SIZE-BASED DYNAMICS OF THE PELAGIC FISH COMMUNITY OFF NORTHERN CHILE

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This thesis is dedicated to my parents for their hard work in building a future for their offspring.

Thesis Abstract

The well-being of humans and their societies depends on goods and services from marine ecosystems. Management of the fish stocks off Northern Chile is based on a single species approach. However, the fish species are not independent, and there is a need to understand the species interactions within the community and with the 3climate variability and human pressures. In this thesis I studied the size-based dynamics of pelagic fish community off Northern Chile.

I investigated temporal effects of climate variability on size-based indicators from the pelagic fishery. I found that catches from the pelagic community have been declining and have become composed of smaller fish. The main signals from the environment were short-term effects, but the trends found were probably combined consequences of climate variability and fishing.

I developed a multispecies size-spectrum model to explore the dynamics of the pelagic community. The model examined the effect of cannibalism and intraguild predation on anchovy and sardine dynamics under different environmental conditions. I found that climate variability and predation interactions are both needed to understand the coexistence and extinction of anchovy and sardine.

The effect of fishing on anchovy dynamics was also explored through the model. Preliminary results showed that fishing below maturity has lower impact on anchovy dynamics than current fishing pattern off northern Chile. In addition the approach of a balanced harvest strategy would be more beneficial for anchovy only when it follows the relative growth rate of the species.

Indicators and models are key tools in implementing the ecosystem-based approach. This thesis has combined these tools with emerging ecological theory about the role of size in the structuring marine ecosystems and, in this way, has set up a basic framework to work towards the ecosystem-based fishery management off Northern Chile.

Contents

List of Figures

List of Tables

Acknowledgement

Declaration

I declare that the work presented within this thesis was written entirely by me and corresponds to my own work with the following exception. The R code developed to implement a multispecies size-spectrum model in Chapter 3 was the product of collaborative work with Richard Law.

"There is not just a way to the ecosystem-based fishery management (EBFM);
the EBFM is the way".
(after Sanskrit)

Chapter 1

General Introduction

1.1 Brief overview of the evolution of the fishery management

That direct and indirect effects of fishing lead to the decline of fish marine populations and affect the structure and function of marine ecosystem, is not exclusive of the last century. Retrospective records suggest that major structural and functional changes due to overfishing occurred worldwide in coastal marine ecosystems as early as the late aboriginal and early colonial stages (Pitcher 2001, Jackson et al. 2001). The negative impact of fishing at all level of organization in marine ecosystems over the last century is, however, much greater than in pre-industrialized times (Pauly and Palomares 2005). A massive expansion of fishing activity took place during 1950s when catches had an extremely rapid growth in the northern hemisphere as well as in the developing world, particularly in trawling, purse seining and long-lining gears. During the 1970s, 1980s and early 1990s the collapses and declines in fish stocks started to be reported. The first collapse with global repercussions was the Peruvian anchovy in 1971-1972, although debates still persist as to whether the collapse was caused by the environment or by overfishing. In the late 1980s and early 1990s most stocks of cod off New England (USA) and Eastern Canada also collapsed (Pauly et al. 2002).

In the late 1990s, in an attempt to assess the current state of the world fisheries since the 1950s, the Food and Agriculture Organization (FAO) concluded (Grainger and Garcia 1996) that by 1994 35% of fisheries resources were in the "senescent" phase (with declining landings), 25% were in a "mature" phase at a high level of exploitation, and 40% were still "developing", while there were none remaining in the "undeveloped" phase. The state of the global fish stock was more striking when Watson and Pauly (2001) corrected the global data from FAO caused by over-reporting catches from China. This revealed that world fisheries landings had been slowly declining since the late 1980s by 0.7 million tones per year. A later FAO analysis of 441 fish stocks with a status based on some stock assessment showed that

74% of them were in the condition of fully exploited, overfished and depleted (Garcia and De Leiva 1998).

By the end of the 1990s, a general awareness existed that the expansion of fleet capacity was the main threat to fish stocks. Global fishing pressures had increased extremely fast from 1950s to 1990s due to geographical extension of fleets and new technologies, and, although the number of fishing vessels showed signals of stabilization, the fishing capacity continued to increase. In addition, the number fishing vessels had decreased in developed countries but had increased in developing ones (Garcia and De Leiva 1998). These evaluations confirmed that a high proportion of the global fish stocks by the late 1990s were under stress owing to the fishing exploitation.

Alongside the expansion of the fishing activity, fishery science evolved from single species models to draw attention to the direct and indirect effects of the fishing, climate variability, and human pressures on marine ecosystems. A general awareness was growing about the need to include a holistic view of fishery management (Ludwing et al. 1993, Botsford et al. 1997, Pauly et al. 2002), opening up a path to the development of the Ecosystem approach to fishery management. Single species models had emerged after the recovery of the fish populations of the North Sea due to the release of fish stocks from fishing activity during Second World War. This recovery of biomass drove scientists to build single species models, assuming that the size of stocks was affected primarily by fishing pressure, leading to an attempt to equate the concept of stability with optimal fishing mortality and therefore maximum sustainable yield (Pauly et al. 2002). However, in practice the control of catches or of fishing effort was rarely implemented, and was vulnerable to socio-political decisions of the fishery managers (Botsford et al. 1997). In addition, severe assumptions in single species models, such as 'compensatory responses' in recruitment owing to reduction in spawning population size, were unrealistic because fish stocks kept showing recruitment failure after severe declines (Pauly et al. 2002). In trying to explain the failure of the recovery and recruitment, the hypothesis of depensatory effect was suggested for Atlantic cod off Newfoundland as a consequence of its lack of resilience (Walters and Kitchell 2001). The increase of smaller sized species that are competitors or predators of juvenile of cod in nursery areas and the preferred prey of adult cod (high proportion on the cod's diet) could

have promoted the decline of the cod stock. Mullon et al. (2005) related the plateau-shaped type collapses (which are, by nature, the most difficult to predict) to hidden increases in exploitation and depensatory mechanisms as being responsible for the lack of resilience of some fish stocks. Depensatory mechanisms describe by Liermann and Hilborn (2001) such as reduced probability of fertilization, impaired group dynamics, predator saturation and conditioning of the environment (the ability to modify their environment to increase survival) were suggested.

However, a depensatory effect was not the only effect of fishing found. Later observations showed the propagation of fishing effects at the community level. Such effects included; a decrease in the mean trophic level of landings in different marine ecosystems (Pauly 1998), a significant reduction in large fish predators in oceanic and shelf ground fish communities compensated for by increases in fast-growing species (non-target) (Myers and Worm 2003), and trophic cascades from the collapse of benthic fish community (Frank et al. 2005). At the same time changes in the life history parameters owing to fishing were also reported. For instance, Jennings et al. (1998) analysed time series (20 and 10 years) of the North Sea demersal fish community showed a change in the species composition leading to increase in growth rate (k) while mean maximum size (L_∞), age at maturity and length at maturity decreased in the fish community. Moreover, fishing has greater effect on species with slower growth and later maturity (Jennings et al. 1999). Fishing was also changing the size structure of marine communities such as those in the North and Celtic Seas. Decreasing trends in the intercept and slope of the community size spectrum, diversity, mean weight, maximum length occurs as consequence of size selective fishing leading to community more dominated by small individuals (Rice and Gislason 1996, Bianchi 2000, Daan et al. 2005, Blanchard et al. 2005). Fishing was suspected of being selective with respect to heritable life traits, with the consequence that exploited populations would evolve in response to harvesting (Law 2000). Decreases in length at maturity could be attributed to the fishery-induced genetic selection (Grift et al. 2003).

Effects of both fishing and climate variability were identified in Celtic Sea and Scotian Shelf (Canada) at community level (Zwanenburg 2000, Blanchard et al. 2005) finding in the first case that the fishing effect could be more important than the climate effect. Indeed, mechanistic links have been discussed more recently as a

synergy effect between fishing and the climate variability (Hidalgo et al. 2011). For instance, Hsieh et al. (2006) found that the loss of year classes owing to fishing could magnify and accelerate the collapse of stocks and/or species because this loss decreases the capacity of stocks to buffer climate variability. Fish populations become more dependent on recruitment and therefore on the environmental variability. Moreover, this effect could also propagates to the community owing to the gradual elimination of large long-lived fishes and replacement by shorter-lived fish species and invertebrates, leaving much simplified food webs lacking of their former 'buffering' capacity (Pauly et al. 2002). Later, Anderson et al. (2008) found that fishing effect of age-truncated or juvenescent populations, leads to unstable population dynamics owing to changing demographic parameters such as intrinsic growth rates.

The empirical evidence accumulated on direct and indirect effects of fishing at population, community and ecosystem level demonstrated clearly that the fluctuations of the population size were dependent not only on fishing mortality but also on multiple factors. These effects needed to be taken into account in the goals of fishery management and in decision making by managers. A call to introduce more elements of ecology (e.g. predator and prey interactions), together with physical forcing and the response of management was made (Botsford et al. 1997, Link 2002a, Pauly et al. 2002, Pikitch et al. 2004). To address the critical need for a more effective and holistic management, a variety of advisory panels recommended the introduction of ecosystem considerations in managing fisheries. The Ecosystem approach to fishery management (also named Ecosystem-based fishery management or Ecosystem Approach to Fisheries) was a new direction for fishery management, reversing the order of management priorities, starting with the ecosystem rather than the target species, and having the overall objective of sustaining healthy marine ecosystems and the fisheries that they support (Link 2002b).

