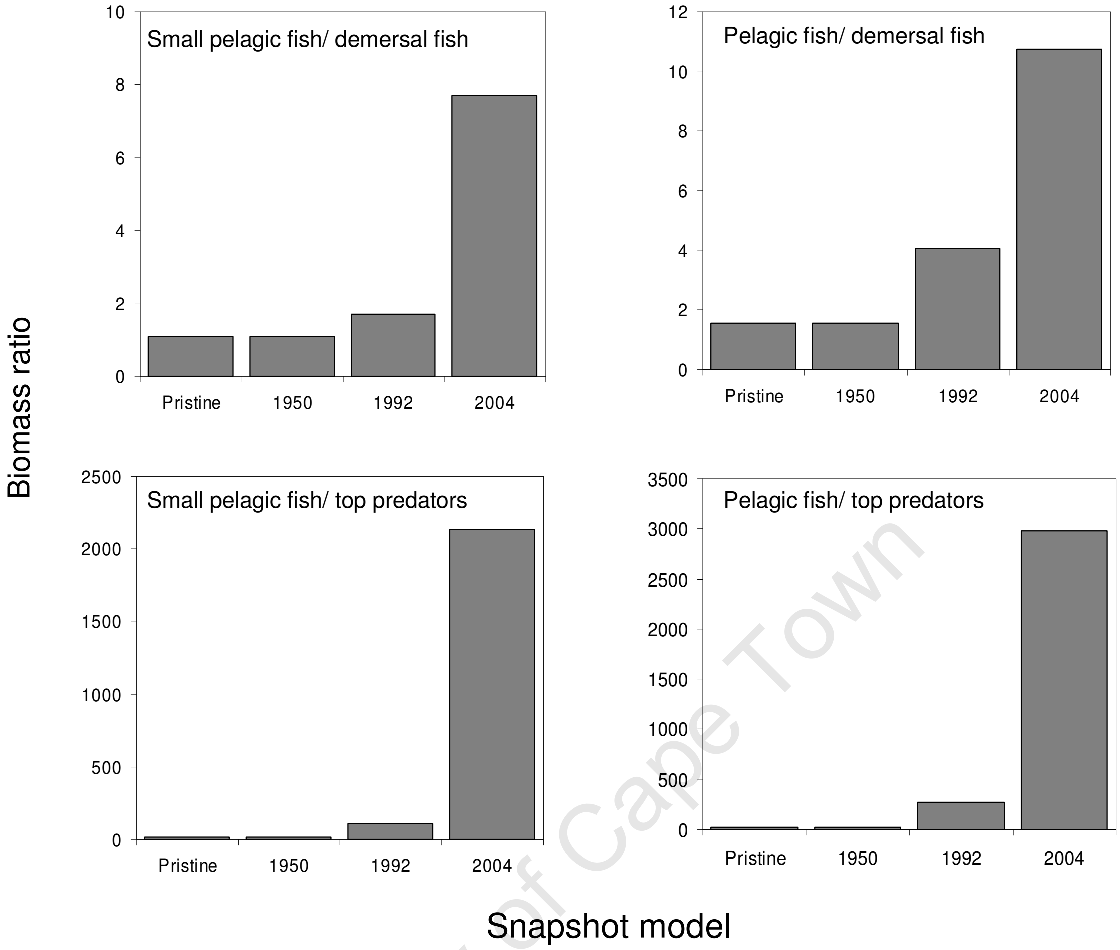


Figure 6.1. Biomass ratios among functional groups from four snapshots models representing the southern Humboldt marine system off central Chile.

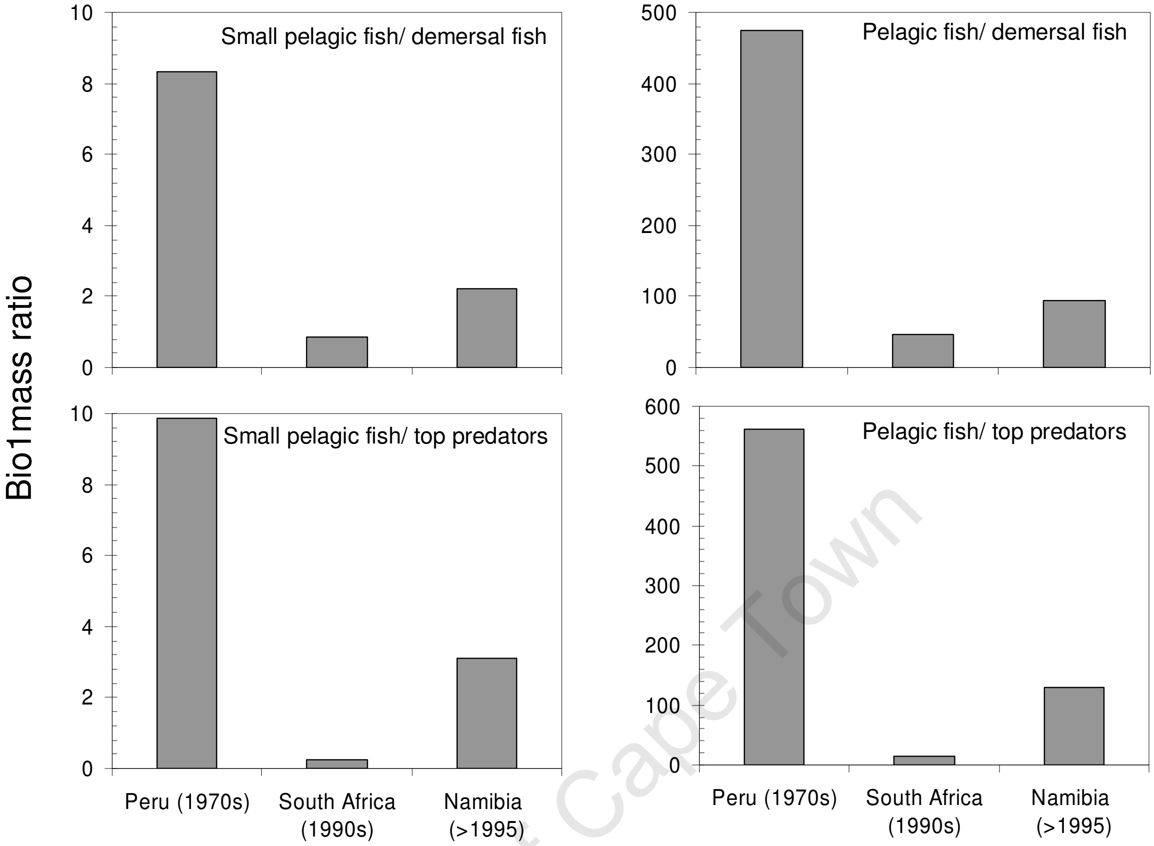


Figure 6.2. Biomass ratios among functional groups in three snapshots models representing the Peruvian system in the 1970s, the southern Benguela Current System off South Africa in the 1990s, and the northern Benguela Current System off Namibia in >1995.

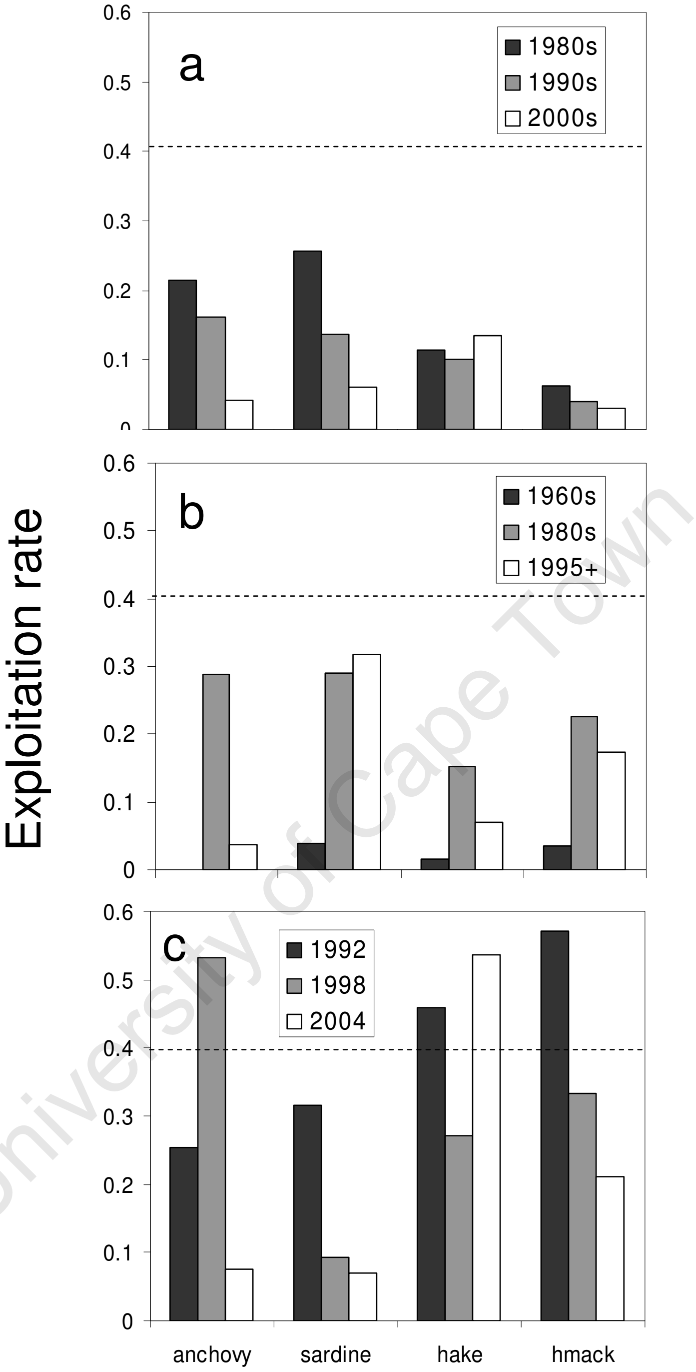


Figure. 6.3. Exploitation rate (F/Z) for important stocks calculated from mass-balanced models representing different time periods in a) southern Benguela System, b) northern Benguela System, and c) central Chile. Horizontal dotted line=Target reference point.

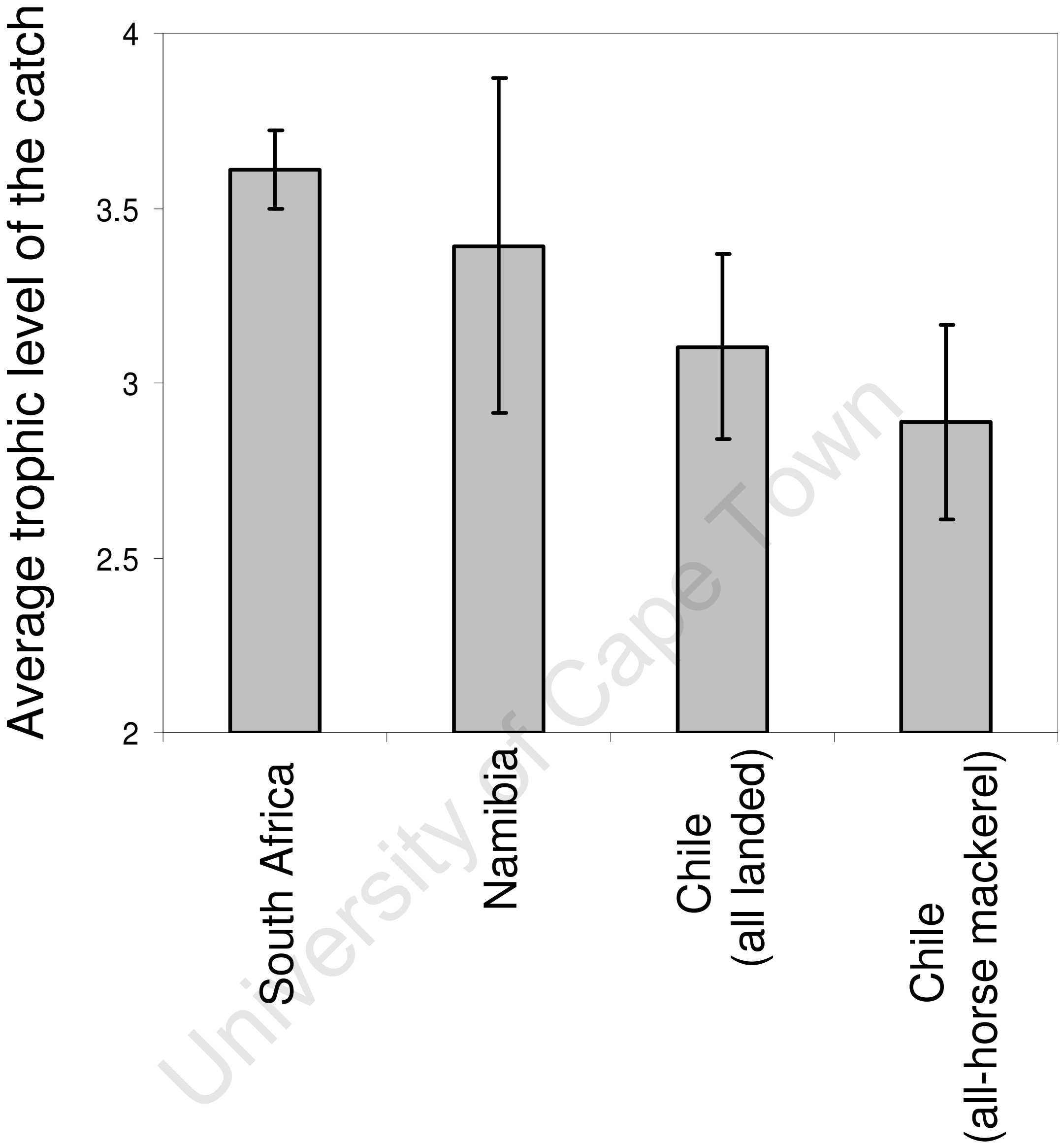


Figure 6.4. Average trophic level of the catch in three upwelling ecosystems. Bars represent +/- one standard deviation from the mean.

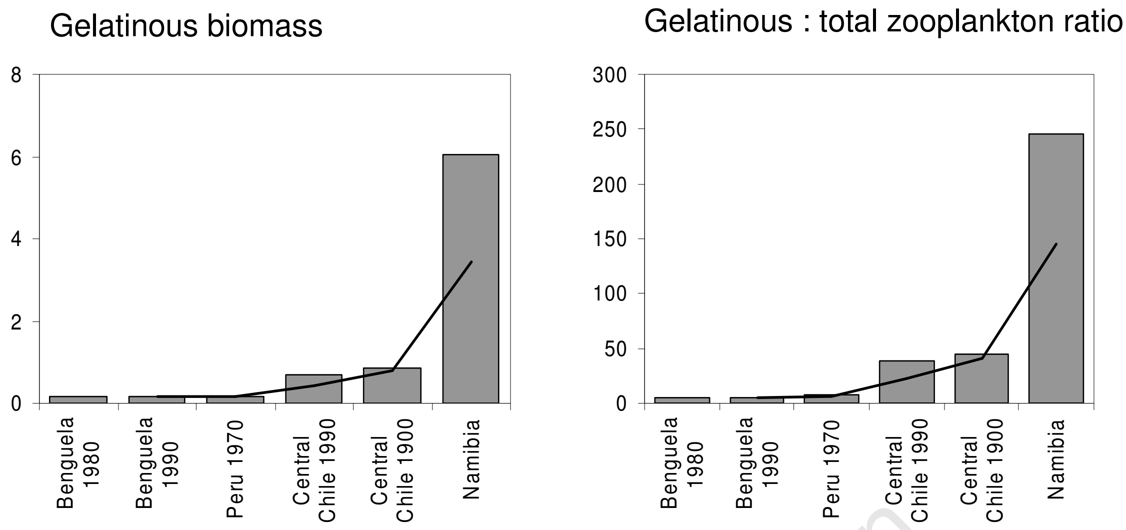
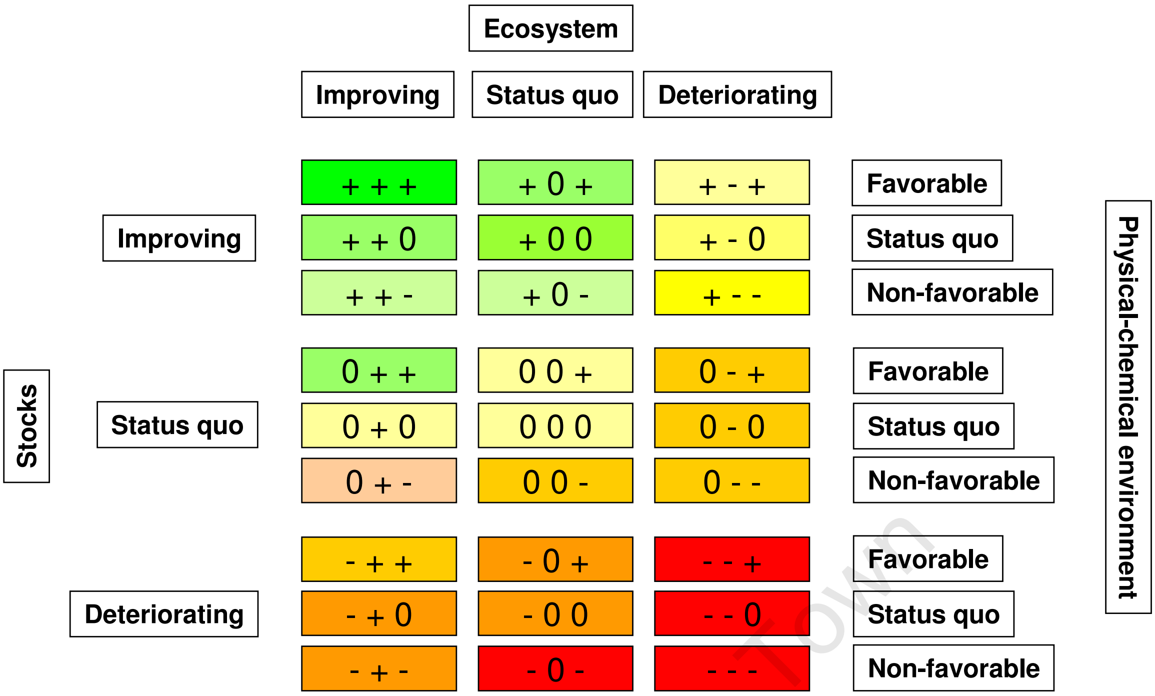


Figure 6.5. Biomass of gelatinous plankton and biomass of gelatinous plankton:crustacean zooplankton in snapshot food web models representing four upwelling ecosystems in different time periods.



	Ecosystem			
Stocks	Improving	Status quo	Deteriorating	Physical-chemical environment
Improving	+ + +	+ 0 +	+ - +	Favorable
	+ + 0	+ 0 0	+ - 0	Status quo
	+ + -	+ 0 -	+ - -	Non-favorable
Status quo	0 + +	0 0 +	0 - +	Favorable
	0 + 0	0 0 0	0 - 0	Status quo
	0 + -	0 0 -	0 - -	Non-favorable
Deteriorating	- + +	- 0 +	- - +	Favorable
	- + 0	- 0 0	- - 0	Status quo
	- + -	- 0 -	- - -	Non-favorable

Figure 6.6. Combinations of stock, ecosystem and environment states that can be used to focalize research effort (improve understanding) and management actions (trigger control rules).

CHAPTER 7

MECHANISMS AFFECTING THE BEHAVIOUR OF ECOSYSTEM-BASED LIMIT REFERENCE POINTS IN AN UPWELLING FOOD WEB MODEL

Abstract

Although bottom-up forcing and overfishing are known to induce shifts on ecosystem states, system changes and their reversibility under each factor are still poorly understood. In this chapter, dynamic food web simulations are conducted to evaluate when and why ecological thresholds may be exceeded and whether bottom-up forcing or fishing are more likely to induce irreversible ecosystem states. Simulations are conducted using a calibrated food web model of the upwelling system off central Chile (33º-39ºS) and the Ecopath with Ecosim software version 5.1. The effects of fishing scenarios are explored by changing fishing mortality according to trophic level. The effects of bottom-up forcing scenarios are explored by changing phytoplankton biomass as function of sea temperature at El Niño Southern Oscillation (ENSO) and decadal scales. Simulations are carried out for 150 years and impacts, system recovery and regime shifts from each scenario are evaluated using trophodynamic indicators and limit reference points for biomass of functional groups as proxies of food web state and ecological thresholds, respectively. Equally distributed fishing along trophic levels is the least harmful fishing scenario, resulting in low biomass limit reference points exceeded and high system recovery. Concentrating fishing at higher and lower trophic levels exceeds reference points and induces ecosystem changes with low-to-medium recovery potential. No limit reference points are exceeded (or regime shift induced) under ENSO scale bottom-up forcing. Decadal scale bottom-up forcing has different effects on the system depending on the sequence in which the high and low phytoplankton biomass period is simulated. A shift from low phytoplankton biomass towards high phytoplankton biomass does not result in biomass limit reference points being exceeded, whereas the opposite sequence results in a large number of limit reference points being exceeded with medium recovery. The interplay between fishing and decadal scale bottom-up forcing indicates that bottom-up forcing can dampen the effects of fishing, whereas fishing increases the number of limits reference points exceeded and decreases the recovery observed under decadal scale bottom-up forcing. Results suggest that fishing (especially unsustainable strategies) is more likely to exceed ecological thresholds and induce regime shifts of low recovery than decadal scale bottom-up forcing.

Keywords: Ecosystem thresholds, fishing and environmental forcing, food web models, Ecopath with Ecosim, central Chile, ecosystem recovery.

Introduction

It is widely recognized that fishing, by impacting living and non-living components, results in deleterious changes in whole ecosystem structure and function (Goñi, 1998; Jennings and Kaiser, 1998; Hall, 1999). For this reason, fishing is considered the main threat to marine ecosystems (Jackson et al., 2001; Pauly et al., 2002, Worm et al., 2006). Ecosystem components, however, are also affected by environmental changes that can result in whole system alterations. Inter-annual El Niño Southern Oscillation events (ENSO), decadal shifts, and the rapid rate of global warming are among the most important environmental forcing factors affecting marine ecosystems (Timmerman et al., 1999; Easterling et al., 2000; Steele, 2004; Chavez et al., 2003). Observed patterns indicate that a significant ecosystem change in structure and function is triggered when either fishing (Cury and Shannon, 2004; Frank et al., 2005; Daskalov et al., 2007) or some environmental factor (Steele, 2004) exceed certain critical levels, i.e., an ecological threshold.

Ecosystem shifts induced by climate and fishing differ. For example, the effects of environmental change on stocks seem to be of low frequency as shown by scale depositions off the California Current System at the centennial (Holmgren and Baumgartner, 1993) and millennial scales (Finney et al., 2002). This evidence supports the hypothesis that, in the absence of fishing, fish stocks "naturally" oscillate under the effect of climate forcing. On the other hand, the decline and collapse of many fish stocks since the second half of the 20th century is related more to fishing than to any environmental factor (Christensen et al., 2003; Myers and Worm, 2003). Unlike the environment, fishing is selective and first decreases the abundance of big individuals that are normally located at high trophic levels in the food web. Therefore, fishing steadily decreases the size and trophic level of populations and marine communities, in a process known as *fishing down the food web* (Pauly et al., 1998a). Although fishing can result in a gradual transition towards communities dominated by small-sized, short-lived and high turnover rate species, overfishing can trigger drastic changes such as stock collapse and whole food web cascades (Cury and Shannon, 2004; Daskalov, 2002; Frank et al., 2005; Daskalov et al., 2007).

The increase in fish stocks observed in the North Sea after World War II, which partially inspired Beverton and Holt (1957) in the first formal description of the use of closed areas in fisheries management, resulted from the fact that productive fishing grounds were inaccessible because of the presence of mine fields. However, the slow and sometimes complete lack of recovery observed for exploited marine populations after more recent collapses (Hutchings, 2000) may indicate that fishing could have exceeded some ecological thresholds. The reversibility of these ecosystem-scale changes is still poorly known, but is of great importance for fisheries science and management due to their potential ecological, economic and social consequences (Worm et al., 2006).

There are a few clear target reference points for the ecosystem approach to fisheries. Ecological thresholds can be considered to be limit reference points because exceeding them can lead to alternate and sometimes undesired ecosystem states. However, since fishing and environmental variability operate at different rates and levels in the food web, ecosystem responses to these forcing factors are likely to differ, i.e., there are ecosystem thresholds for fishing and for environmental variability. Furthermore, due to the likely synergistic effects between fishing and environmental changes, thresholds for fishing can be affected by environmental changes, e.g., overfishing levels might differ in productive or unproductive climatic regime.

Likewise, the decline or recovery of fish stocks and communities under favourable or unfavourable environmental change can be accelerated or delayed by overfishing. For example, the stock of anchovy off Peru collapsed with no signs of recovery in the early 1970s after a rather moderate ENSO event. However, the same stock rapidly recovered after the strongest ENSO event of the century in 1997-98. This almost opposite response of anchovy can be explained by more cautious fishing taking place after the 1980s (Csirke et al., 1996) and the long term context in which both ENSO events occurred, i.e., the influence of decadal fluctuations (Chavez et al., 2003; Alheit and Ñiquen, 2004). Likewise, anchovies were "cleared" from the Namibian system to allow faster sardine recovery during the 1980s (Cury and Shannon, 2004). The anchovy stock collapsed under heavy fishing, but sardine stocks did not recover and, until today, no recovery signs are found in either of these species. In fact, the

Namibian system shifted towards a state dominated by horse mackerel and jellyfishes (Cury and Shannon, 2004; Moloney and Jarre, 2004). Frank et al. (2005) showed how overexploiting an abundant piscivorous fish of high trophic level led to a whole food web cascade. More recently, Daskalov et al. (2007) showed that the two-step trophic cascade observed in the Black Sea was initiated by overfishing marine mammals (first step) and small pelagic fish (second step), increasing system vulnerability to an invasive jellyfish species.

Studying ecosystem responses to fishing and its relationship with environmental changes is important to predict how and when ecosystems will change state, and whether these shifts (of components or of the whole food web) will be reversible. Models are an important component of any assessment of ecosystem response to changes in management and/or environmental conditions (Walters and Martell, 2004). In this chapter a series of fishing and bottom-up forcing scenarios are simulated to explore thresholds, changes of state and reversibility in a food web model representing an exploited upwelling system. A set of ecological indicators and limit reference points are used as proxies of ecosystem state and ecological thresholds, respectively.

Methods

Simulation of fishing and environmental scenarios

Simulations are conducted using a food web model that has been previously fitted to time series of biomass, catch and fishing mortality for the period 1970-2004. Model description and steps followed during the fitting process are fully described in Chapter 3. Although the Ecosim software does not include a formal sensitivity analysis, experience has shown that model results are sensitive to the vulnerability parameter "v" (see Christensen and Walters, 2004; Christensen et al., 2005). As explained in Chapter 3, the fitting process included a searching procedure to i) identify the v values to which model outputs are most sensitive (i.e., those that impact most on the sum of squares) and ii) find the vs from this subset that improve model fit (i.e., reduce the sum of squares between Ecosim predictions and observed data). The v values in the model are thus "tuned" to available data, giving results that more closely matched observed values than would a model with default or arbitrarily chosen v values.

Pre-simulation adjustments

Prior to simulations, the fitted model was run without fishing (i.e., the fishing mortality rate was set to zero for all functional groups) or bottom-up forcing (no forcing function on phytoplankton biomass) until the biomass of all model groups was stabilized. This stabilization was reached at +/- 50 years. Simulated scenarios were conducted from this point onwards for a hundred more years (referred to as the start of the simulation) using the Ecopath with Ecosim software version 5.1 (Christensen and Pauly, 1992; Walters et al., 1997; Christensen et al., 2005).

Simulating fishing forcing

Three scenarios of constant fishing mortality were simulated:

Concentrating fishing in higher trophic levels in the food web

The simulation is conducted by applying a constant fishing mortality rate to all harvestable functional groups (i.e., all functional groups that have been historically targeted by a fleet or have been part of the by-catch in some of the fisheries operating in the study area). The fishing mortality rates were directly proportional to the groups' trophic level, concentrating exploitation at the higher trophic levels of the food web (Table 7.1). The following approach was followed: A fishing mortality equal to 80% of the production: biomass ratio (P/B) was allocated to the harvestable functional group occupying the highest trophic level in the model (i.e., pelagic fish II, TL=5.15). The fishing mortality on the other harvestable functional groups was assigned directly proportional to their TL using the following equation:

$$F_i = 0.8 \times \left(\frac{P_i}{B_i} \right) \times \left(\frac{TL_i}{TL_{pelagicsII}} \right) \tag{7.1}$$

where i represents a harvestable functional group; F is the fishing mortality coefficient, P is production, B is biomass and TL is trophic level.

Concentrating fishing on lower levels of the food web

The simulation is conducted by applying a fishing mortality rate inversely proportional to the trophic level of each harvestable functional group, i.e., concentrating exploitation in low and intermediate trophic levels of the food web. The following approach was followed: a fishing mortality rate of 80% of P/B was assigned to the harvestable functional group occupying the lowest trophic level in the model (macrobenthos TL=2.0). The fishing mortality in the other functional groups was assigned inversely proportional to their TL using the following equation:

$$F_i = 0.8 \times \left(\frac{P_i}{B_i} \right) \times \left(\frac{TL_{macrobenthos}}{TL_i} \right) \qquad (7.2)$$

Distributing fishing according to production along trophic levels

This scenario mimics what could be considered an ecologically-sound fishing strategy, harvesting functional groups according to their production (Bundy et al., 2005). The simulation is conducted by applying a fishing mortality rate to all "harvestable" functional groups in accordance with their respective production:biomass ratio. In Chapter 6 it was proposed that an exploitation rate of E=F/Z=0.4 was an appropriate target reference point. Therefore, the fishing mortality for each group was calculated as:

$$F_i = 0.4 \times \left(\frac{P_i}{B_i} \right) \qquad (7.3)$$

Simulating bottom-up environmental forcing

Five scenarios representing bottom-up environmental forcing in the model, at the inter-annual and decadal scales were explored (Fig.7.1).

Inter-annual ENSO-scale events

The El Niño Southern Oscillation (ENSO) is the most important inter-annual source of variability in the Pacific Ocean and the Earth (McPhaden, 2006) including the southern Humboldt (Strub et al., 1998). Using modelling, Timmermann et al. (1999) predict an increase in both the frequency and intensity of ENSO in the eastern tropical Pacific Ocean under predicted future increases in global temperature. The ENSO cycle has a warm phase (known as El Niño) and a cold phase (known as La Niña) that have different and opposite effects, i.e., phytoplankton biomass decreases during El Niño and increases during La Niña (Watters et al., 2003). Three scenarios were tested:

(i) The model was forced from the bottom-up using a simulated time series of phytoplankton biomass that assumes the current frequency of ENSO events of 4-7 years, which roughly implies one ENSO event per decade (Fig. 7.1a).

(ii) The model was forced from the bottom-up using a simulated time series of phytoplankton biomass that assumes an increase of 100% in the frequency of ENSO events, i.e., two ENSO events per decade (Fig. 7.1b).

(iii) The model was forced from the bottom-up using a simulated time series of phytoplankton biomass that assumes one ENSO per decade, but of 50% higher intensity than scenario (i) (Fig. 7.1c).

Simulated scenarios assumed that ENSO events a) occur at equally spaced steps of time (i.e., same lags); b) have the same span, i.e., one year of a warm anomaly (El Niño) followed by one year of a cold anomaly (La Niña); and c) all have the same intensity, i.e., +/-2ºC (scenarios i and ii) and +/-3ºC (in scenario iii). This range of temperatures was chosen considering i) positive and negative anomalies found in a time series of sea surface temperature off central Chile and changes projected in the frequency and intensity of ENSO under realistic global warming projections (Timmermann et al., 1999).

Decadal shifts affecting phytoplankton biomass

Decadal changes are important features in the whole Pacific Ocean (Chavez et al., 2003) and in the southern Humboldt (Alheit and Ñiquen, 2004; Montecinos et al., 2004). Decadal changes have been related to changes in fish populations and their fisheries along the coasts of the southern Humboldt system (Yáñez et al., 1992; Cubillos et al., 2007). Decadal variability is characterized by a warm (known as El Viejo) and cold (known as La Vieja) phase, the periods of which are thought to be about 50 years (i.e., 25 years of warm conditions and 25 years of warm conditions) (Chavez et al., 2003), although there is some disagreement about the scale (Alheit and Ñiquen, 2004).

Two scenarios of decadal bottom-up forcing were simulated:

i) The model was forced from the bottom-up using a simulated time series of phytoplankton biomass that assumes 25 years of decreased phytoplankton biomass (i.e., warm conditions prevailing in the system) followed by 25 years of higher phytoplankton biomass (i.e., shift towards cooler conditions, Fig. 7.1d).

ii) The model was forced from the bottom-up using a simulated time series of phytoplankton biomass that assumes 25 years of increased phytoplankton biomass (i.e., cold conditions prevailing in the system) followed by 25 years of lower phytoplankton biomass (i.e., shift towards warmer conditions, Fig. 7.1e).