Although at the end 1990s the overfishing effect on marine populations was accepted world-wide, during the following decade the prospects of marine populations, communities and ecosystems were under debated owing to some overfished stocks starting to respond to recovery plans (Worm et al. 2006, Hilborn 2007a, 2007b). Indeed, Worm et al. (2009) pointed out that the commitment to adopting an ecosystem approach to fisheries may have influenced progress in curbing the

overfishing of marine stocks. The EBFM led to a revaluation of management targets for fisheries and the role of managers in meeting broader conservation objectives for the marine environment. After an extensive analysis of global catch data, scientific stock assessments, research trawl surveys, as well as data on small-scale fisheries, the authors concluded that marine ecosystems were currently subjected to a range of exploitation rates, resulting in stable, declining, collapsed, and rebuilding fish stocks and ecosystems, and that management action had achieved a substantial reduction of exploitation rates in some regions.

1.2 Indicators and models

The implementation of the Ecosystem Based Fishery Management (EBFM) involves the development of tools to assess and predict the state of marine communities under different fishery management strategies. Two types of tool are used in the context of EBFM: indicators and models (Rice 2000, Link 2002a, Fulton et al. 2011, Ye et al. 2011). Indicators are needed to monitor changes in the state of populations, communities and ecosystems (Rochet and Trenkel 2003), and they are widely used for environmental reporting, research and management (Jennings 2005). The relevance of indicators lies in their capacity to summarize how the state of a system changes with respect to a specific pressure or impact, their sensitivity to detect impacts, and how readily they can be communicated to managers and stakeholders (Rice and Rochet 2005). Indicators can measure the states of the ecosystem components (e.g., mean length, mean trophic level), the impacts of pressures on the ecosystem (fishing fleet, temperature), and the responses of managers (actions to mitigate, reduce, eliminate or compensate the change) to the changes in ecosystem state (Jennings 2005, Piet et al. 2010). The most developed indicators are the states (those that track the attributes of the components of the ecosystem), and they are used to establish the status of the ecosystem, its changes and the process involved in these changes (Rochet and Trenkel 2003, 2009, Trenkel and Rochet 2010).

Models are key tools for integrating a wide range of system information in a common framework. Models of exploited marine ecosystems can increase understanding of system dynamics; they can identify major processes, drivers (e.g. climate, human pressure) and responses; they can highlight major gaps in knowledge

(Fulton et al. 2011); they can forecast the future and predict ecological responses to climate and human pressure (Chavez et al. 2008). The EBFM models play a key role because they provide a 'road test' mechanisms to explore the expected outcomes in the ecosystems and fisheries of different management strategies (Link 2002a, Fulton et al. 2011, Ye et al. 2011).

1.3 Eastern Upwelling Marine Ecosystems

Eastern Boundary Upwelling Ecosystems (EBUEs) are some of most productive marine ecosystems in the world; the four main are Canary, California, Benguela and Humboldt providing one fifth of the marine fish global catch and contributing significantly to securing food and livelihood strategies in many developing countries (Fréon et al. 2009).

The EBUEs are systems located at the western margins of the continents (eastern part of oceans) on each side of Equator and associated with the subtropical gyres of the Atlantic and the Pacific. The southern flanks of these gyres are driven by the trade winds. Winds towards the equator along the eastern flanks feed the trades and drive the broad and slow eastern boundary Benguela, California, Iberia/Canary and Humboldt currents. Near shore (25–150 km), an interaction with the Earth's rotation (Coriolis force) and presence of the coastal boundary, produces a shallow (~ 50 m) wind-driven offshore surface Ekman flow which is replaced by cool and nutrient-rich waters from below; this process, known as 'coastal upwelling' leaves a strong imprint on sea surface temperature and chlorophyll of EBUEs (Chavez and Messié 2009). In addition, the horizontal shear in the wind stress (wind stress curl) over the open ocean results in a divergence transport known as Ekman pumping. Both coastal upwelling and offshore Ekman pumping produce surface water with high nutrient levels, which lead to the characteristically enhanced biological production of EBUE's (Rykaczewski and Checkley 2008, Chavez and Messié 2009). EBUEs also account for a significant part of gas exchange between the ocean and the atmosphere, particularly CO_2 (Fréon et al. 2009).

The trophic structures of these systems has been described by Chavez and Messié (2009) as productive coastal upwelling habitat where there is a resident food web that interact with migratory species. At the centre of resident food web are populations of small pelagic fish (e.g. anchovy, sardines) feeding on the plankton, and others groups of resident species such as, mackerels, mesopelagic fish, demersal fish, jumbo squid and cetaceans that fed on the small pelagic fish and plankton. These species can also experiences migratory fluxes. In addition, highly migratory species (e.g. sharks, swordfish, whales and tuna) foraging at the edge of coastal upwelling system. Seabirds are also part of system feeding on and competing with fish populations.

The Humboldt Current System (HCS) is particularly important within the EUBEs because it makes the highest contribution to global catches (~71% of the biomass, metric tons) (Fréon et al. 2009) owing to the production of anchovy . The system extends along the coast of South America from 4°S off northern Perú to 40°S off central south of Chile (**Figure 1.1**). HCS encompasses three subsystems: the highly productive year-round Peruvian upwelling system, a lower productivity and rather large ''upwelling shadow" off northern Chile and southern Perú and a productive seasonal upwelling system off central-southern Chile (Montecino and Lange 2009).

1.4 North Chilean Marine Ecosystem (NCME)

The NCME (18°20'S-24°00'S) within the HCS (**Figure 1.1**) is part of a lower productivity and rather large ''upwelling shadow" shared between Chile and south of Perú (Montecino and Lange 2009). The following description refers to the area considered as part of Chilean territory.
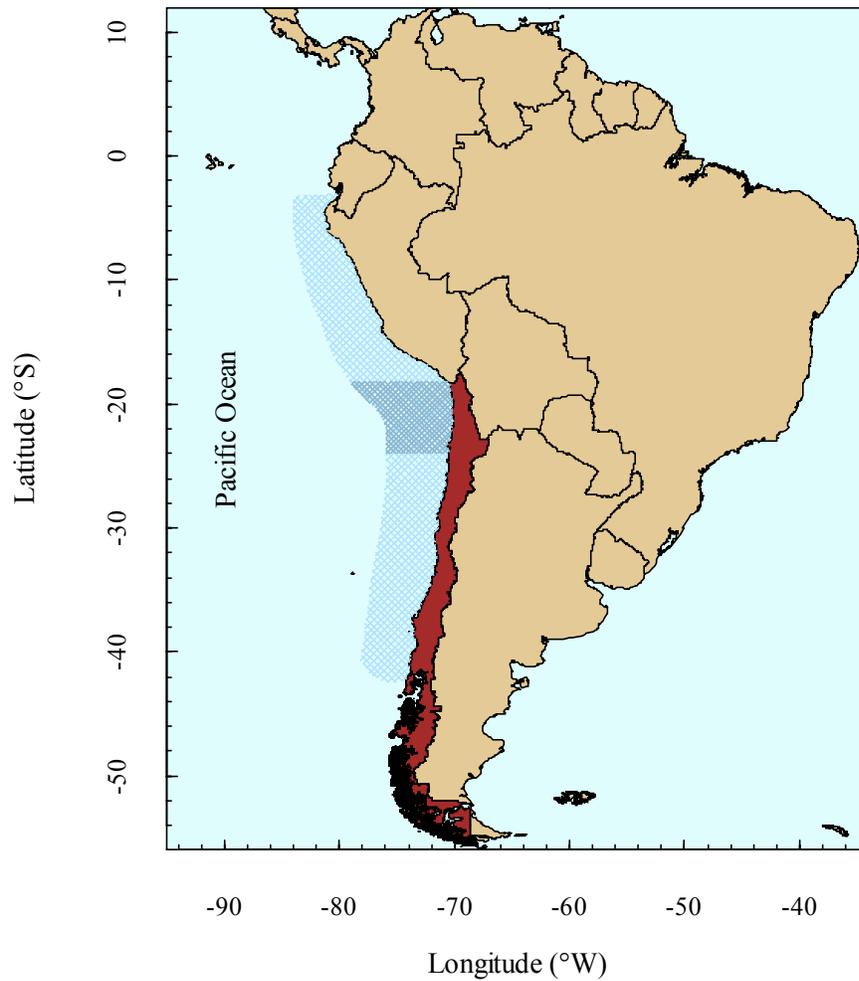
Figure 1.1. The study area the Northern Chilean Marine Ecosystem extends from 18°20'S to 24°00'S (dark blue area) located along the North of Chile (dark brown). Humboldt Current System (HCS) extends from 04°00'S to 40°00'S (light blue area).

1.4.1 Climate variability

As in the other EBUEs, upwelling is the major driving force of the ecological processes in the NCME, promoting high primary production of plankton as well as small pelagic fish.