Simulated scenarios assumed that warm and cold states have the same magnitude (i.e., +-2ºC).

Physical forcing on phytoplankton biomass

The environmental forcing scenarios described above are based on the assumption that changes in sea surface temperature cause variability in the biomass of the functional group representing the phytoplankton. Following Watters et al. (2003) time series of $B_{\text{phytoplankton}}$ at time t were created with an empirical model that relates sea surface temperature with surface chlorophyll concentrations. They found that during recent warm and cold events, the log (pigment concentrations in mg·m^{-3}) in the NIÑO3 region changed by about –0.109/°C (see Table 2 in Watters et al., 2003). This model was used here to create time series of $B_{\text{phytoplankton}}$ that represent changes in sea surface temperature forcing at different scales. The model is described by the following equation:

$$B_{phytoplankton_t} = B_{phytoplankton_{t=0}} \cdot e^{(-0.109\,Xt)} \tag{7.4}$$

where $B_{\text{phytoplankton } t=0}$ is the biomass of phytoplankton in the Ecopath base model at the beginning of the simulation, and *Xt* is the anomaly in the simulated sea surface temperature at time *t.* Thus, the biomass of phytoplankton was forced to decrease during events of warm sea surface temperatures and increase during events of cold sea surface temperatures.

Biomass trajectories obtained using the above model were used to force the food web model from the bottom-up by substituting $B_{\text{phytoplankton t}}$ during simulations.

Simulating the interplay between fishing and environmental forcing

Interactions between environmental forcing and fishing were explored by combining the above described fishing and environmental scenarios. The aim was to explore whether ecologically-based limit reference points exceeded under fishing scenarios are affected by bottom-up changes and vice versa.

Indicators

Indicators and their limit reference points used in this chapter as proxies for ecosystem state and ecological thresholds respectively are shown in Table 7.2.

Assessing impacts and recovery under simulated scenarios

Fishing and environmental scenarios as well as their combinations were run for 100 years. The different fishing and bottom-up forcing scenarios were run in the first 50 years. For the last 50 years the model was run without any fishing (F=0 for all groups) or bottom-up forcing ($B_{phytoplankton}$ was set as $B_{phytoplankton}$ at the beginning of the simulation) so as to evaluate i) the impact of each scenario at the food web level, ii) the reversibility of these impacts and iii) whether induced changes fulfil the definition of true regime shifts (see below).

Assessing impacts

The impact of each scenario was evaluated as follows. At time t=50 years from the beginning of the simulation, the number of groups in which biomass decreased beyond the limit of 50% $B_{initial}$ was recorded and expressed as a percentage of the total groups in the model. This allowed the evaluation of scenarios that produced more/less negative changes in the system (i.e., limit reference points exceeded). The following scale was considered when evaluating impacts: 0-24% low impact, 25-49% medium impact, 50%-74%, high impact, and >75% extreme impact.

Assessing reversibility

Reversibility under each scenario was evaluated as follows. At time t=100 years from the beginning of the simulation, the number of groups in which/whose biomass recovered beyond the limit reference point was recorded and expressed as a percentage of all groups which biomass decreased below 50% at time t=50 years. The following scale was considered when evaluating reversibility: 0-24% poor, 25-49% low, 50-74% medium, >75% high.

Regime shift features

The biomass of trophic guilds and the biomass ratios between piscivores:planktivores and demersal:pelagic fish were used to evaluate whether simulated scenarios induced regime shifts. Criteria in Table 7.3 were used to identify whether changes induced by simulations matched or not the adopted definition of regime shift.

Results

Fishing effects

Results obtained from simulated fishing scenarios are presented in Figs. 7.2 and 7.3. Concentrating fishing in higher trophic levels resulted in 43% of biomass limit reference points being exceeded while concentrating fishing in lower trophic levels and distributing proportionally to production across trophic levels resulted in 56% and 24%, respectively (Table 7.4). In terms of recovery, concentrating fishing in higher trophic levels resulted in the lowest recovery among fishing scenarios (56%), followed by concentrating fishing in lower trophic levels (73%) and distributing fishing proportionally to production of i (80%) (Table 7.4).

Changes in the biomass of trophic guilds and the pelagic:demersal and piscivores:planktivores ratios under simulated fishing scenarios are presented in Fig. 7.3. According to the criteria considered in Table 7.3, the scenarios concentrating fishing in higher trophic levels and lower trophic levels fulfilled the considered criteria for regime shifts. The distribution of fishing according to production across trophic levels accomplished three out of four criteria, with the criterion not met being that of indicators changing beyond +/-50% of their initial value.

Bottom-up forcing at ENSO scale

Results obtained from simulated ENSO scenarios are presented in Figs. 7.4 and 7.5. Although synchronous biomass changes among functional groups are observed in all ENSO scenarios, no biomass limit reference point was exceeded (Table 7.4). In addition, regardless of the intensity or frequency of changes in phytoplankton biomass, all changes under ENSO scenarios were fully reversible (Figs 7.4 and 7.5; Table 7.4).

Changes observed under this bottom-up forcing only matched one criterion out of four considered for regime shifts, i.e., ENSO-induced changes were observed for a range of trophic levels (Fig. 7.5).

Environmental variability at decadal scale

Results from simulated decadal shifts are shown in Figs. 7.6 and 7.7. The hypothetical scenario of a low phytoplankton biomass period followed by a high phytoplankton period was beneficial and no limit reference point was exceeded or even approached. In addition, observed changes were all reversible (Table 7.4) and many groups even increased their biomass leading towards a seemingly stable regime of higher biomass by the end of the simulation (Fig. 7.6a and Fig. 7.7).

In contrast, under the hypothetical scenario of a high phytoplankton biomass period followed by a low phytoplankton biomass period many biomass limit reference points were exceeded. Changes observed under this scenario were of medium reversibility (73%) (Table 7.4). Observed changes under both decadal bottom-up forcing scenarios matched all criteria considered to characterize regime shifts (Figs. 7.6 and 7.7; Table 7.4).

Interplay between fishing and bottom-up changes at the food web level

Results of the interplay between fishing and bottom-up scenarios are presented in Fig. 7.8 and Table 7.4. Because that ENSO scale bottom-up forcing did not exceed biomass reference points or induce regime shifts, they were not included in this comparison.

When fishing scenarios were examined under the low phytoplankton biomass period followed by a high phytoplankton biomass period, results markedly differed with respect to the effects observed under the three fishing scenarios alone. Firstly, the bottom-up forcing decreased the number of limit reference points exceeded in the scenarios concentrating fishing in higher (11%) and lower trophic levels (55%), but it did not affect the number of limit reference points exceeded under the equally distributed fishing scenario. However, this sequence of bottom-up decadal forcing decreased system recovery with respect to fishing scenarios alone (Table 7.4).

The alternative decadal bottom-up forcing (high phytoplankton biomass period followed by a low phytoplankton biomass period) resulted in even more noticeable and negative effects on the system compared to the effects of fishing scenarios alone. More biomass limit reference points were exceeded, but there was improved recovery in the scenario that concentrated fishing in higher trophic levels and reduced recovery in the scenarios where fishing was concentrated in lower trophic levels and proportionally distributed fishing across trophic levels (Table 7.4).

When fishing scenarios were overlapped with the decadal scale bottom-up scenarios, more negative effects in the system were observed compared to the effects of bottom-up scenarios alone (Table 7.4). Recovery was also negatively affected (Table 7.4).

Fishing scenarios had a positive influence on the number of limit reference points exceeded when compared to the effect of the second decadal bottom-up forcing alone. The number of biomass limit reference points exceeded decreased under fishing, but system recovery was also reduced (Table 7.4).

When decadal bottom-up forcing was combined with the fishing scenarios all four criteria considered for regime shifts were met, and system recovery was reduced (Fig. 7.8; Table 7.4).

Discussion

Fishing effects

Scenarios concentrating fishing in either higher or lower trophic levels were found to be non-sustainable in the long-term. In addition, changes were found to be of low-to-medium reversibility. Specifically, concentrating fishing at higher trophic levels of the food web resulted in the collapse of exploited groups with high TL, favouring only birds, cephalopods and mesopelagic fish, which is probably the result of cascading effects. The collapse of high trophic level harvestable groups did not result in an explosive increase of species located in lower trophic levels such as small pelagic fish. In fact, the biomass of these groups declined during the first 50 years of simulation, probably due to biomass increase in predators (cephalopods and birds) and competitors (mesopelagic fish). However, the biomass of macrobenthos increased, which could be a cascading effect of the decline of Chilean hake and other demersal feeding fish. In Chapter 3 and Chapter 4 we have seen that there is evidence to support a strong top-down control of Chilean hake on red squat lobster. Worm and Myers (2003) also found this kind of top-down effect between cod and shrimps in the North West Atlantic. Overall, system recovery under this scenario was found to be low and results observed under this scenario are in accordance with what has been observed and predicted in ecosystems where previously abundant groups located at high trophic levels have been fished out (Hutchings, 2000).

From an ecosystem perspective, concentrating fishing in lower/intermediate trophic levels of the food web (i.e., forage species) is not an advisable strategy either. Although system recovery under this scenario was medium (73%), more limit reference points were exceeded (11) compared to results of concentrating fishing in higher trophic levels (9). In this scenario, the collapse of small pelagic fish directly and negatively affected the biomass of predators. These effects are likely to be of a trophic nature since overfishing on species of high trophic levels can be discounted because of their low fishing mortality in this scenario. The collapse of small pelagic fish indirectly and positively impacted the biomass of macrobenthos, which strongly increased, overriding the effect of fishing on this group. This effect may be related to the likely top-down control exerted by Chilean hake and possibly also other demersal feeding fish, which were reduced in abundance as a result of reduced availability of small pelagic fish prey, but which also feed on macrobenthos. Overfishing of forage species, specifically small pelagic fish, can have important and detrimental effects on their food webs as has been also proposed by Shannon et al. (in press).

This raises an important point in terms of single species management that is not normally considered, i.e., recovery/rebuilding plans for species located at high trophic levels need to be based on a reduction of fishing mortality on these species, but also release from fishing for their prey. Careful management of forage species management is required. As discussed in Chapter 6, one alternative to deal with this issue is to allow a certain amount of production of forage fish to be available (left in the sea) as potential prey for predators.

Using EwE food web simulations, Bundy et al. (2004) found that, regardless of the trophic pattern chosen, exploitation always disturbs the ecosystem. However, the degree of disturbance will depend on fishing rates and how these are distributed across trophic levels. In Bundy et al.'s (2004) study, concentrating exploitation at lower trophic levels was less disruptive than equal exploitation across trophic levels, which, in turn, was less disruptive than concentrating exploitation at higher trophic levels (Bundy et al., 2004).

Results obtained in this chapter indicate that fishing according to the production of each functional group at 40% of group production was far less disruptive than the other two strategies explored. Only four limit reference points were exceeded and the system exhibited a high recovery. Some cascading type effects seems to emerge mostly in the case of sea lions and macrobenthos under changes in predators such cetaceans and hake, which seem to override the effect of fishing on these functional groups. In this sense, the present study suggests that proportional exploitation across trophic levels may be an ecologically sound management strategy. The discrepancy between these results and those of Bundy et al. (2004) can be caused by the nature of the food web models (different systems and number of groups), the scenarios simulated and the assumptions about the vulnerability parameter. A model fitted to time series data was used in this chapter, but Bundy et al. (2004) did not use a model that had been fitted to time series. Assuming default vulnerabilities in dynamic simulations is a dangerous assumption because we do not know how biomasses will respond to simulated forcing factors (Christensen et al., 2005).

Bottom-up effects

No biomass limit reference points were exceeded or even approached under ENSO scale bottom-up changes. The only exception was horse mackerel for the scenario ENSO 2 (Fig. 7.4b). In addition, all changes in the biomass of model groups observed at ENSO scale bottom-up forcing were 100% reversible. These results are in agreement with previous modelling exercises where pulsed oscillations on ENSO scale affecting phytoplankton biomass were propagated rather smoothly through the food webs (Watters et al., 2003; Milessi, 2005; Milessi et al., 2005). Specifically, Milessi (2005) and Milessi et al (2005) simulated ENSO and fishing scenarios in the same ecosystem. However, they used a food web representing the coastal system off central Chile in year 1992 that was not fitted to time series (Neira and Arancibia,

2004) and only analyzed inter-annual changes induced by bottom-up and top-down forcing.

Regardless of their frequency and intensity, ENSO scale bottom-up forcing did not induce regime shifts (as defined by the criteria in Table 7.4) in the model scenarios examined. It is well known that ENSO not only affects the abundance and production of phytoplankton, but also production rates, distribution and catchability of fish at higher trophic levels. The effects of different assumptions on the biological effects of ENSO and their ability to cause regime shifts should be included in future studies. Results of the simulations conducted in this chapter are in accordance with the current understanding of ENSO effects on ecosystems and how they seem to be dependent on longer time scale events, such as long-term warm (El Viejo) or cold (La Vieja) phases (Chavez et al., 2003; Alheit and Ñiquen, 2004). However, the response of the system to a series of ENSO events in a rapid succession by itself and in combination with fishing could lead to a different dynamics and should be explored further in future research.

Bottom-up changes on the decadal scale could lead to different changes in the system depending on the sequence in which the low and high phytoplankton biomass is allocated during the simulation. This is presumably related to the starting conditions, implying that the model may be sensitive to this. However, system recovery under these scenarios was medium to total indicating that if the decadal change is a continuous oscillation (as ENSO events, but on a longer time scale) from high to low phytoplankton biomass and back, bottom-up decadal changes are likely to cause reversible shifts in the ecosystem. However, the differences in response from the low-high and high-low bottom-up forcing of phytoplankton biomass could be related to the way primary production is used in the model. The ecotrophic efficiency of phytoplankton was set to 0.3 (i.e., only 30% is used, see Chapter 2). The result of this assumption is a low bottom-up limitation and, therefore, the simulated shift from low to high phytoplankton biomass had little impact in the whole food web. Conversely, the simulated shift from high to low phytoplankton biomass may have resulted in a bottom-up limitation with more strong impacts in the food web.

Interplay between fishing and bottom-up forcing factors

Results suggest that one of the bottom-up decadal scenarios dampened the effects of fishing, while the alternative scenario led to more limit reference points being exceeded even in the best fishing scenario (equally distributed fishing along trophic levels). The interpretation of these results is that overfishing could be compensated for a productive regime, but even a sustainable long-term management strategy can be jeopardized by an unproductive regime.

When fishing scenarios were overlapped with bottom-up forcing, limit reference points were exceeded compared to no limit reference points being exceeded under the period of low phytoplankton biomass followed by a period of high phytoplankton biomass. Counter intuitively, fishing scenarios slightly decreased the limit reference points exceeded under the opposite decadal bottom-up forcing. Overall, fishing scenarios always affected system recovery under bottom-up forcing.

The effects of fishing and bottom-up forcing simulated here may be affected by intrinsic limitations in the model used. For example, the effect of fishing observed here may be underestimated since the model aggregates biomass of adults and juveniles (except for Chilean hake) and it has been shown that disaggregated models are more sensitive to fishing than aggregated ones (Cox et al., 2002.). In addition, the effect of by-catch and discards are not considered here, nor the effects of fishing gears on benthic habitat and biota. On the other hand, the effects of the bottom-up forcing may be overestimated since, for example, many groups are mobile and could change their distribution by large-scale spatial displacement. In addition, considering the long duration of simulations, some degree of physiological compensation, and even genetic adaptation, could occur in some groups.

It is premature to expand the scope of results of this chapter to other marine systems, specially upwelling ecosystems, because the model may depend on initial condition and structure. However, it would be interesting to promote simulation experiments as the one conducted here in models representing comparable and/or contrasting food webs models as to obtain general conclusions regarding the effect of fishing and environmental forcing on marine ecosystems.

Results obtained in this chapter suggest that fishing strategies such as concentrating fishing on higher and lower trophic levels may be unsustainable and can induce regime shifts of low to medium reversibility. Considering the high environmental variability in upwelling systems, distributing fishing proportionally to production across trophic levels may be the best scenario because changes in biomass of groups suggest low impacts and high reversibility. Regular bottom-up pulses at ENSO scale, as simulated here, may result in low impacts at the level of the food web and are unlikely to induce regime shifts. Decadal bottom-up forcing is likely to induce reversible regime shifts. Overall, fishing appears to have more negative effects on ecosystems than bottom-up forcing, is more likely to lead to ecological thresholds being exceeded, and the reversibility of fishing-induced changes is low to medium under no bottom-up forcing, and low under bottom-up forcing.

These results highlight the need to avoid exceeding ecological thresholds, specially those induced by fishing, and emphasize the importance of considering fishing and environmental variability at the decadal scale rather than simply focusing on inter-annual variability.

Table 7.1. Trophic level, production:biomass ratio in each potentially exploited functional group and the fishing mortality coefficient (F) applied in each fishing scenario. Scenario 1=concentrating fishing in higher trophic levels; Scenario 2=concentrating fishing in lower trophic levels; Scenario 3=equally distributed fishing across trophic levels.

Group name	**Trophic level**	**P/B ($year^{-1}$)**	**F scenario 1 ($year^{-1}$)**	**F scenario 2 ($year^{-1}$)**	**F scenario 3 ($year^{-1}$)**
macrobenthos	2.00	5.70	1.8	4.56	2.28
anchovy	2.15	1.16	0.4	0.86	0.46
Araucanian herring	2.14	1.20	0.4	0.90	0.48
mesopelagic fish	3.83	1.20	0.7	0.50	0.48
horse mackerel	4.04	0.84	0.5	0.33	0.34
Chilean hake (large)	3.65	0.54	0.3	0.24	0.22
Chilean hake (small)	3.36	1.61	0.8	0.77	0.65
pelagic fish I	4.26	0.44	0.3	0.16	0.18
demersal fish14	3.98	0.70	0.4	0.28	0.28
demersal fish I	4.04	0.63	0.4	0.25	0.25
chondrichthyans	3.00	0.37	0.2	0.19	0.15
pelagic fish II	5.15	0.50	0.4	0.16	0.20
cephalopods	3.85	3.66	2.2	1.52	1.46
sea lion	4.92	0.51	0.4	0.17	0.20
cetaceans	4.64	0.14	0.1	0.05	0.05
Average F			0.58	0.73	0.51

Table 7.2. Indicators and corresponding reference points used to evaluate results of fishing, bottom-up forcing scenarios and their interplay.

Indicator	**Reference point**	**Used to evaluate**
Biomass of all groups in the system (B_i)	Limit reference point: $B_{i,\ t=t0} = 50\%\ B_{i,\ t=t0}$	Number of Limit reference points exceeded in each scenario
Percentage of groups that fall bellow 50% of their $B_{initial}$ at 50 years of simulation	0–24% low 25–49% medium 50–74% high >75% extreme	Impact of each scenario
Percentage of groups that recovers to >50% of $B_{initial}$	0 – 24% poor 25 – 49% low 50 – 74% medium >75% high	System recovery under each scenario
Biomass of trophic guilds	+/- 50% $B_{initial}$	Regime Shift features
Piscivores/planktivores biomass ratio ($B_{piscivores}/B_{planktivores}$)	+/- 50% respect to ($B_{piscivores}/B_{planktivores})_{initial}$	Regime Shift features
Pelagic/demersal ratio ($B_{pelagic}/B_{demersal}$)	+/- 50% respect to ($B_{pelagics}/B_{demersal})_{initial}$	Regime Shift features

Table 7.3. Criteria used to define regime shift and indicators used.

Criteria	**Indicator**
1) Sudden or abrupt shift from one dynamic regime to another	Shift duration is much lower than regime(s) duration, e.g., annual versus decadal changes.
2) High amplitude shift from one steady state to another	Shift includes changes in the indicators in excess of 50% in the indicator
3) Low frequency events	Inter-decadal variability is higher than inter-annual variability, e.g. the variability between regimes is higher than the variability within regimes.
4) Evident at "multiple trophic levels"	Changes are observed in multiple functional groups, e.g., from lower trophic level species (e.g., primary producers) to high trophic level species (e.g., top predators).

Table 7.4. Number of Biomass limit reference points exceeded and recovery observed under simulated scenarios.

Scenario	Description	Number of B_{Limit} exceeded	%	Number of recoveries	%
Fishing 1	Concentrating fishing at higher trophic levels	9	43	5	56
Fishing 2	Concentrating fishing at lower trophic levels	11	52	8	73
Fishing 3	Proportionally distributed fishing across trophic levels	5	24	4	80
Bottom-up 1	Interannual variability (one ENSO per decade)	none		none	
Bottom-up 2	Interannual variability (two ENSO per decade)	none		none	
Bottom-up 3	Interannual variability (one ENSO per decade increased intensity)	none		none	
Bottom-up 4	Decadal variability (low to high phytoplankton biomass)	none		none	
Bottom-up 5	Decadal variability (high to low phytoplankton biomass)	15	71	11	73
	Fishing 1 and Bottom-up 4	8	38	4	50
	Fishing 1 and Bottom-up 5	14	67	10	71
	Fishing 2 and Bottom-up 4	5	24	2	40
	Fishing 2 and Bottom-up 5	13	62	8	62
	Fishing 3 and Bottom-up 4	5	24	3	60
	Fishing 3 and Bottom-up 5	14	67	6	43

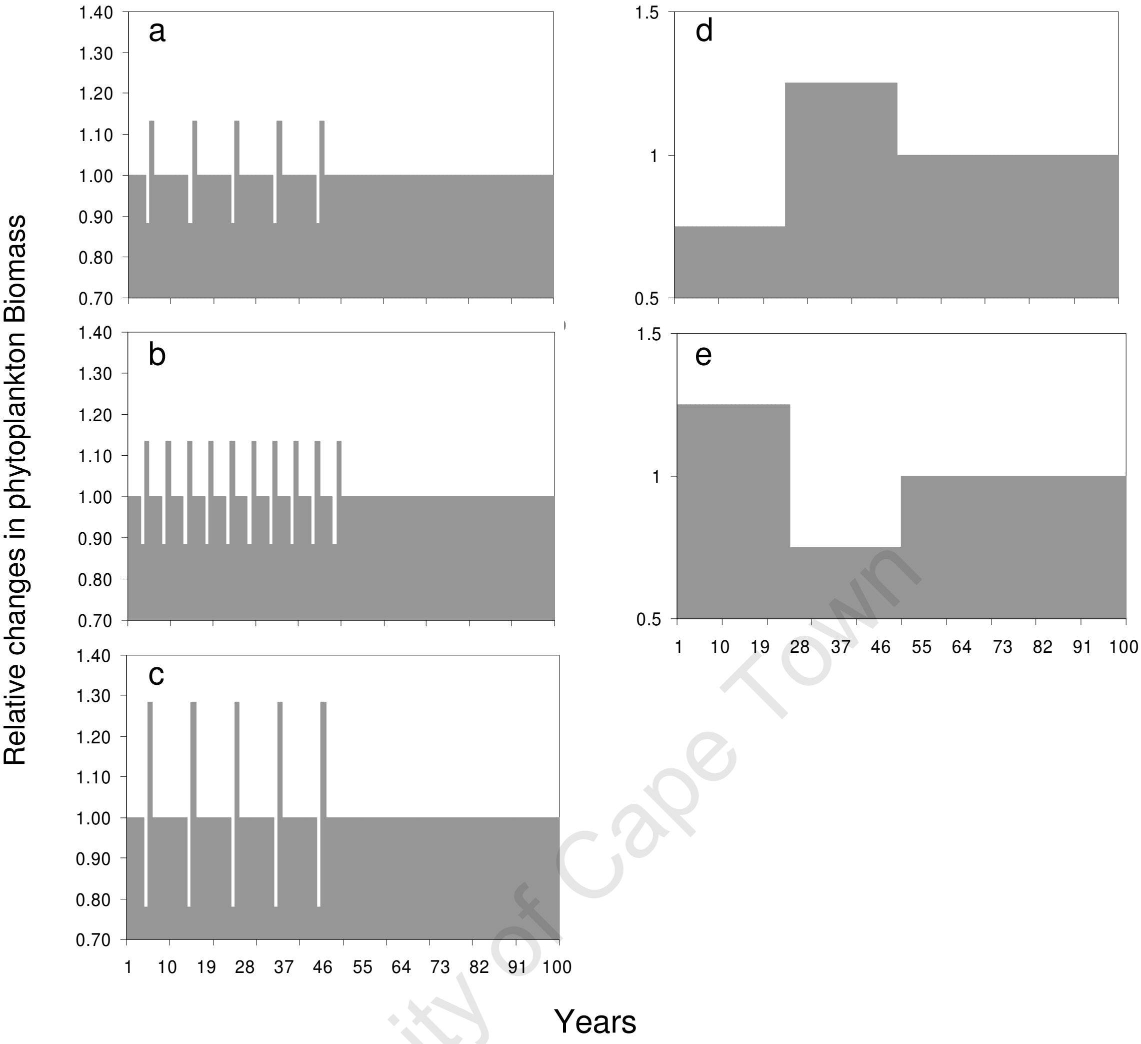


Figure 7.1. Bottom-up forcing scenarios simulated at El Niño Southern Oscillation (ENSO) and decadal scales. a) One ENSO event per decade; b) 2 ENSO events per decade; c) one ENSO event per decade but at 50% higher intensity; d) 25 years low phytoplankton biomass followed by 25 years of high phytoplankton biomass; d) 25 years of low phytoplankton biomass followed by 25 years of low phytoplankton biomass.

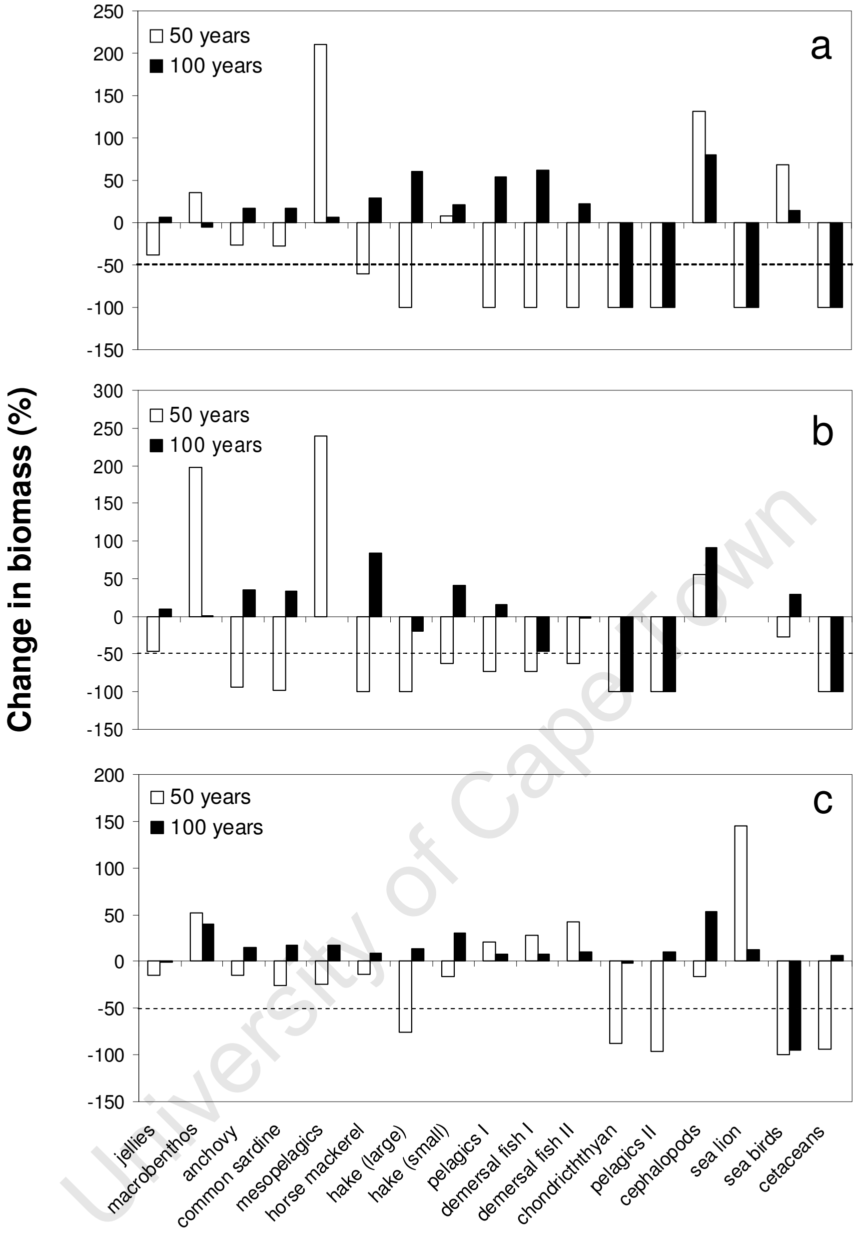


Figure 7.2. Changes in model groups' biomass under simulated fishing scenarios. a) Concentrating fishing at higher trophic levels; b) Concentrating fishing at lower trophic levels; and c) proportionally distributed fishing along trophic levels. Dotted horizontal lines indicate the limit reference point (i.e., 50% $B_{i,\ t=t0}$).

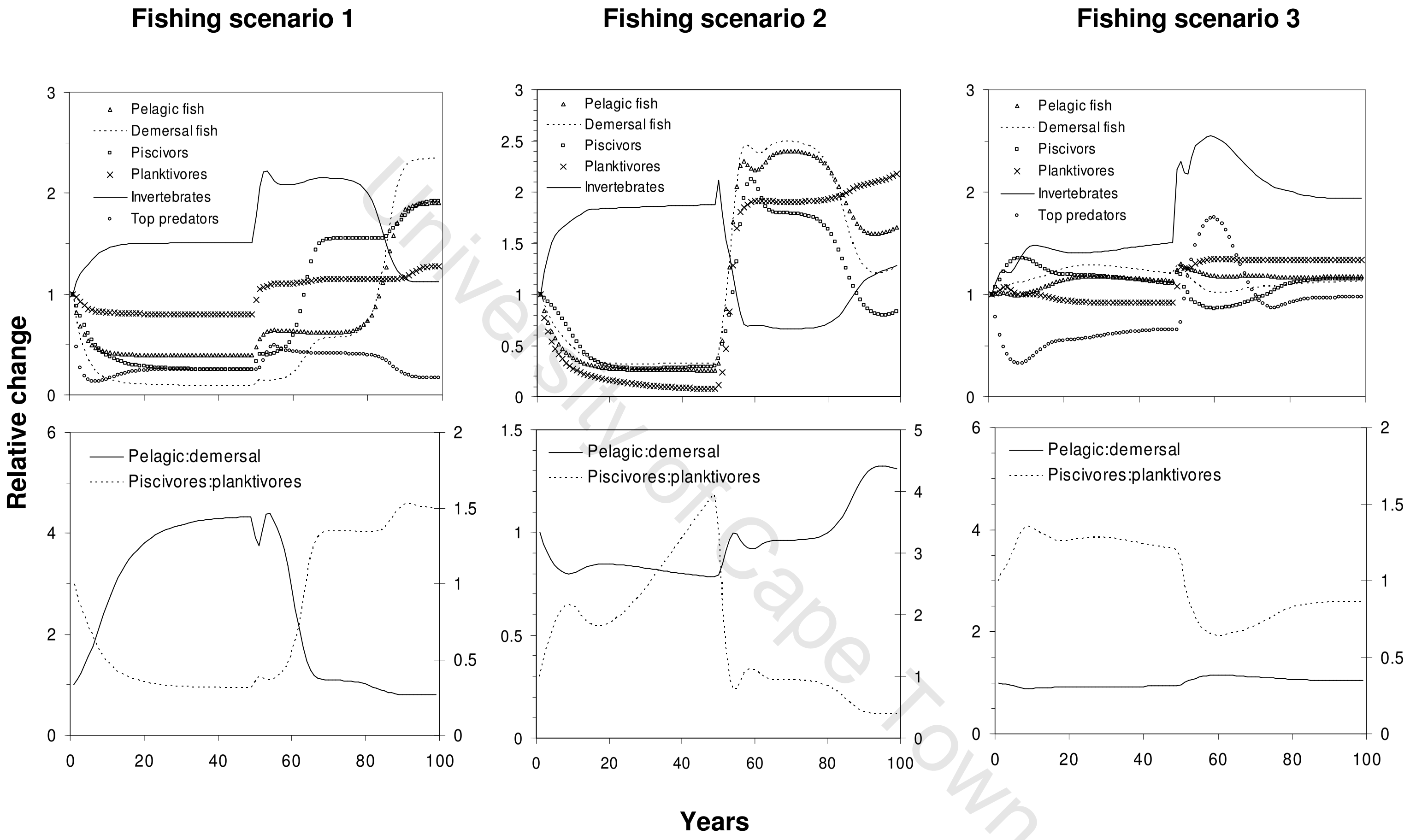


Figure 7.3. Changes in trophic guilds, the pelagic:demersal ratio and piscivores:planktivores ratio under fishing scenario 1 (concentrating fishing in higher trophic levels), fishing scenario 2 (concentrating fishing at lower trophic levels) and fishing scenario 3 (relatively distributed fishing along trophic levels).