Off northern Chile coastal upwelling prevails throughout the year due to the predominance of south and south-west winds with maximum values in summer and minimum values in winter (Pizarro et al. 1994). Temperature and salinity patterns (surface and depth) confirm that upwelling occurs year-round, strongest in summer and weakest in winter, bringing fresh water to the surface near-shore (Blanco et al. 2001). Upwelling events in summer can take place for a duration of 4 to 15 days (Barbieri et al. 1995). Upwelling plumes extend 50-60 km (from the centre of the upwelling) during summer and autumn, and 40-50 km in winter and spring. Ocasionally, large filaments can reach 75-125 km from the centre of the upwelling with northeast direction. Topography of the coast (e.g. cape and bay) interacts with upwelling intensifying the events (Strub et al. 1998).

Yáñez et al. (2008) point out that upwelling process can be affected by physical processes of different spatial and temporal scales. Within seasons, coastal trapped waves dominate. Strong intra-seasonal variability of the sea level, coastal currents and sea surface temperature (SST) have been ascribed to coastal trapped waves generated by oceanic equatorial Kelvin waves (Hormazabal and Shaffer 2002). At an inter-annual scale (every 5 to 7 years) the south eastern Pacific is under influence of the ENSO cycle which influences the NCME. The ENSO cycle has two phases "El Niño" or warm year and "La Niña" or cold years. During El Niño years, winds towards the west dominate circulation along the surface of the tropical Pacific Ocean, increasing the SST, weakening the upwelling, increasing in depth of the thermocline, and therefore reducing plankton productivity. Conversely, during La Niña, winds towards the east dominate, thermocline is shallow, coastal waters expand and upwelling become stronger (Bertrand et al. 2008b). At an inter-decadal scale the influence of the Pacific Decadal Oscillation has been suggested (Thatje et al. 2008) together with global warming (Timmermann et al. 1999). Yáñez et al. (2008a) suggest three regime shifts for NCME. From 1950 to 1971, when positive values on the Southern Oscillation Index (SOI) for the Pacific Ocean were observed, the NCME was characterized by low SST and a downward trend in average sea level. From 1973 to 1987, there was a shift to a warmer temperature, a higher value of sea level, and a SOI with lower values. Several authors argue that a third shift could have been taking place from 1989 onwards, returning the complete HCS to a cool condition (Chavez et al. 2003, Alheit and Niquen 2004, Lehodey et al. 2006, Yáñez et al. 2008a).

1.4.2 Pelagic Food Web

The main biological components of the pelagic food web in the NCME are shown in **Figure 1.2**. One feature of the food web is the relative short trophic pathways, such that, aside from zooplankton (mainly copepods and euphausiids), there are only three trophic levels of consumers; small-sized planktivorous fish, medium-sized omnivorous fish, with larger fish predators, mammals and sea birds being the top predators. The dominant planktivorous are anchovy (*Engraulis ringens*) and sardine (*Sardinops sagax*). The second group, medium-size fish predators are represented by the jack mackerel (*Trachurus murphyi*) and cephalopods (*Dosidicus gigas*) feeding on small pelagic fish and/or zooplankton. The large pelagic fish predators are migratory species such as swordfish (*Xiphias gladius*) which feed on fish, and mammals such as, sea lions (*Otaria flavescens*) and seabirds that also consume fish (Thiel et al. 2007). This general description can be complemented with the studies of Medina et al. (2007) and Barros (2007). Their work suggests other functional groups or species that could be important in the pelagic environment of NCME including sharks, and the diverse community of mesopelagic fish (Sielfeld et al. 1995, 2010), which has become relevant in terms of biomass in HCS since 1998 (Marzloff et al. 2009). Mackerel (*Scomber japonicus*) would be an important species for the pelagic fishery, as well as palm ruff (*Seriolella violacea*), eastern pacific bonito (*Sarda chilensis*) (Barros 2007, Medina et al. 2007).
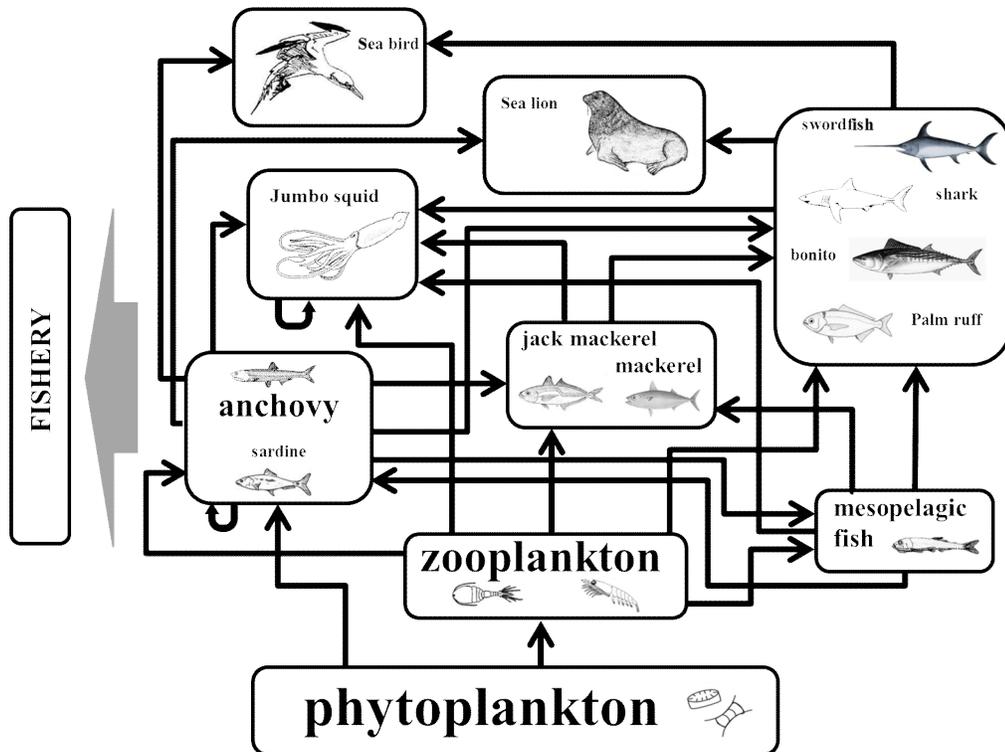
Figure 1.2. Conceptual model of the exploited pelagic food web of the NCME (Font size is indicative of the relative proportions of biomass in the system; grey arrow show mortality owing to fishing).

1.4.3 History of the Pelagic Fishery

An important fraction (e.g. 42% in 2004) of the Chilean pelagic landings is caught in the North Chilean Marine Ecosystem. Anchovy and sardine successively constitute the bulk of the landings (Yáñez et al. 2008a), however species such as jack mackerel and mackerel are also part of the landings.

Major exploitation of pelagic fish community in the NCME started in the middle of 1950s with landings almost exclusively of anchovy (**Figure 1.3**). However, the greatest development took place in the late 1970s and early 1980s, reaching a peak of over 3 million tonnes in 1986. These high landings were sustained by sardine and jack mackerel rather than by anchovy. Since the late 1980s, the landings decreased owing to the collapse of the sardine fishery, and the main species caught became

anchovy. Landings of jack mackerel decreased gradually, but since 2001 became relative lower than in the 1990s and stable. In addition, landings of mackerel (bycatch of the jack mackerel fishery) became important from the beginning of the 1990s.

How the physical forcing interacts with the pelagic food web and the fishery in the HCS has been a major subject of study, especially in the context of anchovy, ENSO events and regime shifts. Although, the decadal variability seem to produce the same type of effects in the pelagic communities of HCS as short term event such as ENSOs, a regime shift seems to lead to a complete long-lasting reorganization of the pelagic community (Alheit and Niquen 2004). Thus, a 'cold' environment leads to increased biomass in lower trophic levels and changes in the ichthyoplankton community (Alheit et al. 2009). Changes in the size structure, spawning period and distribution of anchovy may be observed (Niquen and Bouchon 2004, Alheit et al. 2009). Changes in the species composition of the fishery and the community as well as in its trophic structure have also been described (Bertrand et al. 2004b, 2008b, Niquen and Bouchon 2004).
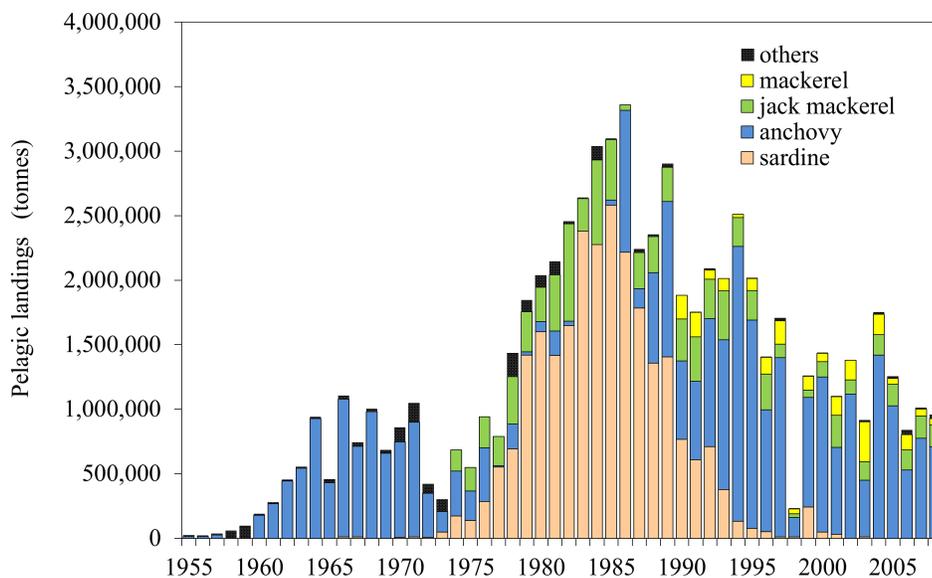
Figure 1.3. Historical annual landings of the industrial pelagic fleet at the NCME. (Graph was constructed with official landings records from SERNAPESCA 1955-2008).

Management of pelagic fishery in NCME has been and is based on a single species approach. During the first 30 years of the pelagic fishery, it was an open-access. This means that the right to catch fish was free and open to everybody. In the 1980s, this strategy, driven by the adoption of new policies, resulted in severe overexploitation, overcapitalization of fishing activity, and the collapse of numerous fisheries in Chile (Castilla 2010) such as the sardine fishery. Between 1986 and 1991, owing to the clear evidence of the decreasing areas of fishing ground and landings (particularly of sardine), the open access to the fishery was closed, as the only policy possible to implement a control on the fishing mortality (Peña-Torres 1997). In 1991, new fishery legislation was passed in Chile. This legislation was the Chilean Fishery and Aquaculture Law (FAL) which included conservation, sea zoning, reallocation of fishing right for artisan and industrial fleets, and new management schemes (Castilla 2010). As a consequence of the new FAL, the total allowable catch (TAC) system to control fishing mortality was established. Quota allocations to individuals (artisans) and registered industrial vessels were assigned. Together with this, different management regime, sea-zoning schemes along the Chilean coast was established. The artisan-exclusive zone, a region of 9.3 km (5 nautical miles) was established (Castilla 2010), and the industrial fleet was banned within this area and controlled through the use of a geographical positioning system (GPS) which became compulsory in 2001. Quota allocations in the NCME were divided among artisans and the industrial fleet, with the industrial fleet having historical rights to a large proportion of TAC (~84% of the biomass, metric tons). Other fishing regulations, such as size-at-entry and seasonal closures, persisted over the years to protect the recruitment, spawning and mature individuals of anchovy, sardine and jack mackerel. As mackerel is a bycatch species of jack mackerel fishery also experience the same size-at-entry than jack mackerel (Böhm per. com.)

Although, Chile joined a diplomatic agreement in 2001 in the Conference of the Economic Commission for Latin America and the Caribbean (CEPAL) to adopt an EBFM, fishery management is still based on single species approach, with management goals looking after the sustainability of individual species, and not taking into account the effect of fishing activity on marine communities and ecosystems. In spite of the lack of the implementation of the EBFM in Chile in the context of fishery management, scientific work has kept developing. Thus,

ecosystem models such as ECOPATH with ECOSIM (Christensen et al. 2005) have provided insight about the structure, state and vulnerability to human and climate pressure of the Northern and Central Chile marine systems. For instance, Medina et al. (2007) used the model for a snapshot of the system in 1989, describing the main components of the fish community and the main characteristics of pelagic environment in NCME and identified gaps of knowledge. Barros (2007) explored through simulation the effect of climate variability, fishing and vulnerability to predation (zooplankton) as drivers of anchovy-sardine alternation in the NCME. Neira (2008) assessed when and why ecological thresholds may be exceeded and whether bottom-up forcing or fishing is more likely to induce irreversible ecosystem states. Simulations suggest that fishing rather than decadal bottom-up forcing is more likely to result in ecological thresholds being exceeded, inducing regime shifts with low likelihood of recovery. In addition, the author also assessed the changes of food web structure off central-south Chile during 20th century identifying: i) an increase in the fishing mortality on the fish stock and food web, ii) a decrease in the removal of large predators, iii) an increase in the relative abundance of small pelagic fish, all of which lead to a current state of system (2005) which is stressed and vulnerable to external forcing.

1.5   The importance of body size in marine ecosystems

Body size is a trait that captures a significant proportion of the ecologically relevant characteristics of organisms in an ecosystem. If body size is not taken into account, a large amount of biological information can be loose (Woodward et al. 2005). Moreover, aquatic ecosystems are strongly size-structured, with many species growing continuously throughout their lives by up to five orders of magnitude in body mass (Cushing 1975). At the individual level, body size determines to a large extent key life-history processes such as growth, ingestion, metabolic, birth and death rates. These are all correlated with body mass through a power law relationship ($Y=aM^{b}$) (Peter 1983, Lewis et al. 2008). The range of prey sizes consumed by a predator expands with increasing predator body size (Scharf et al. 2000, Barnes et al. 2008, 2010b) and moreover, the relation between body mass and population density (numerical abundance) in a log-log space declines in the ocean with slope around -1

(Sheldon et al. 1972, Jennings and Mackinson 2003). Body size is an excellent predictor of trophic level within the community (Jennings et al. 2001). Drivers such as climate variability and fishing can influence size structure by speeding up growth and predation rates and targeting large fish, and therefore modify the functioning of fish assemblages, with consequences for productivity and resilience of some fish populations and communities (Shin et al. 2005, Daufresne et al. 2009, Law et al. 2012).

In addition, size is a basic trait used in many indicators and models to identify and predict the effect of climate variability or fishing in marine communities in the context of EBFM. Shin et al (2005) describe size-based indicators are statistics summarizing the size distribution of fish assemblages and populations. They provide relevant integration of the effects of fishing on community structure and processes, environment-induced or genetic variability in life history characteristics, predator-prey relationships, or competitive interactions. In addition, the underlying processes that drive size-based indicators can be understood intuitively by non- scientists, are cost-effective and straightforward, and reference directions of change can be established on the basis of theoretical, empirical, and modelling studies. Furthermore, size-based models and in particular size-spectrum models seem to be promising tools because i) they can take into account the whole ecosystem (Travers et al. 2007), ii) they are based on the empirical evidence that abundance scales with body size (Sheldon et al. 1972), iii) require a relatively small number of parameters, and iv) they can be used in data-poor situations. Also, because they assume that 'large fish eat small fish', they allow relevant processes such cannibalism and interspecific predation to be taken into account. These processes are crucial to understanding the dynamic and functioning of marine communities, e.g. size-selective predation may lead to the occurrence of Allee effects (De Roos et al. 2003), the recovery of long-live fish species (depensatory effects), and the alternation of sardine and anchovy species (Irigoien and Roos 2011).

1.6   Thesis aims and structure

The general aim of this thesis is to contribute to the understanding of the dynamics of the pelagic community off northern Chile and to the implementation of EBFM.

By using empirical and theoretically approaches, I try to combine EBFM with emerging ecological theory on the key role of body size in the structure and function of marine ecosystems.

In **Chapter 2**, I study the observed changes in size-based fishery indicators in the Northern Chile fish stocks at the levels of species and assemblages, together with environmental indicators over the period of 1990 to 2008. I also examine the effect that climate variability could have on the size structure of the fisheries resources. In **Chapter 3,** I describe the pelagic fish community off northern Chile in terms of species composition, trophic and distributional characteristics. I present a mathematical model of the multispecies size-spectrum model developed in this thesis, and describe how parameters for the model were gathered. I also discuss the overall structure of the model, its consistency with empirical studies, future applications, and its limitations. In **Chapter 4,** I use the multispecies size spectrum model to show that the well-known alternation of sardine and anchovy in upwelling marine ecosystems can be influenced by the combined effects of the environment and predation. Cannibalism and interspecific predation can be drivers of the extinction or coexistence of anchovy and sardine, depending on how environmental forcing acts on the size-structure of the plankton community. In **Chapter 5,** I show work in progress on the effect of fishing mortality on the pelagic fish community off northern Chile. Specifically, I use traditional size-at-entry and balanced harvest strategies to study the effects of fishing on anchovy, through four population and fishery indicators. I discuss the steps that will be needed to test the findings and the potential implications for anchovy fishery management. The thesis ends with a General Discussion in **Chapter 6** where I highlight the main contributions of thesis to the knowledge of dynamics of the pelagic fish community off northern Chile. The chapter also discusses the main caveats and limitations of the research, and the future directions of this work in the context of the application of EBFM in the North of Chile.

Chapter 2

Environmental effects on size-based indicators of the exploited fish assemblage off Northern Chile

2.1 Abstract

Understanding the relative impact of human and environmental pressures on marine fish communities is a key challenge. Size-based indicators carry information about the effects of climate variability and fishing on the size distribution of fish. Environmental data was used to investigate the effect of the climate variability on size-based indicators from commercial catches off northern Chile from 1990 to 2008. I found that sea surface temperature showed no trend over time but contained a number of anomalies corresponding mainly to El Niño/La Niña events. Chlorophyll-a increased significantly over the period 1997 to 2008. Changes in the fish community and in the fishery occurred including collapse of the sardine fishery, an increase in the smallest jack mackerel caught and a downward trend in the size-structure of the whole assemblage of the catch. Only short-term effects of the environment variables on the indicators of anchovy and sardine were found affecting the mean length and the catch per unit effort respectively. I conclude that catches from the pelagic community off Northern Chile shown an increase in fish of smaller body size and of anchovy species. It is argued that these trends arisen from the combined effect of climate variability and fishing. Implications for the whole community as well as recommendations for monitoring are discussed.