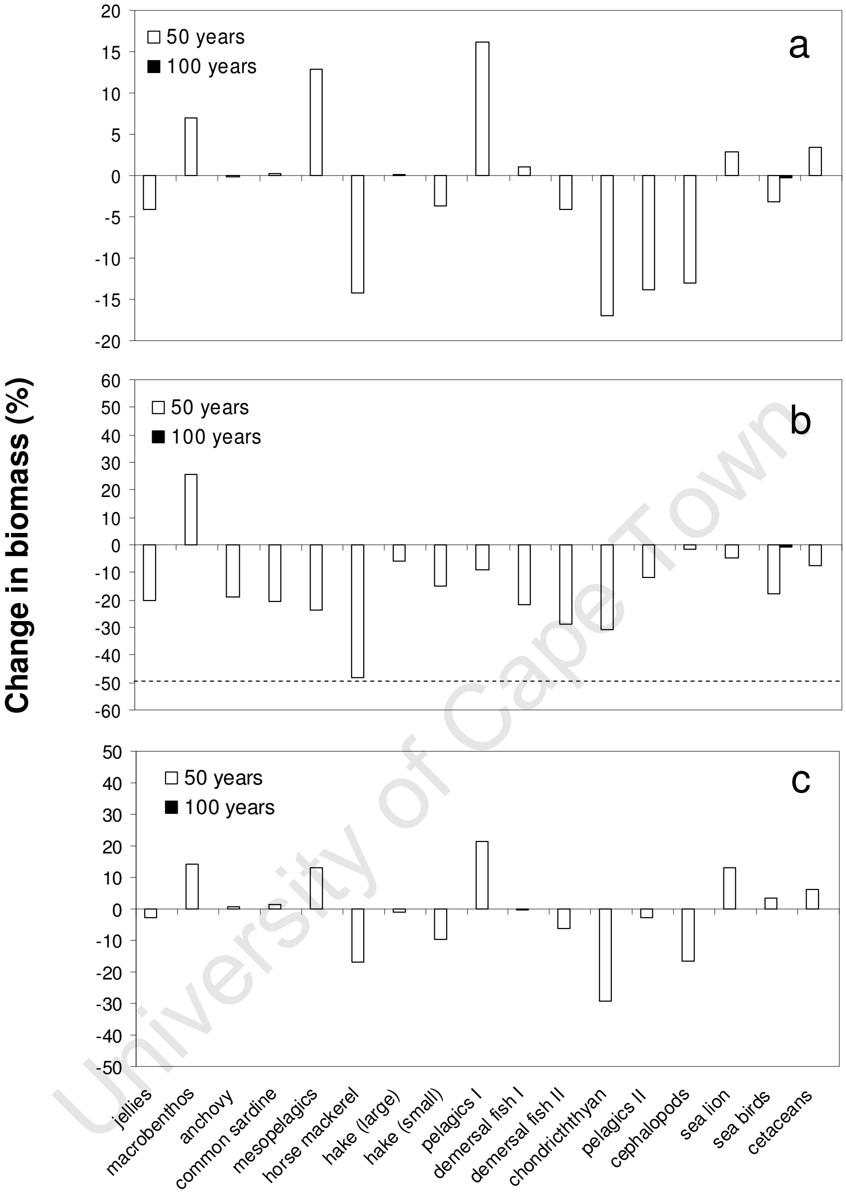


Figure 7.4. Changes in model group biomass under simulated El Niño Southern Oscillation (ENSO) scale bottom-up forcing scenarios. a) One ENSO event per decade; b) Two ENSO events per decade; and c) One ENSO event per decade but with 50% higher intensity than in scenario (a).

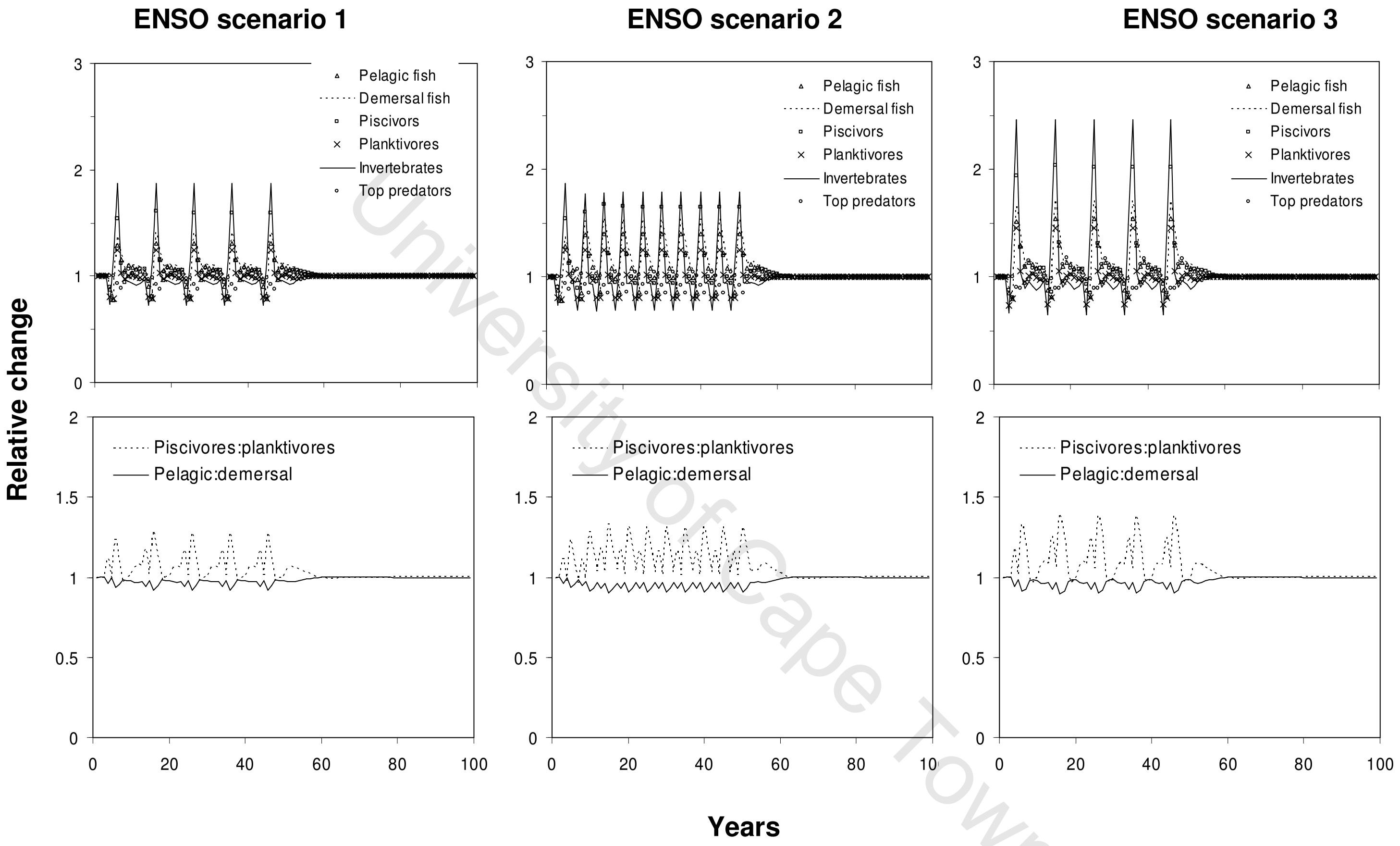


Figure 7.5. Changes in trophic guilds, the pelagic:demersal ratio and piscivores:planktivores ratio under simulated El Nino Southern Oscillation (ENSO) scale bottom-up forcing scenarios. Key: ENSO scenario 1= 1event per decade; ENSO scenario 2= 2 events per decade; and ENSO scenario 3= 1 ENSO event per decade but with 50% higher intensity than in ENSO scenario 1.

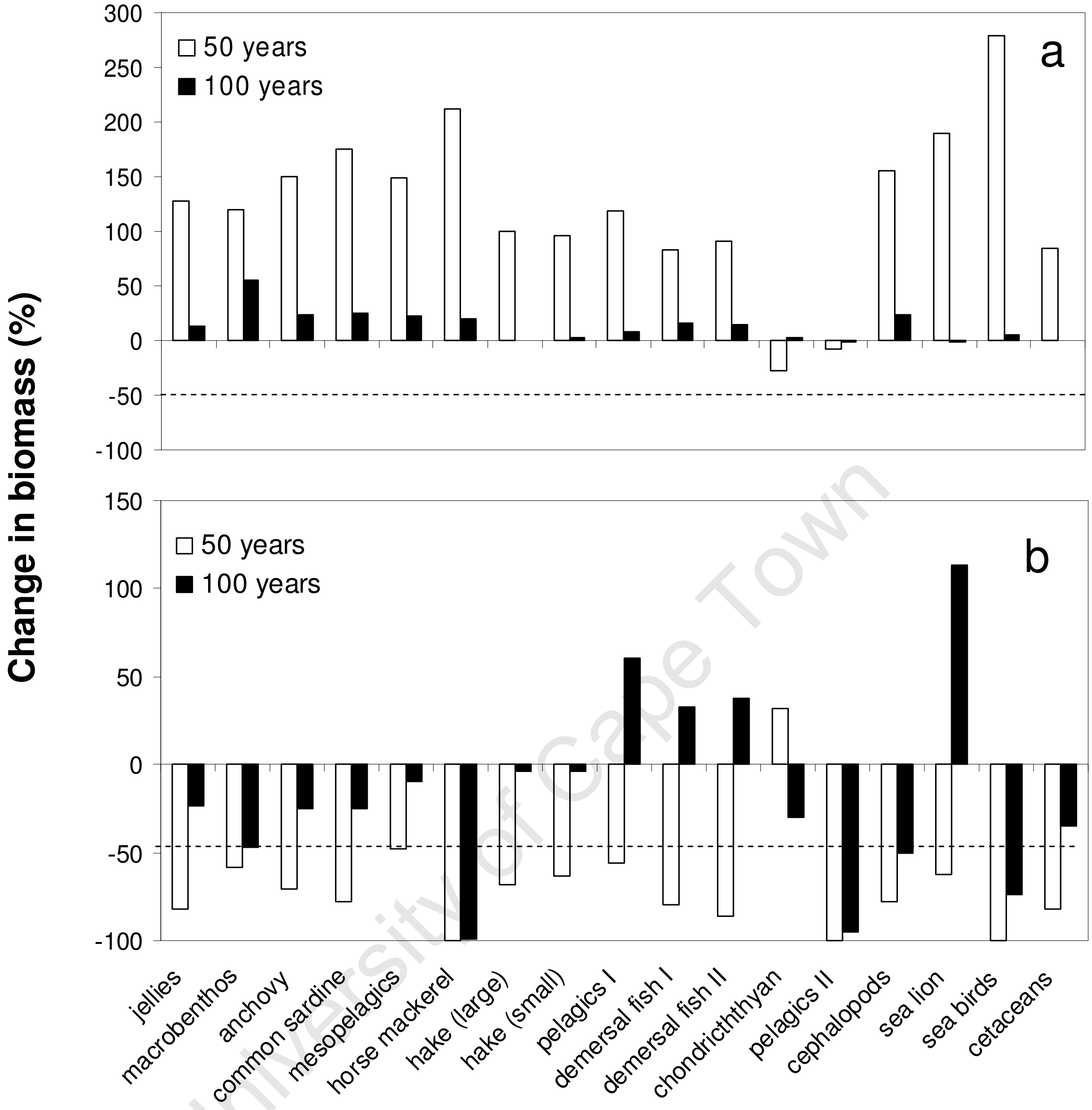


Figure 7.6. Changes in biomass of model groups under simulated decadal bottom-up forcing. Key: a) 25 years of low phytoplankton biomass followed by 25 years of high phytoplankton biomass; b) 25 years of high phytoplankton biomass followed by 25 years of low phytoplankton biomass. Dotted horizontal line denotes the limit reference point (i.e., 50% $B_{i,\, t=t0}$).

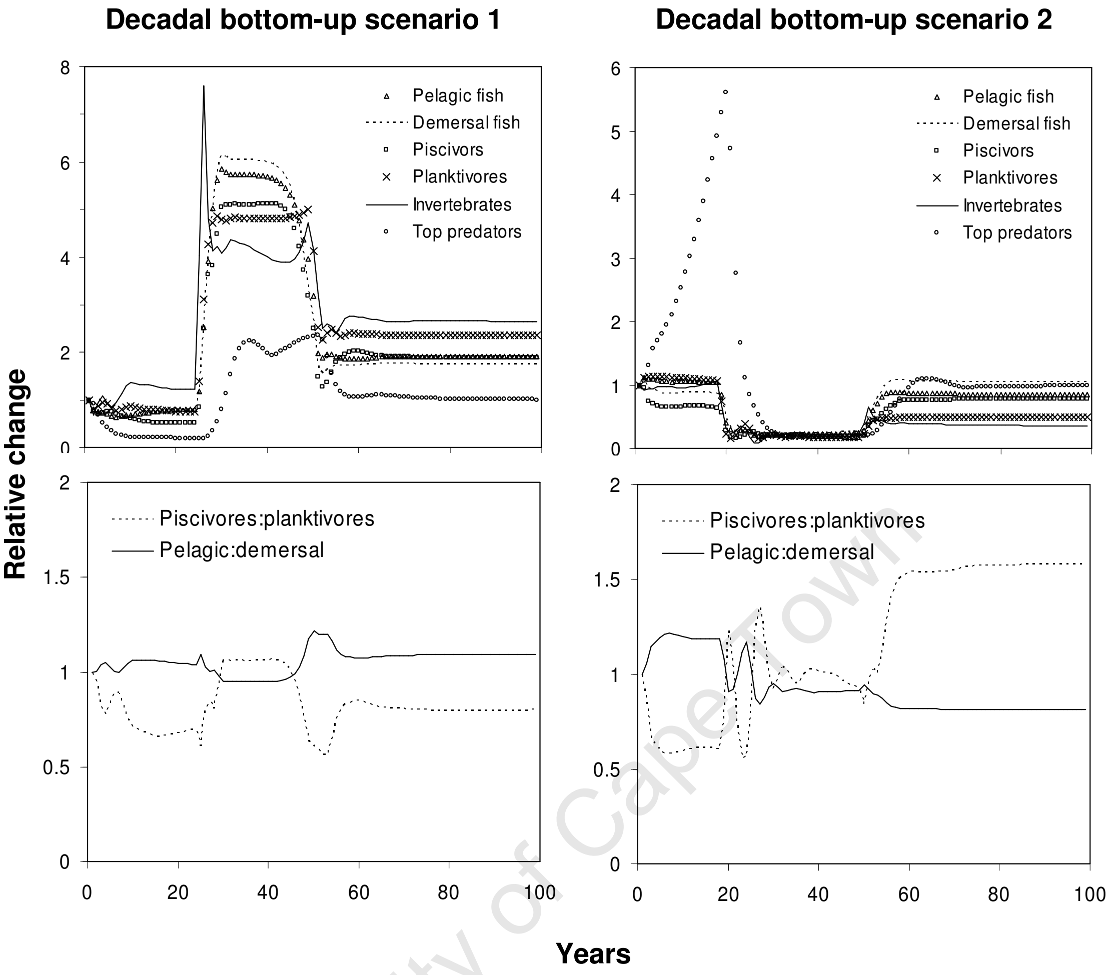


Figure 7.7. Changes in trophic guilds, the pelagic:demersal ratio and piscivores:planktivores ratio under simulated decadal bottom up scenarios. Key: Decadal bottom up scenario 1=25 years of low phytoplankton biomass followed by 25 years of high phytoplankton biomass; Decadal bottom-up scenario 2=25 years of high phytoplankton biomass followed by 25 years of low phytoplankton biomass.