2.2 Introduction

The development of the ecosystem approach to environmental management of marine communities implies the need to account for multiple pressures on ecosystems (Rochet et al. 2010). However, understanding the relationships between natural and human pressures and ecosystem health is challenging, particularly in marine ecosystems owing to their complex nature, dynamic environmental processes

and influences from human activities (Halpern et al. 2008). Indicators are now widely accepted tools to monitor changes in the state of population, communities and ecosystems, and several are needed to identify the impact of multiple pressures in a system (Rochet and Trenkel 2003, Rochet et al. 2010). An indicator's relevance lies in its capacity to summarize how the state of a system changes with respect to a specific pressure or impact, how sensitive it is in detecting impacts, as well as how communicable it is to managers and stakeholders (Rice and Rochet 2005).

Body size is an important characteristic in ecosystems because organisms obey scaling laws that dictate how biological features change with size (Peters 1983). In marine ecosystems, organisms can grow many orders of magnitude throughout their lifetime and body size can be a stronger a predictor of the trophic role of on individual organism than species identity (Jennings et al. 2001). Size-based indicators have been shown to detect declines in the abundance of larger individuals and species that occur from the direct and indirect effects of fishing on populations and communities (Shin et al. 2005). Fishing mortality can reduce abundance/biomass and reduce mean body size (Beverton and Holt 1957) and under heavy fishing pressure these effects can permeate through the system leading to declines in the body size of fish communities, either by removing the largest size fish in the community and, indirectly, by relaxation of predation pressure as the abundance of large fish declined (Shin et al. 2005, Heath and Speirs 2012). Size-based indicators will also carry information on environmentally-driven changes in size distributions such as recruitment success and food- and temperature-dependent growth.

There is growing theoretical and empirical support for the possible forms of the relationships between the size-based indicators with environmental or human pressures (Trenkel and Rochet 2010). For instance, increments in temperature are thought to speed up growth and predation rates, shifting towards smaller sizes individuals, populations and communities (Daufresne et al. 2009, Shackell et al. 2010). Increased primary productivity can either decrease mean size in the short term due to recruitment pulse or in the longer term lead to larger sizes (Beverton and Holt 1957).

The Humboldt Current System (HCS) along the coast of South America is widely known for its high productivity of small pelagic fish (particularly anchovy) and its climate variability at different temporal scales (e.g. interannual, decadal and

centennial) (Montecino and Lange 2009). Climate variability in the HCS is driven by the El Niño/La Niña-Southern Oscillation (ENSO) taking place in an interannual scale (every 5 to 7 years) and the regime shifts (decacal) (Alheit et al. 2009). These two types of temporal variability are of significant magnitude and cause major alterations in the whole ecosystem (Alheit and Niquen 2004).

Under El Niño or a warm regime, the system can be characterized by the approaching of warm subtropical oceanic waters to the coast off Perú and Chile (increase in the sea surface temperature), a deeper thermocline, a weaker upwelling and lower productivity. Opposite conditions take place during La Niña-'normal' or a cold regime with a prevalence of cold coastal water, a shallow thermocline, stronger upwelling and higher productivity (Bertrand et al. 2004b, 2008b, Alheit and Niquen 2004, Yáñez et al. 2008a, Chavez et al. 2008, Alheit et al. 2009). These changes are thought to lead to increases in biomass of low trophic level organisms such as meso-zooplankton under cold temperatures and decreases in warmer periods. Changes in the species composition of ichthyoplankton community have been also identified (Alheit et al. 2009).

The effect of the climate variability on higher trophic levels in the HCS has been studied mainly for commercially species and particularly for anchovy. Under El Niño conditions changes in the size structure, the intensity and duration of spawning and the spatial distribution of species can take place (Niquen and Bouchon 2004, Alheit et al. 2009). Species becoming more patchily distributed, closer to the coast and/or deeper into the water column and can migrate from North to South (Bertrand et al. 2004b, Niquen and Bouchon 2004, Yáñez et al. 2008a). These disruptions lead to changes in the species composition, trophic structure of the community as well as the fishery, which may change from mono-specific (anchovy based) to multi-specific (e.g. sardine, jack mackerel) (Bertrand et al. 2004b, 2008b, Niquen and Bouchon 2004). For instance, Niquen and Bouchon (2004) found that anchovy size-structure is characterized by the absence of young individuals prior to El Niño events and by an increase of them at the end. Juveniles (1-2 years old) of sardine predominate during the event. Reproductive activity of anchovy is diminished and sardine and mackerel increases. Owing to displacement from the north to the south, species such tuna, pacific mackerel, jack mackerel, skipjack, and mesopelagic species increase in Peruvian waters.

Although the decadal variability may affect the pelagic community of HCS in similar ways as a short term event (e.g ENSO), the decadal changes are thought to lead to a complete and permanent reorganization of the pelagic community (Alheit and Niquen 2004). For example, under a "warm period" anchovy biomass decreased significantly. The hypothesized reasons for this have been linked to 1) shifts in the size structure of zooplankton towards small sizes and 2) increases in the vulnerability and spatial availability of egg, larvae, juveniles and adults of anchovy to predators (e.g. mackerel and horse mackerel). At low abundance and spatial occupancy, anchovy populations are thought to increase their localized density (due to hyperaggregation) and this may lead to increased cannibalism as well as increased vulnerability to fishing and predation (Alheit and Niquen 2004, Gutiérrez et al. 2007, Yáñez et al. 2008a, Bertrand et al. 2008b). In the opposite phase of the decadal variability a 'cold regime' is thought to cause an increase in favorable habitat conditions for anchovy and at the same time unfavorable conditions for sardine larvae and eggs. Sardine biomass decreases, along with its spatial occupancy (Alheit and Niquen 2004, Gutiérrez et al. 2007, Yáñez et al. 2008a).

While the effect of the environmental variability on pelagic fish populations in the HCS has been well studied in terms of its abundance, biomass, spatial distribution, species composition and catches, little is known about its effect on the size distributions of species or community assemblages. The goal of this study is to investigate the effects of environmental variability on size-based indicators of pelagic fishery off Northern Chile. I suggest that a shift towards small body size could have taken place in the size-structure of the catches from pelagic fish assemblage of NMCE as consequence of the persistent environmental change. Yáñez et al. (2008a) proposed that NCME went through a regime shift of cold sea surface temperatures at the end of 1980s. The permanence of cold SST in the system could have triggered a series of changes in the habitat of pelagic fishery resources, and in particular of anchovy and sardine. Following the mechanism proposed by Alheit and Niquen (2004) and Alheit and Bakun (2010) for the HCS, the hypothesis in this Chapter is that the prevalence of cold temperature concomitant with a shallow thermocline increased the productivity in coastal water leading to better feeding and recruitment of anchovy. The conditions in NCME that favoured anchovy were deleterious for sardine and therefore a sustained failure in recruitment of sardine led

to a decrease in its abundance and the yield. After El Niño 1997-1998 a drastic decrease of abundance of jack mackerel and mackerel in Peruvian waters and central Chile was also observed (Bertrand et al. 2004b). These concomitant changes in pelagic system of NCME may have led in the long term (1990 – 2008) to a size-structure of the catches dominated by small body size and single species.

To explore these temporal changes, I use detailed size-structured information from the pelagic fisheries operating in the NCME, which is available for the dominant species that comprise the pelagic fish assemblage: anchovy (*Engraulis ringens*), sardine (*Sardinops sagax*), mackerel (*Scomber japonicus*) and jack mackerel (*Trachurus murphyi*). Size-based indicators were developed at population and assemblage level; it was examine whether linear trends have occurred over the time period from 1990 to 2008, and whether or not they are related with environmental variables such as sea surface temperature and productivity (chlorophyll-a).

2.3 Methods

2.3.1 Background

The study area was the NCME (**Figure 1.1**) known for its permanent upwelling sustaining a high level of primary production (Thiel et al. 2007). The pelagic fish community is characterized by a relatively short food chain. Besides the phytoplankton and zooplankton, three trophic levels of consumers can be distinguished: planktivorous fish (anchovy, sardine and mesopelagic fish), large fish predators such as jack mackerel, mackerel, and top predators (sea lions and birds) (Barros 2007, Medina et al. 2007). Commercial exploitation of the fish assemblage started in the mid 1950s targeting mainly anchovy and sardine, and later was extended to jack mackerel. These species encompass a range of life histories, from fast somatic growth (e.g. anchovy–von Bertalanffy growth rate (k) = 0.88 year^{-1}; Cubillos 1991) and early maturity such as anchovy (**Table 2.1**), to species with slow growth (e. g. jack mackerel-von Bertalanffy growth rate (k) = 0.094 year^{-1}; Gili et al. 1995) and late maturity such as jack mackerel (**Table 2.1**). The mean trophic level of the catches has been estimated to be 2.7, indicating that fishing removes mainly low trophic level species (Medina et al. 2007).

Table 2.1. Length at maturity (L_m), asymptotic length (L_∞) and maximum age (A_{max}) of the species studied.

Species	L_m (cm)	L_∞(cm)	A_{max} (year)	References
anchovy	12.5	20.25	4	Cubillos (1991), Canales and Leal (2009), Serra and Canales (2009)
sardine	26	38.6	10	Serra et al. (1979), Cárdenas and Mendo (1985), Froese and Pauly (2000)
mackerel	26	44.4	10	Aguayo and Steffens (1986), Pardo and Oliva (1992), Froese and Pauly (2000)
jack mackerel	25.5	70.8	19	Gili et al. (1995), Cubillos and Alarcón (2010), Arcos et al. (1995).

2.3.2 External pressures

To detect environmental variability effects on the species and on the overall exploited assemblage, three sources of environmental data were used to construct environmental indices. First, sea surface temperatures (SST, °C) from 1990 to 2008 for the NCME were obtained from Advanced Very High Resolution Radiometer (AVHRR) pathfinder (http://poet.jpl.nasa.gov/), at a spatial resolution of 4 km. Second, as a proxy indicator of the productivity, monthly averages of Chlorophyll-a (CHL) were obtained from the sea-viewing Wide Field-of-View satellite sensor (SeaWiFS) from http://oceancolor.gsfc.nasa.gov/ at a spatial resolution of 9 km. These records were only available for the period 1997 to 2008. Values of SST and CHL were converted to annual mean. Third, SST data from the El Niño 3.4 region from http://www.cpc.noaa.gov/data/indices/ were used to identify the presence of El Niño (warm event) or La Niña (cold event) conditions in the Equatorial Pacific Ocean and related with SST in the NCME. Anomalies meeting or exceeding +/-0.5°C for three consecutive months were used to identify a warm or cold event.

2.3.3   Indicators

Size-based indicators were calculated at the species and at the assemblage level, spanning from 1990 to 2008 (with the exception of sardine indicators owing their extremely high rarity in the years 2003 to 2008). The data came from the archives of the Institute of Fisheries Development Chile and consisted of logbooks of fishing boats, length frequency distribution of the catch disaggregated to species, and individual weight and length measurements. The number of the total individuals caught by length class (in cm) by year and species was raised to the total landings taking into account the stratified sampling design of the commercial purse seine fleet (Saavedra 2006). Note that in using fishery information I am looking at changes at population and assemblage level, but also changes in fishing activity in response to the biological changes and environmental variability.

Using the above information, size-based indicators were calculated as follows:

2.3.3.1 Species indicators

Mean length $(\bar{L}_i)$. This indicator was calculated as:

$$\bar{L}_i = \frac{\sum_j N_{i,j} \, l_j}{\sum_j N_{i,j}}$$

where, $N_{i,j}$ is the numbers of individuals of species i caught in the length class j, l_j is midpoint of the length class j. It is expected that unfavourable environmental conditions can lead to a reduction of the mean length of catches as consequences of a migration of the larger individual from their permanent habitat and therefore fishing zone (Niquen & Bouchon 2004). On the other hand, favourable environmental conditions can lead to a decrease in the mean length of catches due to recruitment success and in the long term to increase the number of larger size individuals caught.

Maximum length $(L_{0.95})$. The maximum length $(L_{0.95})$ indicator was obtained as the 95% percentile of the size distribution sampled in each year by species (Rochet et al. 2005). Changes in the selectivity (towards smaller sizes) in the jack mackerel fishery

took place in 2001, and this indicator helped to differentiate if a potential reduction in the $\overline{L_i}$ of catches was due to an increase in the number of small individual caught or to a reduction in the number of the individuals with larger body size caught.

Catch per unit effort (lnCPUE). The natural logarithm of catch per unit effort (CPUE) was used as an indicator of the number individuals caught of all size per fishing trip. CPUE was obtained for each species by dividing the number of individuals caught in each year by the number of fishing trips taking place per year. The duration of fishing trips was not possible to determine from information available.

Catch per unit effort of adults (lnCPUEA). This indicator was calculated as the same lnCPUE, but included only the number of individuals with length greater than the length at maturity (**Table 2.1**).

2.3.3.2 Assemblage indicators

Mean length ($\overline{L}$). This indicator quantifies the average size of the fish in the catches ignoring species differentiation.

$$\overline{L} = \frac{\sum_j N_j l_j}{\sum_j N_j}$$

where, N is the numbers of individuals caught in the length class j, l_j is midpoint of the length class j.

Mean maximum length (L_{max}). This quantifies the life-history trait composition within the catches of the assemblage:

$$L_{max} = \sum_{i=1}^{4} \frac{N_i l_{i,\infty}}{N}$$

where, N_i is the numbers of individuals caught of the species i, $l_{i,\infty}$ is the asymptotic length of species i (**Table 2.1**), and N is the total numbers of individuals in the catches of the exploited assemblage.

Slope and intercept of size spectra. By definition size spectra represent the logarithm of abundance or biomass of a community as a function of the logarithm of body size (Duplisea and Castonguay 2006). The slope reflects the relative abundance of small and large fish in the community whereas the intercept reflects the overall productivity of the system. Although the slope and intercept had been used mostly as indicators of the fishing impact in aquatic communities, is possible to expect that the slope of size spectra from the catches also became steeper as consequence of reduction in body size of the individuals caught. An increase in the intercept is also expected if the main composition of catches shifted towards smaller body sizes.

To calculate the slope and intercept from fisheries data, individual length (cm) was transformed to weight (g) using the species-specific length-weight regression coefficients and body weights were transformed to a logarithmic scale with base 2. Biomass (g) per fishing trip was binned in intervals 0.4 (g) on this logarithmic scale. The size spectrum, in this case the relationship between log2 normalized biomass against midpoint class of log2 body mass class, was obtained for each year from 1990 to 2008. The log2 scale was chosen based on the range of body of the size-structure of the catches.

Body masses in the range 16 – 450 g were considered when estimating the slope and intercept of the spectra. This was less than the full range of body mass in the data (1 – 1875 g) because it was only this part of spectrum that is under full exploitation by the fishing gear. Size spectra were standardized to remove the correlation between the slope and intercept by subtracting the mean from the independent variable (Trenkel and Rochet 2003). A linear regression analysis was applied in order to estimate the slope and intercept of the annual size spectrum in the fish assemblage.

2.3.3.3 Trends analysis

The trend analysis of all indicators and environmental indices was used to identify whether linear decreases or increase occurred over the time, which expresses a continuous (permanent) change in the system (Trenkel and Rochet 2010).

To test for monotonic trends over time in the environmental and biological indicators, linear regression analysis was used. The analysis started by fitting a linear

regression to each indicator time series using ordinary least-squares (OLS). The linear model had the form $y=\hat{\beta_0}+\hat{\beta_1}x+\varepsilon$, where y corresponds to an indicator, $\hat{\beta_0}$ is the intercept of single regression, $\hat{\beta_1}$ is a parameter for the predictor variable x (year), and ε is the error assumed $N(0,\sigma^2)$. An ANOVA was carried out to identify if a linear model was significantly better than a null model (only intercept, no linear change) using an F ratio test. The Durbin-Watson test was used to test for autocorrelation in the residuals and Shapiro-Wilk test for normality. A maximum lag of three years for autocorrelation was considered adequate owing to the short length of the time series. The critical value for rejecting the null hypotheses of no autocorrelation and normality was taken as $\alpha=0.05$. When autocorrelated residuals were present a linear model with generalized least-squares (GLS) was fitted which allows the error to be time dependent, in this case using an autoregressive process of order 1 (Blanchard et al. 2010). When residuals showed a significant departure from normality, the linear trend was fitted using robust linear regression (RLM) (Venables and Ripley 2002). Few cases were identified with both conditions and GLS fitting was carried out for them. Coefficient of determination (R^2) for the GLS was calculated according to Nagelkerke (1991) and for the RLM the adjusted R^2 coefficient was based on Renaud and Victoria-Feser (2010).

2.3.3.4 Environment – indicator relationships

Linear environment-indicator relationships were studied to assess the direct effect of the environment (SST or CHL) on each indicator at species and assemblage levels. For each environment-indicator pair a linear regression model using GLS was fitted. A forward selection of the predictor variable (SST or CHL) was carried out starting from a null model (intercept only). To identify if a linear model was significantly better than a null model an ANOVA and F-ratio test were used. Since CHL data were only available from 1997-2008, the effect of this variable was only possible to study for a small subset of data. A significance level $\alpha=0.05$ was used for all models except for CHL where $\alpha=0.1$ was used because of the short time series of data.

2.4 Results

2.4.1 Trends in external pressures

SST did not show a significant trend over the study period 1990-2008 (**Figure 2.1a**) (OLS: p-value=0.417, R^2=0.040). However, important anomalies of the SST were identified during this period (**Figure 2.1a**), which coincided with El Niño (positive) or La Niña (negative) events detected in the regional index El Niño3.4 SST. Warm events in NCME were observed in the years 1992, 1997, 1998, with 1997 being the highest (> +1°C) (**Figure 2.1a**). The coolest anomaly in NCME was observed in 2007 (< -0.5 °C). Although other cold and warm events have been observed in the NCME (Yáñez et al. 2008a) they were not clearly visible in the local SST time series (**Figure 2.1a**).