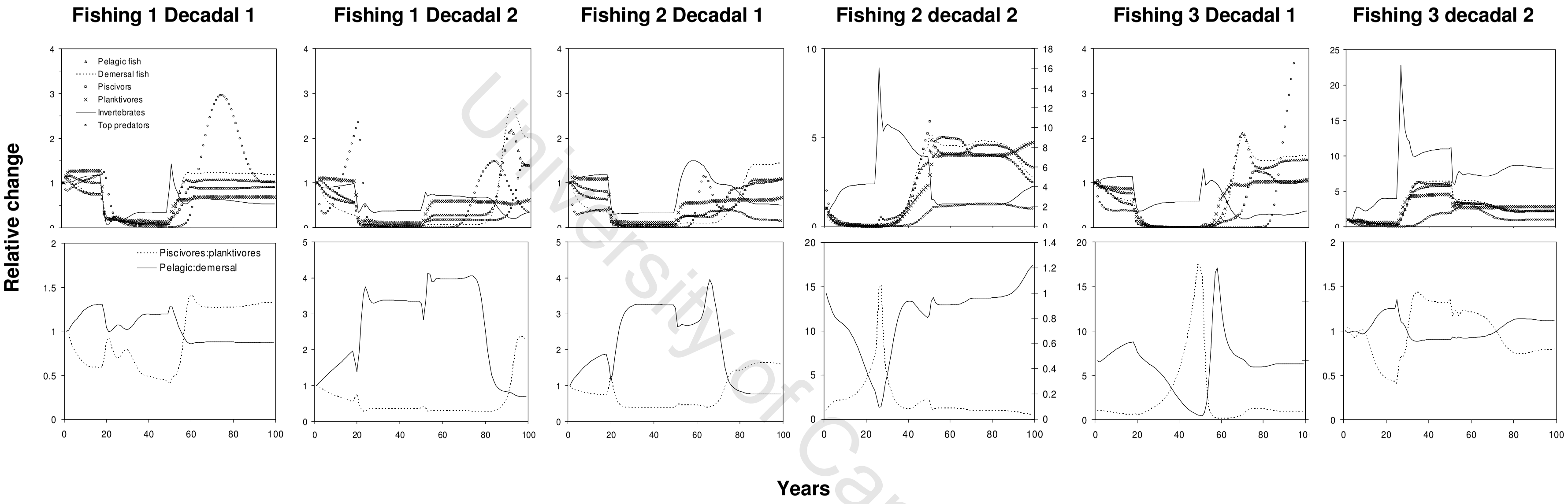


Figure 7.8. Changes in trophic guilds, the pelagic:demersal ratio and piscivores:planktivores ratio under the interaction among fishing and decadal bottom-up forcing. See legend in Figure 7.6. Key: fishing scenario 1 (concentrating fishing in higher trophic levels); fishing scenario 2 (concentrating fishing at lower trophic levels); fishing scenario 3 (relatively distributed fishing along trophic levels); Decadal bottom up scenario 1=25 years of low phytoplankton biomass followed by 25 years of high phytoplankton biomass; Decadal bottom-up scenario 2=25 years of high phytoplankton biomass followed by 25 years of low phytoplankton biomass.

CHAPTER 8

GENERAL DISCUSSION AND SYNTHESIS

Each of the preceding chapters contains an in depth discussion of relevant findings. This Chapter attempts an overall discussion rather than a “discussion of the discussions”. Specifically, hypothesis set out in Chapter 1 are revisited here in the light of results to propose an understanding of the main ecological features of the ecosystem under study. In particular, the discussion will focus on changes in food web structure and the relative effects of the main forcing factors affecting the food web. An overall synthesis is then attempted by integrating results from Chapters 6 and 7 in terms of the key aspects that should be considered in the implementation of an ecosystem approach to fisheries in central Chile.

1. Effects of fishing on Ecosystems: Is the ecosystem degraded compared to the “pristine” states? Snapshot models that were constructed and compared in Chapter 2 indicated that the food web structure in the Southern Humboldt System off Central Chile differed from the pristine or pre-industrial period towards the more recent periods. An important increase in fishing mortality at the stock and food web levels was observed, together with a decrease in the importance of removal of biomass by predators, and increase in the relative abundance of species with small body size, short life span and low trophic level. Trends in global indicators derived from network analysis and food web structure are in accordance with what is theoretically expected in stressed ecosystems and suggest that the food web could be more susceptible to external forcing and negative ecological interactions (Odum, 1985).

2. Forcing factors: What are the relative roles of fishing, the environment and trophic structure in the observed variability at stock and food web levels? The Ecopath with Ecosim software allowed the evaluation of the relative contributions of fishing mortality series, trophic controls (vulnerability parameters) and environmental forcing (hypothetical bottom-up changes in primary production) on observed stock dynamics between 1970 and 2004. Results indicated an important effect of fishing and environmental forcing (hypothetical decadal shift in primary productivity) on the food web dynamics, likely mediated by the existence of trophic flow controls between some predator-prey interactions.

3. Dynamic quantification of predation mortality and forage species management: Who eats and controls whom? Are vulnerability parameters indicative of significant trophic relationships that support the existence of trophic controls in the system? The best-fitted model in Chapter 3 suggested a likely top-down flow control for the Chilean hake-red squat lobster interaction ($v>2$), whereas the interaction between Chilean hake and small pelagic fish may be mainly bottom-up controlled ($v<2$). The statistical strength of the correlation between the biomass of these two prey-predator pairs supports the hypotheses of top-down trophic control of Chilean hake on red squat lobster. Positive (bottom-up) effect of small pelagics on hake was less conclusive, and nonlinearities in this prey-predator pair should be studied further. The analysis also suggests lack of top-down effect (by Chilean hake and the fishery) on small pelagic fish, but a significant top-down effect of the fishery on Chilean hake. There was no significant effect of sea surface temperature on the analysed stocks, which may not be surprising considering the short span of the time series. This should not prevent research on the short-term effect of environmental forces on stock and food web dynamics. Overall, there is a need to expand our limited understanding on controls in this food web, evaluating their effects on the management of these fishery resources. The number of species across animal taxa suggests a wasp-waist pattern off central Chile, as hypothesised by Rice (1995) and observed by (Cury et al., 2000) in the southern Benguela ecosystem. However, the pattern in production and biomass across the same taxa in the Chilean system resembles a hypothetical dome-shape or pot-belly pattern, with small pelagic fish being one of the most abundant and productive taxa and likely one of the main pathways by which primary production flows to upper trophic levels.

4. Fishing and ecosystem variability: Has an increase in fishing effort/catch led to a decrease in the trophic level of the catch (TLm), a decrease in magnitude of network properties and an increase in the turnover rate of the community? Indicators of fishing pressure suggest that the upwelling ecosystem off central Chile supported high levels of exploitation in the 1990s and a series of sequential stock collapses: horse mackerel (1997), red squat lobster (2000) and hake (2004). A decrease in the magnitude of trophodynamic and network indicators was found suggesting an increase in the turnover rate of the exploited community and a decrease in ecosystem maturity and stability. Overall, changes at the food web level are in accordance with what is expected from the theory of fishing on ecosystems. Management should aim for additional holistic actions to secure sustainability of stocks and ecosystem wellbeing.

Related to the above question: Have these changes affected system variability or is this property primarily driven by decadal changes in the environment (i.e., regime shifts)? Changes in trophodynamic, network and maturity indicators are not related to the rate of change in variance of the landings of important groups/stocks, which decreases over time (except for horse mackerel where increases). This indicator has observable changes in the vicinity of known environmental changes at the ENSO and decadal scales supporting the hypothesis of system variability primarily driven by changes in the environment.

5. Ecosystem-based fisheries management: What are the objectives, indicators, reference points and control rules? Chapter 6 focussed on six tractable ecosystem-based objectives for the ecosystem approach to fisheries (EAF), i.e., avoid overfishing, allow rebuilding, secure reversibility of impacts, acknowledge and maintain species interactions, applying the precautionary approach and maintain ecosystem integrity. For each objective, a series of indicators were presented and some reference points (mainly limit) were discussed and/or proposed. As Pitcher and Pauly (1998) pointed out, the proper role for EAF should go beyond stocks sustainability and aim stock and food web rebuilding. Chapter 6 proposes that until agreement is found regarding what levels are the targets of rebuilding, the aim of EAF should be to avoid fishing-induced ecosystem shifts of low reversibility, especially to states unable to meet food security and expected benefit for the society.

6. Ecosystem shifts and reversibility: However, when and why are ecosystem limits approached and exceeded? Does fishing or environmental variability lead to ecosystem regime shifts of low reversibility? The unavoidable uncertainty in input parameters precludes interpreting model results as precise predictions of future trend in the biomass of functional groups. However, simulation experiments are still useful to studying how physical variability and fishing strategies can influence food web dynamics (Watters et al., 2003). Simulations conducted in Chapter 7 suggest that fishing rather than decadal bottom-up forcing is more likely to result in ecological thresholds being exceeded and to induce regime shifts with low likelihood of recovery. The interplay between fishing and decadal scale bottom-up forcing indicates that bottom-up forcing may dampen the effect of fishing, while fishing increases the negative effects of a low productivity decadal bottom-up forcing.

SYNTHESIS OF THE ECOLOGY OF THE ECOSYSTEM

A. Ecosystem states and shifts in the southern Humboldt

Criticism can be always raised against the way models and indicators are constructed and interpreted. This thesis is not an exception. Uncertainty in data input and sensitivity of models and indicators to these uncertainties are potential shortcomings. Over-aggregation of taxa in both models and indicators may have led to oversimplification of many processes and patterns. It is widely accepted that even strong correlations do not necessarily imply causality among variables. While acknowledging these caveats, it is also necessary to point out that we will never be able to measure and model every single aspect of ecosystems in a precise way. Therefore, imperfection in knowledge should not be used to justify inaction since incomplete scientific understanding is better than no understanding at all. Much research effort is needed to improve technical aspects (e.g., data collection, precision of estimates, model realism and limitations, indicator robustness, among others) and results of this thesis can be considered a starting point towards future ecosystem-based fisheries research in the southern Humboldt system off central Chile. This should be combined with a further consideration of the consequences of limiting factors in current management.

The synthesis of results from Chapter 2 to 5 allows identifying at least three major fishing-related shifts in the upwelling system off central Chile in the last century. These shifts have gradually changed the composition of marine species and overall ecosystem functioning (Fig. 8.1). The first shift was triggered by the decimation of marine mammals (cetaceans and sea lions) in early 1900s. The second shift occurred in 1950s with the onset of demersal fisheries targeting fish (Chilean hake) and crustaceans (squat lobsters). The third shift is related to the increase in the fishery of pelagic species (small pelagic fish first and medium pelagic later) due to opening of markets to fish meal and oil and over-exploitation of the main stocks during late 1990s.

These enabled identification of at least four states in the system (Fig. 8.1):

1. Pristine (>1900s). Top predators were abundant and probably at their carrying capacity. Food resources (fish and crustaceans) were below their carrying capacity due to predation. Community structure and function probably varied under "natural bottom-up forces". Likely, overall food web turnover rate was low while the reversibility of changes high.

2. Removal of marine mammals and onset of industrial fishing (1950). In this state, marine mammals (cetaceans and sea lions) had been decimated and some prey, now released from predation, may have increased in the system. This change may have affected system structure and function. Furthermore, the fishery targeted abundant demersal fish (possibly near their carrying capacity due to release of predation by some marine mammals) and crustaceans (likely below their carrying capacity due to predation by demersal fish). Small pelagic fish were likely abundant, but not fished due to lack of market for fish oil and meal. Some top-down effects (cascades) may have occurred due to the decrease in marine mammals and demersal fish.

3. Fully exploited state (1970-1995). Demersal stocks declined under fishing pressure (and possibly also by regime shifts in the mid 1980s), crustaceans may have increased due to lack of predation. This change may have altered energy flows in the benthic pelagic environment and the benthic-pelagic coupling in the system. Pelagic stocks dominated the catch and the system (likely due to development of oil and meal markets and better environmental conditions since a bottom-up regime shift may have occurred in mid-1980s towards more upwelling and higher primary production conditions).

4. Present state (>2000): Characterized by low abundance of marine mammals and possibly other top predators (far from their carrying capacity), the main demersal (Chilean hake), medium size pelagic (horse mackerel) fish stocks as well as the main benthic crustaceans (squat lobsters) are collapsed (i.e., far from their carrying capacity), with benthic crustaceans perhaps released from top-down control by Chilean hake. Small pelagic fish are abundant due to a combination of good environmental conditions and low fishing mortality. In this state, the system may be in an exacerbated wasp-waist control due to potential lack of keystoneness of groups located in high trophic levels (Libralato et al., 2006). In this state, food web turnover rate is high, but system reversibility to fishing and/or environmental changes may be low compared to the pristine/pre-industrial states.

For how long this state can last and in what direction the system may move are uncertain. Unless rebuilding measures are taken and good environmental conditions occur, the system is unlikely to move backwards to conditions observed in early 1990s or 1950s, and certainly not to the pristine state. Therefore, it is possible that the system may be trapped in a low biomass state with the fishery depending almost exclusively on the productivity of small pelagic fish, which are known to strongly depend on environmental variables. If fishing removes most of the production of small pelagic fish, insufficient surplus production could be left at sea as to support a recovery of dependent and related predators. The collapse of the stocks of small pelagic fish may be regarded as a serious ecosystem threat and should be avoided.

Fishing shifts analyzed above may have gradually changed the ecosystem from one governed by “natural forces” in the pristine state to one governed by increasing human impacts during 1900s culminating in the strongest effects in mid 1990s. In the present state (>2000), fishing forcing has decreased compared to the 1990s and the system may have moved back to a state dominated by natural forces acting either from the bottom-up or from the waist. However, as food web structure has changed, ecosystem resilience and the reversibility of changes may be lower than in the pristine state (Fig 8.1).

B. Ecological features derived from this thesis relevant for an ecosystem approach to fisheries in the southern Humboldt system

Results from Chapter 2 to Chapter 7 highlight several main points of the ecology of the Southern Humboldt system off central Chile relevant for the ecosystem approach to fisheries in this region:

1. The change in food web structure found before and after industrialized fishing emphasizes the central need of ensuring the ecological wellbeing by rebuilding stocks and the food web, if the delivery of system goods and services required by the society are not met or in jeopardy.

2. Fishing mortality is an important source of mortality in the more recent models and therefore a central aim of management should be to avoid overfishing of fully exploited stocks. On the other hand, fishing mortality should be managed as to allow the rebuilding of overfished stocks in a period of 10 years.

3. In addition to fishing, the environment (physical and biological) has been shown to affect stocks and food web dynamics. The rates, processes and effects of physical and biological variability are still poorly evaluated and, therefore, a precautionary approach should guide management directing research effort towards decreasing uncertainties on the effects of natural mortality (i.e., predation and environmentally-driven recruitment) on exploited stocks.

4. In terms of physical bottom-up environmental impacts, it seems important to focus on the temporal scales at which ecosystem goals can be monitored. Since ENSO events are unlikely to induce alternate stable states, it seems that the decadal scale should be the focus of EAF management, specifically changes in ecosystem state and productivity (regime shifts).

5. In terms of trophic interactions, answering who controls whom seems to be more important than who eats whom for stock and food web dynamics, and should be the focus of management. Specifically, a dynamic quantification of predation mortality may be useful for the assessment and management of red squat lobster. On the other

hand, forage species management (i.e., allowing a determined amount of forage fish biomass to remain at sea to sustain predators) may be necessary in the case of bottom-up effect of forage species (e.g., small pelagic fish) on top predators and predatory fish. Forage species management is also a key point in facilitating rebuilding of decimated stocks.

6. Trends in ecological indicators pointed out that beyond stock variability, fishing has affected the whole food web. These changes are in accordance with what is expected from the effects of fishing on ecosystems and, therefore, rebuilding plans should be aimed to consider the whole food web as well as individual stocks.

7. The study emphasises that EAF should avoid fishing-induced regime shifts since they may be poorly reversible.

C. Ecosystem approach to fisheries in Chile: the way forward

Currently, there is a generalized perception that world fisheries are a sunset industry, spiralling down both the ecological and human wellbeing as traditional management has normally failed to maintain target stocks in sustainable levels. Garcia et al. (2003) asked: will EAF be able to reverse this image? I concur with the authors in that developments in fishery science are just one part of the answer since political will, good governance, participation, and education are also key aspects of a successful EAF. However, the evolution of EAF should accelerate as science better articulates feedbacks between ecological effects and economic consequences, then leading to policy choices and formal commitment among sectors (Murawski, 2007).

Again, incomplete knowledge should not be used as an excuse for inaction. This study has shown that although scarce, available data, models and indicators can address issues of global interest for EAF in central Chile, e.g., identify main interactions among target and non target species, analyse the effect of fishing and environmental variability on stocks and food web dynamics, and evaluate ecosystem state and change using available ecosystem indicators.

Following Pikitch et al (2004), the main steps towards the implementation of EAF are shown in Fig. 8.2. Chilean management system is based on information derived from catch and abundance of target species (basically fishing mortality and spawning biomass). In this stage, EAF must rely in effective single-species management (i.e, avoiding overfishing and allowing rebuilding) and precautionary actions for other ecosystem components (i.e., reduce by-catches and discards, avoid harmful gears and protect representative proportions of benthic habitats).

However, ecosystems are more than the sum of their parts and, by definition, single-species objectives are not enough to secure the conservation of ecosystem properties. The next step implies moving forward to a targeted management approach focused on improving data collection systems and the re-analysis of existing data in the context of the ecosystem. Ecosystem indicators (and their corresponding reference points) and measures of ecosystem status for high-priority ecosystem interactions need to be important components of a comprehensive EAF.