CHL showed a significant upward (GLS: p-value=0.069, R^2=0.252) trend (**Figure 2.1b**) from 1997 to 2008.
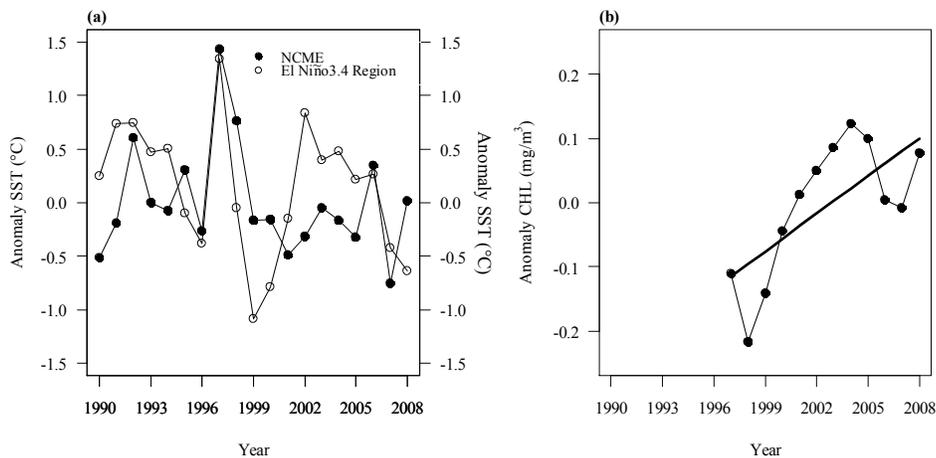
Figure 2.1. Time series of environmental indexes. (a) SST anomaly at the NCME and at El Niño3.4 Region. (b) CHL at the NCME. (The line represents the statistically significant linear trend found in the environmental variables).

2.4.2 Trends in indicators

Significant negative linear trends in the indicators were detected for all species except anchovy (**Table 2.2; Figure 2.2a, 2.3a**). This species only showed important outliers in $\overline{L}_i$ and lnCPUEA that occurred during the El Niño event in 1997-98. Downward linear trends in three sardine catch indicators were detected (**Table 2.2; Figure 2.2.b, 2.3.b**). Mackerel indicator trends included a downward trend only in lnCPUEA though not in the body size ($\overline{L}_i$, $L_{0.95}$) (**Table 2.2.; Figure 2.2.c, 2.3.c**). A downward trend in lnCPUEA, mean and maximum length of jack mackerel catch indicators was also evident, but not in lnCPUE (**Table 2.2.; Figure 2.2.d, 2.3.d**).

At the assemblage level, a significant steepening of the size spectrum slope over time was detected from linear models (OLS: p=0.022, R^2: 0.229), but no trends were observed in the other indicators $\overline{L}$, L_{max}, and the intercept of size spectra (**Figure 2.4. a, b**).
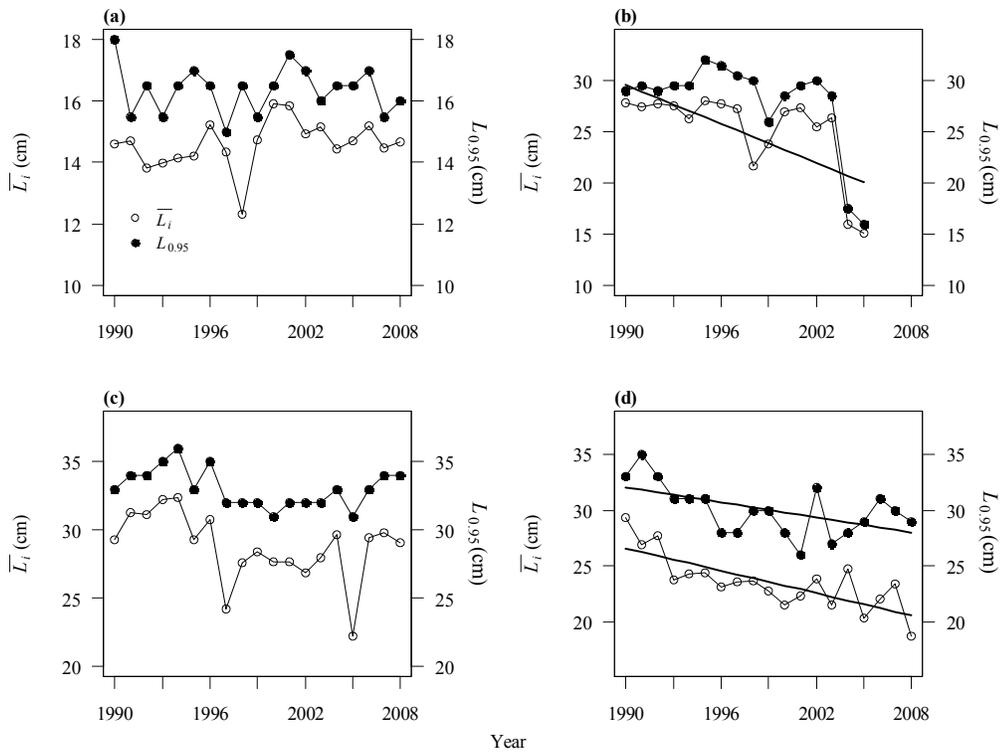
Figure 2.2. Time series of the size-based indicators: Mean length ($\overline{L}_i$) and Maximum length ($L_{0.95}$). (a) Anchovy, (b) Sardine, (c) Mackerel and (d) Jack Mackerel. (The lines indicate a significant linear trend in the indicator).

Table 2.2. Statistical tests of linear trends in indicators over time at the species-population level. First number is the probability of no trend from an ANOVA F-test; the second number is the coefficient of determination R^2 of a time series regression. Bold numbers identify a significant trend at $\alpha=0.05$, and D the direction of the trend in the indicator: ($\uparrow$) increase, ($\leftrightarrow$) no change, ($\downarrow$) decrease.

species	$\overline{L}_i$ Linear p-value (R^2)	D	$L_{0.95}$ Linear p-value (R^2)	D	lnCPUE Linear p-value (R^2)	D	lnCPUEA Linear p-value (R^2)	D
Anchovy	0.112 (0.105)	$\leftrightarrow$	0.751 (0.006)	$\leftrightarrow$	0.050 (0.207)	$\leftrightarrow$	0.274 (0.069)	$\leftrightarrow$
Sardine	**0.029 (0.227)**	$\downarrow$	0.085 (0.161)	$\leftrightarrow$	**<0.001 (0.453)**	$\downarrow$	**<0.001 (0.448)**	$\downarrow$
Mackerel	0.137 (0.102)	$\leftrightarrow$	0.417 (0.035)	$\leftrightarrow$	0.217 (0.096)	$\leftrightarrow$	**0.036 (0.233)**	$\downarrow$
Jack mackerel	**<0.001 (0.327)**	$\downarrow$	**0.015 (0.301)**	$\downarrow$	0.445 (0.035)	$\leftrightarrow$	**<0.001 (0.623)**	$\downarrow$
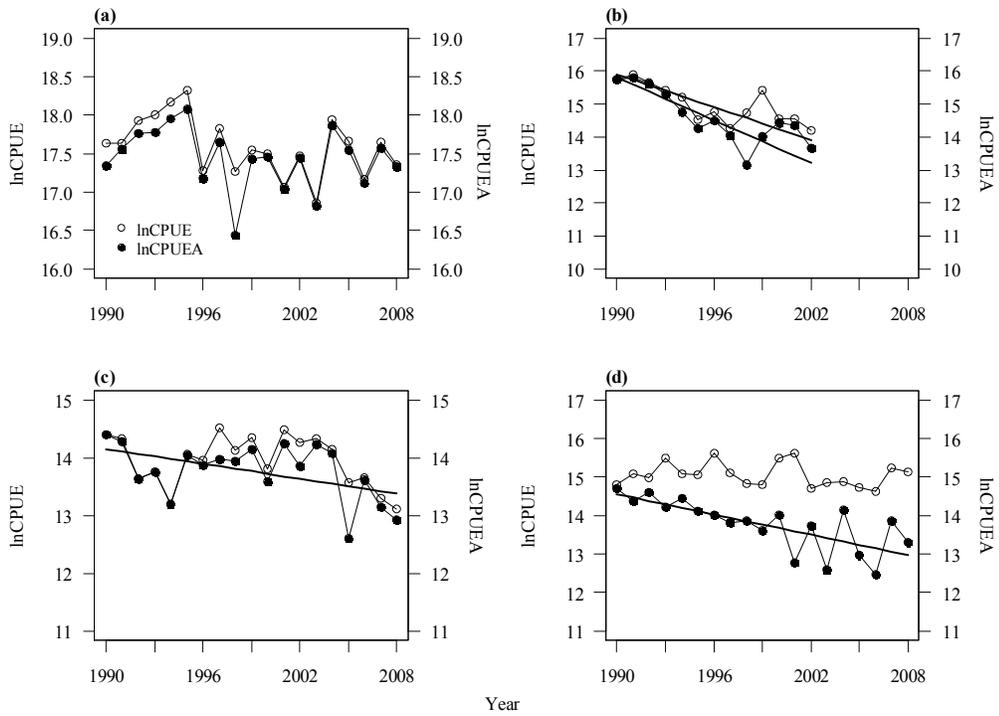
Figure 2.3. Time series of the indicators: lnCPUE and lnCPUEA. (a) Anchovy, (b) Sardine, (c) Mackerel and (d) Jack mackerel. (The lines indicate the significant linear trend in the indicator).
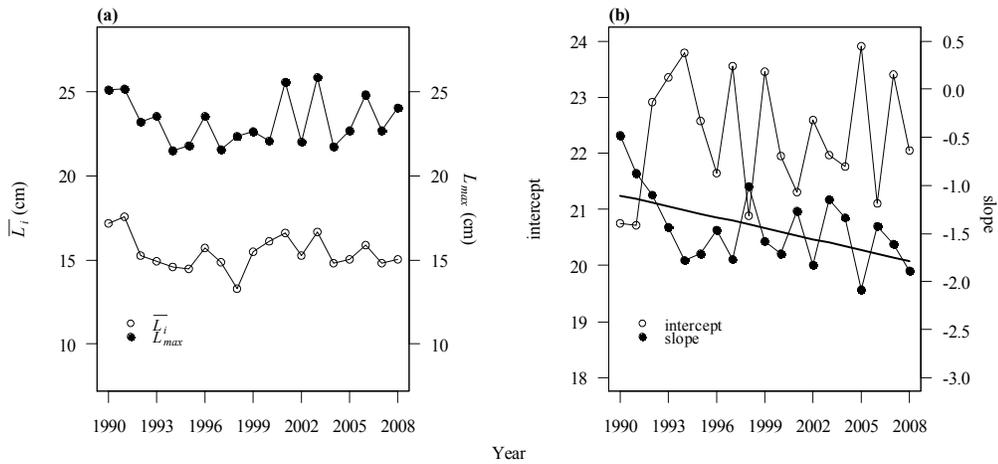
Figure 2.4. Time series of the assemblage size-indicators: (a) Mean length ($\overline{L}$) and Mean maximum length (L_{max}). (b) Intercept and slope of the catch size-spectrum. (The lines indicate the significant linear trend in the indicator).