The next step corresponds to a management system based on the performance and monitoring of reliable indicators, which would be used to translate proper ecosystem-based fisheries management objectives. In this later step, knowledge about how ecosystems respond to fishing pressure, gained through each step in the evolution from exclusive single-species fisheries management towards a full EAF (facilitated by an adaptive management approach) would allow identification of mechanisms behind ecosystem change. This process could decrease the inherent uncertainty that drives fisheries management (Botsford et al., 1997; Pikitch et al., 2004) or at least decrease false precision in current single-species management (Walters and Martell, 2004).

We must keep in mind that the intention behind implementing an EAF is to improve fisheries management (Garcia et al., 2003). Chilean fisheries management need to move through the steps in Fig 8.2 keeping in mind “ten commandments”(Francis et al, 2007): i) use a holistic, risk adverse and adaptive perspective, ii) always scrutinize key assumptions, iii) maintain old-growth age structure in fish populations, iv) characterize and maintain natural spatial structure in fish populations, v) characterize and maintain viable fish habitats, vi) characterize and maintain ecosystem resilience, vii) identify and maintain critical food web connections, viii) account for ecosystem change through time, ix) account for evolutionary change caused by fishing, and x) implement an approach that is integrated, interdisciplinary and inclusive.

The above commandments imply that the "ecosystem information" needs to be scaled-down to the spatial and temporal scales relevant for the management of target species. Likewise, current fisheries research need to be scaled-up from single-species issues to an ecosystem-based understanding as to evaluate when and how fisheries will put ecosystem components (including target species) at risk (ecosystem wellbeing) and when and how ecosystem changes will compromise the socio-economic aspects of fisheries (human well being). Practical ways to implement this are discussed bellow.

The first approach to a more comprehensive EAF is to identify ecosystem inputs (e.g., the effects of the physical and biological environment) and fishery outputs (e.g., the effects of fishing gears on marine biota and habitats). Table 8.1 summarizes some ecosystem inputs and fishery outputs that could be easily incorporated during the first steps of the implementation of a full EAF in central Chile.

Later, and following Ward et al. (2002), more specific aspects to implementing EAF need to be carried out. First, stakeholders and their interest (directly interested/or affected by the fisheries) must be clearly identified and the eco-regions where fisheries are operating must be mapped, including species habitats and oceanographic features. Then, ecosystem values (habitats, specie and uses) and the main potential threats of the fishery to these values need to be identified, for example using ecological risk assessment (Fletcher, 2005). This leads to establishing the objectives and targets for the ecosystem and the stocks together with strategies to achieve identified/agreed targets. Information systems including the monitoring of stocks and ecological indicators must be designed clearly stating information needs and research priorities. An important point is that the performance of the EAF system needs to be periodically assessed, including a review process and redesign when needed. Finally, EAF needs to evolve together with stakeholders and training and education packages for fishers, managers and general public need to be implemented.

Approaches to support the move towards an EAF based in targeted management and in the performance indicators are being developed elsewhere. Three examples are selected from the literature related to the implementation of EAF in South African fisheries, since this experience could be more comparable to the Chilean process (e.g., both countries have developing economies that benefit from the fish productivity of the two major upwelling systems in the southern hemisphere). The following tools are being tested in South African fisheries: i) computing program to follow the implementation of EAF using fuzzy-logic designed to support multicriteria decision making in fisheries (Paterson et al. 2007), ii) a battery of knowledge-based systems to support EAF (Jarre et al., in press), and iii) an EAF monitoring tool using risk assessment results setting criteria for measure progress with implementing an EAF (Nel et al., 2007).

An example of a basic knowledge-based decision tree (Fig. 8.3) shows how the main objectives for EAF can be considered altogether in a management and research program of Chilean fisheries. This tree includes objectives, indicators, reference points and control rules triggered when objectives are not met. Furthermore, this tree allows visualizing how ecosystem-based research can improve/complement single-species management by estimating predation mortality for stocks and allowing biomass of forage species to improve biomass of target species where known strong trophic relationship exist.

D. Final thoughts

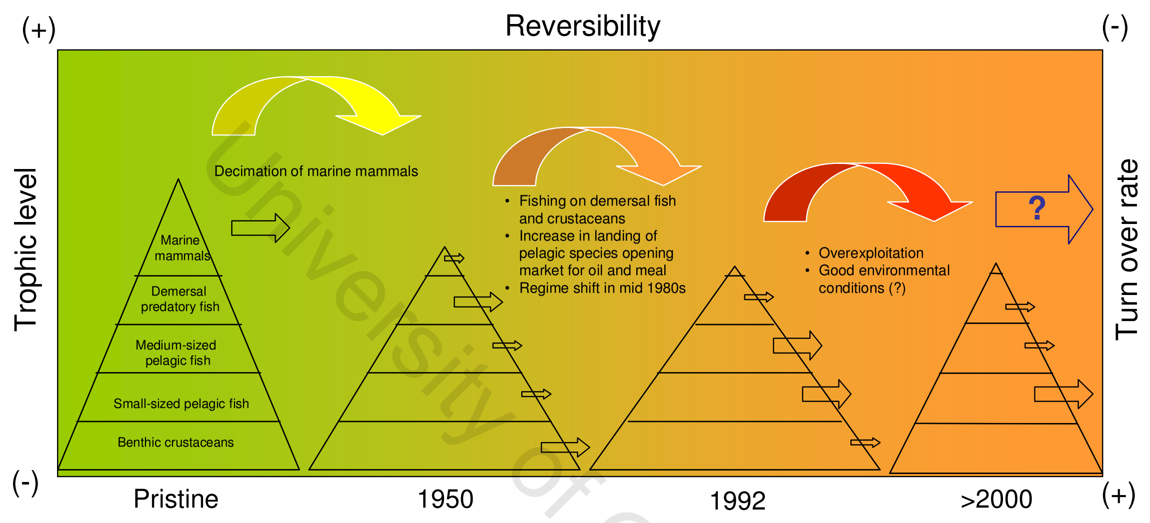
This is the first major attempt to approach ecosystem-based fisheries in central Chile. Although caveats exist, hypotheses and conclusions put forward in this document are a contribution to our still poor understanding of this system and its fisheries. Hopefully, this study will open ground for the next generation of hypotheses and conclusions supported by more and better data, and maybe more robust indicators and models. Meanwhile, results of this thesis are suggestive of a series of ecosystem processes, interactions, dynamics and shifts in the marine food web of central Chile that are of interest for an ecosystem approach to fisheries. These changes cannot be derived by simply observing the dynamics of a few exploited stocks and the need for the development of ecosystem-based science and management arise as the main strong recommendation for Chilean fishery scientists, managers and stakeholders. Chilean fisheries can no longer be managed under the assumption that “each fish is an island” since this approach has not secured sustainability. Current lack of ecological data and scientific understanding impedes also the implementation of a fully ecosystem-based fisheries management. However, inaction is not an option and EAF does not manage ecosystems, but people interested in fish and their fisheries. In this sense, simple but effective low cost steps can be taken to improve fisheries management in central Chile because EAF is, after all, an evolution (not a revolution) to improve fisheries management.

Table 8.1. Fishery outputs and ecosystem inputs that can be incorporated in an ecosystem-based analysis and management of the main fisheries operating in central Chile.

Issue	Rational	Current Management	Recommended Actions
A. Fisheries outputs			
A.1. Overfishing	The abundance of the main stocks in the system are at alarmingly low levels without clear sings of recovery Management should focus on avoiding overfishing and allowing rebuilding of stocks.	No management plan has been implemented.	1. Set F_{Limit} and B_{limit} for each target species. 2. For overfished stocks set F to levels that allow stock rebuilding to target levels in a time period of ten years.
A.2. Discards	The mortality of discarded fish is source of uncertainty and, likely, underestimation of fishing mortality.	Unmeasured.	1. Conduct laboratory and field experiments to quantity discard mortality.
A.3. By-catch	By-catch species are species of commercial value and other are charismatic groups (e.g., sharks, turtles, marine mammals, etc.). Reducing by-catch is a benefit for biodiversity.	Some mitigation measurements.	1. Promote ecologically friendly gears. 2. Define time and area closures. 3. Set limits for the proportion of by-catch. 4. Develop handling protocols. 5. Identify by-catch of vulnerable species.
A.4. Impacts of fishing gears on habitats	Trawling is the most intensive benthic disturbances at sea. An area equivalent to the total oceanic continental shelf is trawled every two years.	Not considered.	1. Set Marine Protected Areas (at least 20% of each habitat type). 2. Gear modifications to reduce destructive effects on sea bed.
B. Ecosystem inputs			
B.1. Recruitment	Size-selective gears have truncated the size-structure of some stocks in central Chile (e.g., hake and horse mackerel see Chapter 5), and their population dynamics may be more dependent on recruitment.	Mechanisms affecting recruitment are poorly understood.	Conduct research (i.e., retrospective forecasting of recruitment, modelling, etc.) to improve our understanding of the recruitment, causal forces and their implications for fisheries management (i.e., forecasting recruitment).

Table 8.1. Continuation

Issue	Rational	Current Management	Recommended Actions
B.2. Decadal variation	Ecosystem and stocks productivity are altered. Management must approach this source of variation that can play a big role in stock collapses. The interplay between decadal shifts and overfishing can lead to undesirable (economic, social and ecological) ecosystem states of low reversibility.	Not considered.	Develop an early warning system for regime shifts and explore regime-specific fishing rates.
B.3. Total predation	Predation mortality (M2) is the main source of natural mortality (M) and sometimes of total mortality (Z). M2 is dynamic, i.e., changes with the ontogeny of the fish and the size of predator populations. Constant M2 (and M) is a weak assumption in fishery models.	Not considered.	Explore linking single-species and multi-species models, i.e., quantify dynamic M2 coefficients using available multi-species models and compare stock dynamics with those assuming constant M.
B.4. Forage species management	Forage species are crucial in ecosystems because they are the prey for some fish (targeted by the fisheries) and other predators. Allowing rebuilding of stocks could benefit from extra allocation of biomass of forage species (targeted by a fishery).	Not considered.	Allocate biomass to be left at sea for dependent predators. An index of the population size of predators can be used as measurement of success.
B.5.Size-based analysis of exploited communities	M2 at the sea is (mostly) size-based and the size spectrum integrates feeding interactions as well as responses to exploitation and management, the size-based is a growing management-oriented area.	Not considered.	1. Collect data on the mean size in the catch/survey for exploited/retained species. 2. Calculate the slope of the community size-spectrum and monitor changes through time.



- Top predators abundant and probably in their carrying capacity.
- Food resources (fish and crustaceans) below their carrying capacity due to predation.
- Community structure and function probably varying under "natural bottom-up forces".

- Top predators decimated.
- Demersal fish (maybe now in their carrying capacity due to release of predation) and crustaceans abundant (but below their carrying capacity due to predation by demersal fish).
- Small pelagic likely abundant but not fished due to lack of market for fish oil and meal.
- Medium pelagic (horse mackerel) probably low increasing strongly since 1970

- Fully exploitation (1970-1995).
- Demersal stocks decline under fishing pressure (maybe regime shifts).
- crustaceans increase due to lack of predation (?).
- Pelagic stocks dominate the catch and the system (likely due to better environmental conditions).
- A bottom-up regime shift may have occurred in mid-1980s towards more upwelling and primary production conditions.

- Reduced populations of marine mammals (far from their carrying capacity).
- Hake collapsed (far from carrying capacity),
- Horse mackerel collapsed (far from their carrying capacity).
- Squat lobsters collapsed crustaceans (far from carrying capacity, but maybe released from top-down control).
- Small pelagic abundant due to a combination of good environmental conditions plus low fishing mortality.

Figure 8.1. Hypothetical ecosystem states and shifts in the southern Humboldt in the last century derived from the synthesis of this thesis. The food web is represented as pyramids and the arrows indicate the level in which the fishery was operating. The size of the arrows is proportional to the catch. The size of the pyramids is not indicative of the biomass or flows in each period.

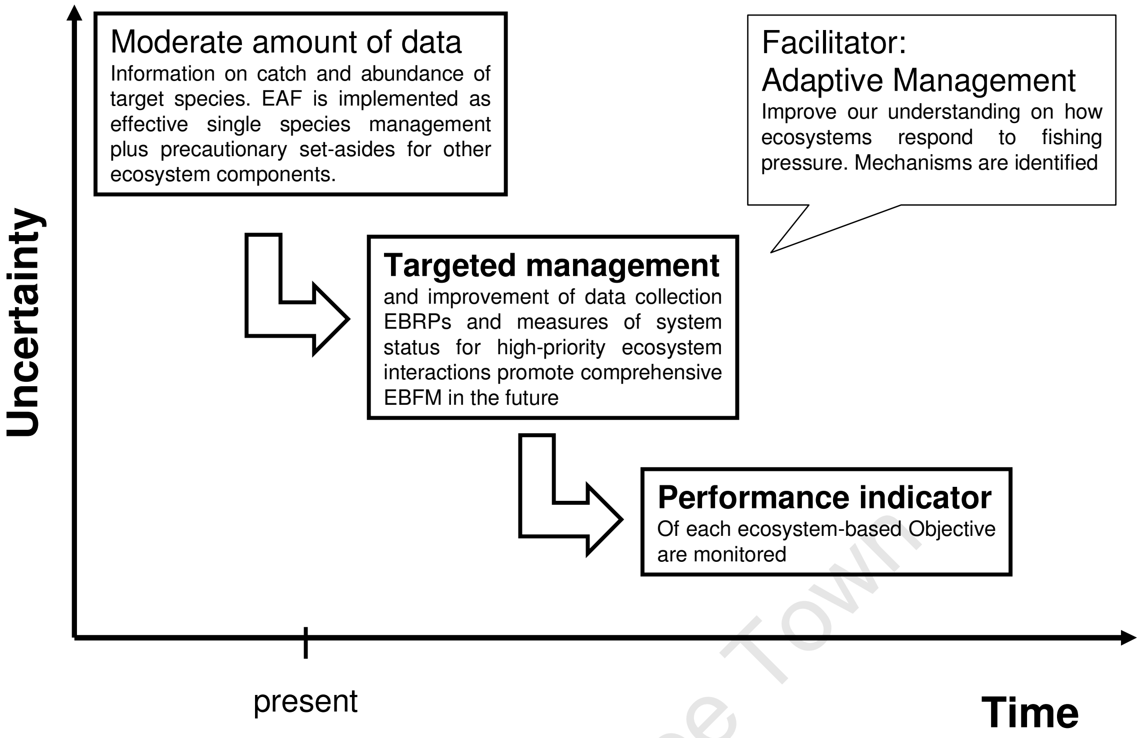
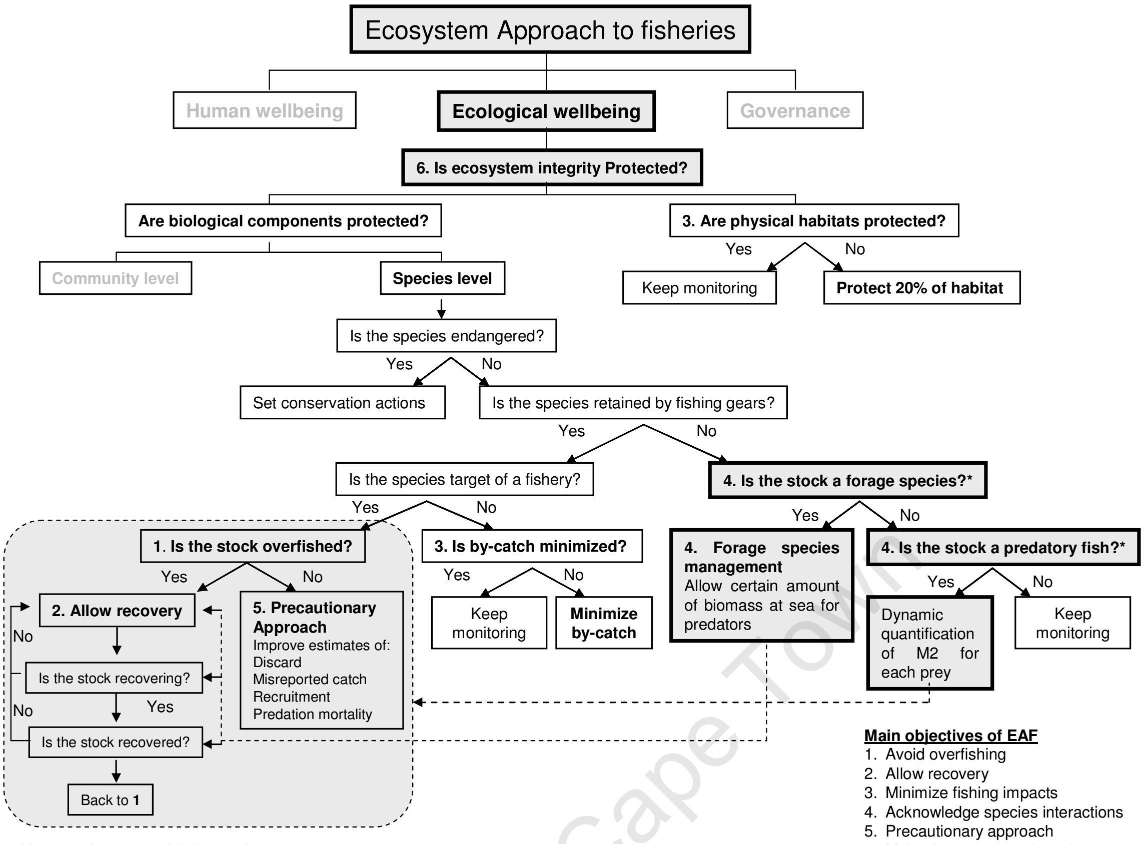


Figure 8.2. Steps towards the implementation of Ecosystem Approach to Fisheries.



*with strong known trophic interactions

Figure 8.3a. Basic decision tree to include ecosystem-based objectives in fisheries management (only the ecosystem wellbeing is considered). The figure shows ecosystem considerations at the physical habitat and species level. Indicators and reference points for each objective are discussed in Chapter 6. Note the narrowness of singe-species fisheries management objectives (grey box) compared to a more holistic ecosystem approach to fisheries. In addition, note how ecosystem-based research can improve/complement single species management (dotted lines) by estimating predation mortality for stocks and allowing biomass of forage species to improve biomass of target species. Shaded boxes indicate how information produced in this thesis could contribute to the development of this approach.

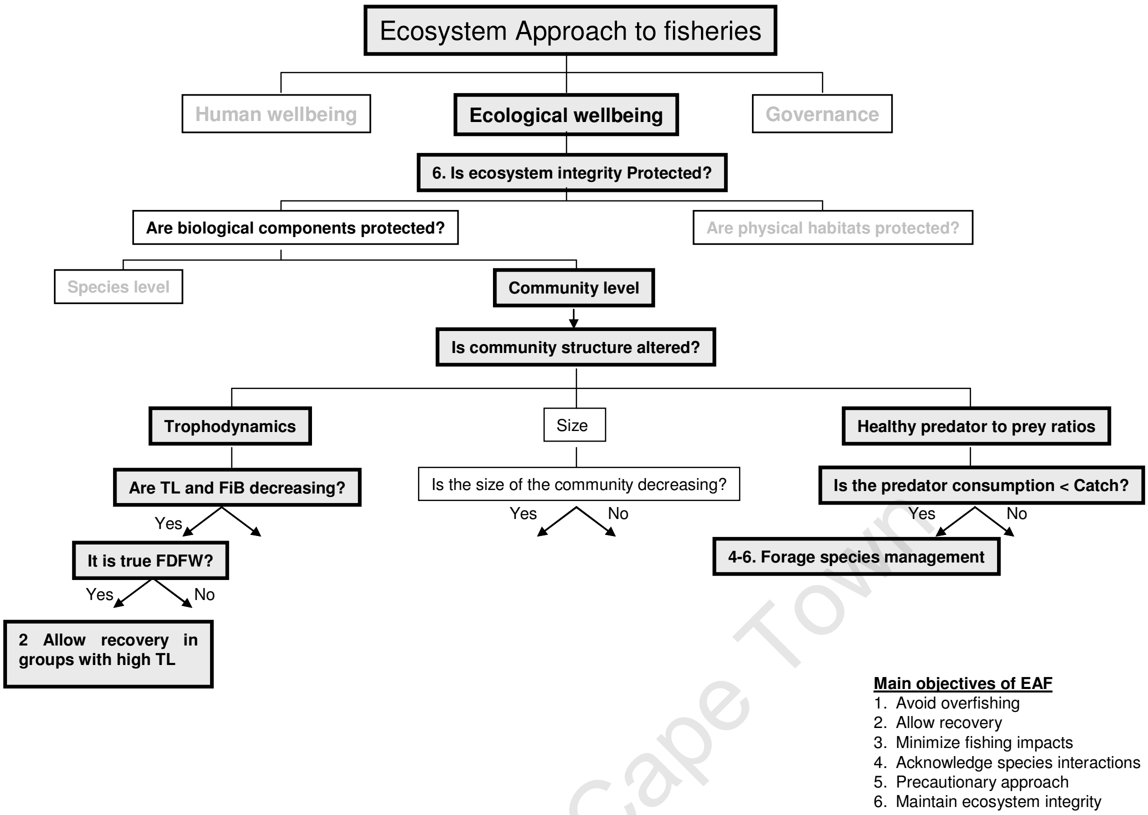


Figure 8.3b. Basic decision tree to include ecosystem-based objectives in fisheries management (only the ecosystem wellbeing is considered). The figure shows ecosystem considerations at the community level. Indicators and reference points for each objective are discussed in Chapter 6. Shaded boxes indicate how information produced in this thesis could contribute to the development of this approach. Key: FDFW=fishing down the food webs; TL=trophic level.

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APPENDICES

Appendix 1. Input data for the models representing the upwelling system off central Chile in four time periods.

Table 1. Data source and method of parameter estimation for the ecosystem model representing the upwelling system of central Chile marine ecosystem model, year 1992. Key: (Eq1)=equation 1 (see text); Eq2=equation 2 (see text); G=General knowledge of the same species/group; GC=Gut content; GE=Guess estimated; OR=Official Report from the Chilean Fisheries Service; SA=Stock assessment.

Group/Parameter	B_i $t*km^{-2}$	P_i/B_i $Year^{-1}$	Q_i/B_i $year^{-1}$	Y_i $t*km^{-2}*year^{-1}$	DC_{ji}	EE_i	GE_i
1. phytoplankton		8		-		0.300	
2. zooplankton I		20	20	-	G;20	0.999	
3. zooplankton II		10	14; 20	-	G;13	0.999	
4. zooplankton III		12		-	G;12	0.999	20
5. jellies		14	14	-	20	0.150	20
6. macrobenthos	SA	SA	4; 21	OR; 19	G; 21		
7. anchovy	SA	SA		OR; 19	GC; 3		11
8. Arauc. herring	SA	SA		OR; 19	GC; 3		11
9. mesopelagic fish		11	14	-	1	0.999	
10. horse mackerel	SA	SA	13	OR; 19	GC		
11. hake (small)		SA	2	-	GC; 15		
12. hake (large)	SA	SA	2	OR; 19	GC; 15		
13. pelagic fish I	SA	SA		OR; 19	GC; 7		
14. demersal fish I	GE; Eq1	SA		GE; Eq2	GC; 15		
15. demersal fish II	GE; Eq1	SA		GE; Eq2	GC; 15		
16. chondrichthyans	GE; Eq1	SA		GE; Eq2	GC; 15		
17. pelagic fish II		SA		OR; 19	GC; 5		
18. cephalopods		14		OR; 19	20; 16		14
19. sea lion	GE on 9	13	GE on 13	-	GC; 9		
20. sea birds	GE	13	13	-	13; 14		
21. cetaceans	GE	14; 18	6; 18	-	17;18		

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Table 2. Input parameters in the food web model representing the upwelling system of central Chile year 1992 (from Neira and Arancibia, 2004). B=Biomass (ton km^{-2}); P/B=production:biomass ratio (ton km^{-2} year^{-1}); Q/B= consumption:biomass ratio (ton km^{-2} year^{-1}); EE= Ecotrophic Efficiency; P/Q= production:consumption ratio; UF= unassimilated food; Y=landings (ton km^{-2} year^{-1}).

Model group/parameter	B	P/B	Q/B	EE	P/Q	UF	Y
1. phytoplankton		120		0.300			
2. zooplankton I		482	1928	0.999		0.20	
3. zooplankton II		45	155	0.999		0.35	
4. zooplankton III		13		0.999	0.410	0.20	
5. jellies		0.58	1.42	0.150		0.20	
6. macrobenthos	2.01	3.57	14.10			0.20	0.228
7. anchovy	8.35	2.88			0.100	0.20	6.102
8. Araucanian herring	11.59	2.45			0.100	0.20	8.952
9. mesopelagic fish		1.20	12.00	0.999		0.20	
10. horse mackerel	13.79	0.82	14.20			0.20	6.48
11. hake (large)	4.29	0.61	5.16			0.20	1.188
12. hake (small)	4.49	2.50	8.32			0.20	0.243
13. pelagic fish I	13.38	0.44			0.100	0.25	3.95
14. demersal fish I	1.68	0.70			0.200	0.20	0.196
15. demersal fish II	0.78	0.70			0.200	0.20	0.021
16. chondrichthyans	0.44	0.36			0.150	0.20	0.134
17. pelagic fish II	0.32	0.50			0.100	0.20	0.106
18. cephalopods		3.50		0.999	0.330	0.20	0.001
19. sea lion		0.25	20.00	0.999		0.20	
20. sea birds	0.07	0.50	20.00			0.26	
21. cetaceans	0.02	0.15	10.00			0.21	
22. detritus	100						

Table 3. Input parameters in the food web model representing the upwelling system of central Chile year 2005, 1950 and 1900.

Model group/Parameter	B	P/B	Q/B	EE	P/Q	Y
Model representing 2005						
macrobenthos	2.008	3.569	14.104			0.044
Anchovy	29.975	2.88			0.1	6.53
Araucanian herring	33.971	2.45			0.1	5.87
mesopelagics		1.2	12	0.999		0
horse mackerel	3.19	0.823	14.2			1.89
hake (large)	5.975	0.605	5.159			1.39
hake (small)	8.62	2.5	8.323			
pelagics I	14.388	0.44			0.1	0.69
demersal fish I	0.234	0.7			0.2	0.042
demersal fish II	0.552	0.7			0.2	0.044
chondricththyan	0.234	0.362			0.15	0.053
pelagics II		0.5		0.999	0.1	0.032
cephalopods	6	2.1	4.4			2.728
sea lion		0.25	20	0.999		
sea birds	0.065	0.5	20			
cetaceans	0.023	0.15	10			
Model representing 1950						
macrobenthos	1.6	3.569	14.104			0.25
anchovy		2.88		0.999	0.1	0.15
Araucanian herring		2.45		0.999	0.1	0.296
mesopelagics		1.2	12	0.999		0
horse mackerel		0.823	14.2	0.999		0.02
hake (large)	4.38	0.7	5.159			1.31
hake (small)	1.5	3.125	8.323			0
pelagics I		0.44		0.999	0.1	0
demersal fish I	1.683	0.7			0.2	0.05
demersal fish II	0.78	0.7			0.2	0.002
chondricththyan	0.436	0.362			0.15	0
pelagics II	0.318	0.5			0.1	0
cephalopods		3.5		0.999	0.33	0
sea lion		0.25	15	0.999		0.036
sea birds	0.065	0.5	20			0
cetaceans		0.15	8.5	0.999		0.039
Model representing 1900						
macrobenthos		3.569	14.104	0.999		
anchovy		2.88		0.999	0.1	
Araucanian herring		2.45		0.999	0.1	
mesopelagics		1.2	12	0.999		
horse mackerel		0.823	14.2	0.999		
hake (large)		0.605	5.159	0.999		
hake (small)		2.5	8.323	0.999		
pelagics I	13.38	0.44			0.1	
demersal fish I		0.7		0.999	0.2	
demersal fish II		0.7		0.999	0.2	
chondricththyan	0.436	0.362			0.15	
pelagics II	0.318	0.5			0.1	
cephalopods		3.5		0.999	0.33	
sea lion		0.25	20	0.999		
sea birds	0.065	0.5	20			
cetaceans	1.093	0.15	8.5			

Table 4. Diet composition of the predators included in the model representing the upwelling system off central Chile in year 1992 (Neira and Arancibia, 2004). Colum number corresponds to the number assigned to each functional group in Table 1.

Prey \ Predator	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
1. phytoplankton	0.40	0.50	0.40	0.50		0.90	0.90													
2. zooplankton I	0.20	0.50				0.05	0.05													
3. zooplankton II			0.60	0.50		0.05	0.05	0.40									0.60			
4. zooplancton III								0.60	0.96	0.05	0.20	0.76	0.43	0.50			0.10			
5. jellies									0.02											
6. macrobenthos										0.14	0.04		0.07		0.24					
7. anchovy										0.15	0.29						0.04	0.12	0.25	0.07
8. Araucanian herring										0.14	0.27						0.06	0.17	0.35	0.10
9. mesopelagics									0.02			0.18		0.10			0.05		0.13	0.10
10. horse mackerel										0.02						0.48		0.18		0.11
11. hake (large)										0.01			0.00					0.28	0.02	0.08
12. hake (small)										0.17	0.07		0.04					0.20	0.17	0.06
13. pelagics I																0.50				
14. demersal fish I										0.00								0.00		
15. demersal fish II																		0.06		
16. chondricththyan																				
17. pelagics II																				
18. cephalopods												0.06				0.02	0.10		0.08	0.33
19. sea lion																				0.10
20. sea birds																				
21. cetaceans																				0.00
22. detritus	0.40				1.00															
Import										0.33	0.12		0.46	0.40	0.77		0.05			0.05
Sum	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00

Table 5. Diet composition of the predators included in the model representing the upwelling system off central Chile in year 2005.

Prey \ Predator	10	11	12	14	15	16	17	18
1. phytoplankton								
2. zooplankton I								
3. zooplankton II	0.05							
4. zooplancton III	0.85	0.10	0.25	0.43	0.50			0.04
5. jellies	0.01							
6. macrobenthos		0.07	0.06	0.07		0.24		
7. anchovy		0.12	0.06					0.13
8. Araucanian herring		0.12	0.06					0.14
9. mesopelagics	0.04	0.20	0.35		0.10			0.15
10. horse mackerel							0.17	
11. hake (large)				0.00				
12. hake (small)		0.30	0.07	0.04				0.15
13. pelagics I							0.17	
14. demersal fish I								
15. demersal fish II								
16. chondricththyan								
17. pelagics II								
18. cephalopods							0.67	0.15
19. sea lion								
20. sea birds								
21. cetaceans								
22. detritus								
Import	0.05	0.09	0.15	0.46	0.40	0.77		0.24
Sum	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00

Appendix 2. List of changes carried out to accomplish the mass-balance in each Ecopath model constructed in Chapter 2.

A) Model 2005

Hake (adults)

In hake adults, the ecotrophic efficiency (EE) resulted to be higher than 1 mainly because the group was under very high fishing mortality. Therefore, the biomass of this group was increased (from X to Y) using the value estimated for the vulnerable fraction of the stock instead of the spawning biomass. This change resulted in EE_{hake}= 0.536.

Jumbo squid

In jumbo squid EE was 1.946, mainly due to high predation mortality. Specifically, the cannibalism was excessive.

The following changes were carried out:

- The proportion of cephalopods on cephalopods diet was decreased from 39% to 15% with the difference (24%) directed to imports. This change resulted in EE=1.191.
- The Q/B ratio was decreased from 5.5 to 4.4 (i.e., 20%) and the P/B ratio increased from 1.75 to 2.1 (20%).

B. Model representing the system in 1950

Hake (adults)

The biomass was increased from 3.01 ton km^{-2} to 4.38 ton km^{-2}. The P/B ratio was increased from 0.605 year^{-1} to 0.7 year^{-1}. Considering that the most of predation mortality in this group was explained by sea lions, the fraction of hake in the diet composition of sea lion was reduced in 50%.

Hake (juveniles)

The biomass of this group was increased from 1.15 ton km^{-2} to 1.5 ton km^{-2} (i.e., 30%). In addition, the P/B ratio was increased from 2.5 y^{-1} to 3.12 y^{-1} (i.e., 25%). Considering that the most of predation mortality in this group was explained by sea lions and cannibalism, the fraction of hake in the diet composition of hake (adults) and sea lions was reduced in 50% and 30%, respectively.

Sea lions

The Q/B ratio was reduced from 20 y^{-1} to 15 y^{-1} (i.e., 25%).

The fraction of sea lion in the diet of cetaceans was decreased in 50% and the Q/B ratio of cetaceans decreased in 15%.

C. Model representing the pristine state 1900 Model

Sea lions

The first run of the model resulted in a $EE_{\text{sea lions}}$=2.55 in. The main problem identified in this group was the high predation by cetaceans. The fraction of sea lion in the diet of cetaceans was decreased in 50% and the Q/B ratio of cetaceans decreased in 15%.
In the absence of any estimate of biomass for this group, the model was allowed to calculate $B_{\text{sea lions}}$ assuming EE=0.999.