45

2.4.3 Environment-indicator relationships

Single direct effects of the environment were detected on certain indicators in anchovy, sardine, but not in mackerel, jack mackerel or in the whole assemblage (**Table 2.3**). They corresponded to a negative effect of SST on $\bar{L}_i$ of anchovy and also negative effect of CHL on lnCPUE of sardine (**Table 2.3**).

Table 2.3. Statistical models of indicators as functions of environmental pressures. Results selected (ANOVA, F-test) that were giving significant improvements over a null model (ANOVA, F-test) are shown. P-values correspond to the ANOVA, F-test. R^2 is the coefficient of determination of the selected model. Numbers in brackets correspond to the standard error of each parameter.

Component	Indicator	Model selected	$\hat{\beta}_0$	$\hat{\beta}_1$	p-value	R^2
anchovy	$\bar{L}_i$	$\sim\hat{\beta}_0+\hat{\beta}_1 SST$	29.870 (6.538)	-0.763 (0.327)	0.041	0.243
sardine	lnCPUE	$\sim\hat{\beta}_0+\hat{\beta}_1 CHL$	18.331 (1.408)	-7.792 (2.466)	0.019	0.798

2.5 Discussion

The findings showed short-term effects of the environment on the indicators of anchovy and sardine, and downwards trends in the size structure of the catches of sardine, jack mackerel and at the assemblage level.

The environmental effect on anchovy was associated with El Niño 1997-1998 is believe produced temporal disruption in the distribution of anchovy, and therefore the normal fraction of anchovy population (adults) available to be caught in the regular fishing zone was absent. The decrease in mean length of anchovy took place in 1998 when the anomaly of temperature was slightly lower than the maximum value in 1997, indicating a post-El Niño condition normally characterized by absent of adults individual (Niquen and Bouchon 2004). In 1999 the mean length of

anchovy catches recovered and the lack of persistent trend in the mean length time series support the hypothesis of temporal effect rather than an increase in the recruitment.

El Niño effect on the size structure of anchovy catches has been identified in previous study in the HCS. For instance, Ñiquen and Bouchon (2004) reported in the Peruvian system a notorious change in the distribution of anchovy body size during the El Niño events 1972-73, 1982-83 and 1997-98. At the onset of the event predominance of adults characteristic and at end of the event juveniles or small body sizes of anchovy prevailed. These changes are due to temporal modifications of habitat that ended with anchovy becoming patchier, changing its distributions southwards and deepening into waters and therefore adult availability to the fishery (Bertrand et al. 2004b, 2008b, Yáñez et al. 2008a).

The trends found in sardine indicators were in line with the present state of collapsed of its fishery and low abundance state of the population at the NCME (Serra and Canales 2009). A similar condition has been reported in the Peruvian ecosystem for the fishery and the population (Gutiérrez et al. 2007, Valdés et al. 2008). The scarce data points after 2000 in sardine catches together with the short time series in CHL call for care in interpreting the statistically negative effect of the CHL on the numerical catches of sardine as directly linked. However, this pattern could be a consequence of a failure of sardine to effectively use the high productivity available in the area owing to its association with more offshore waters during colder conditions (Bertrand et al. 2004b, Alheit and Niquen 2004, Niquen and Bouchon 2004, Gutiérrez et al. 2007).

The simultaneous decrease in the size-based indicators of jack mackerel suggest a sustained decrease in the numbers of larger individual caught, but also an increase in the number of individuals caught under the size of maturity (juveniles). I think that these trends are reflecting modifications in the fishing selectivity in the NCME and in the condition of the spawning stock biomass of the population off of the Chilean coast. The increase of small individuals caught is not likely to be explained by an increase in recruitment since the spawning stock has been defined as 'under critical values' (SUBPESCA 2010). Thus, the decrease trend in the mean length seems to be a consequence of an increase in the number of individuals caught under the size of maturity from a shift in selectivity that took place in 2001 in the NCME (Serra, per

com). The downward trends found in the body size of largest individuals caught together with the number of individual caught above the size of maturity of jack mackerel has been also reported by the stock assessment (Serra and Canales 2009).

The steeping of the slope of the size spectrum in the catches of the assemblage indicate a gradual change in the catches of the purse seine fleet being progressively more dominated by smaller fish. This is the result of the combined effect of each species trends in term of numbers of individuals caught and their changing body size distributions, that seems to be driven by both the environment and fishing. Although, no correlation with SST or CHL and the slope of the size spectrum were found, external evidence in the Humboldt Current system provides supporting evidence for a possible environmental effect. Gutiérrez et al. (2007) characterize the dynamics of sardine and anchovy in the Peruvian system since 1983 to 2003 in three periods: 1983-1992, 1993-1999; 1999-2003. The first - second period is described as a transition period towards the dominance of anchovy and the second - third period as anchovy dominating the pelagic community. The authors related these transitions with cooler conditions in the HCS, suggesting that the trend observed at assemblage level in NCME can be partially explained by environmentally driven changes in the ratio of sardine: anchovy. However, the trends observed also involved jack mackerel catches which reflected the influence of changes in the fishery. The size-at-entry to the fishery was reduced from 26 to 21 cm in 2001 (Böhm per com).

These findings carry a warning from a community point of view that the current fishing activity in the NCME is sustained mainly by a small sized species and at a community level could have implications such as slow down the growth rates of its predators (jack mackerel, mackerel etc.) owing to the removal of prey by the fishing (Andersen and Pedersen 2010). This could lead to a delay in the time required to rebuild predator populations even if the fishing mortality in predator populations is reduced. This type of predator-prey dynamics has been postulated as one of reasons for the lag observed in the recovery of demersal community after a long period of low harvesting in Scotland (Heath and Speirs 2012).

The majority of the combinations between size-based indicators with environmental indices studied did not yield to statistical significant results. This may be due to a low number of observations and therefore the SST time series used here did not register the trend toward the cooler condition identified in other HCS. The CHL time

series also was as yet rather short (1997-2008) for this type of analysis, although its clear positive trend matched with marked increase in productivity during the same time period in other upwelling regions (Belkin 2009, Demarcq 2009).

In this study fishery-dependent data was used to analyse the effect of the environment on the overall catches from the pelagic fish assemblage of NCME. As fishing can be an important driver in marine communities, particularly in decreasing trend of the body size, it is necessary to carry out studies of this nature with fishery-independent data. The methodological approach used here could be used to analyse survey data in this region and infer the status at a community level as well at the species. However, no standardized fishery independent survey time series for the NCME were available that allowed me to evaluate the whole community. While ad hoc surveys have been carried out, there is no established monitoring programme in place to track changes in the abundance and distribution of both the commercial and non-commercial species or the overall size-structure of the pelagic community. Although the fishery data available are limited they can still be used to evaluate to some extent changes that are occurring in the commercial species. To seriously move towards implementing an ecosystem-approach to fisheries in this region, the development of and commitment to an appropriate and regionally/temporally coordinated monitoring program is recommended.

Chapter 3

A multispecies size-spectrum model for the Northern Chilean Marine Ecosystem

3.1 Abstract

Modelling marine communities in the Humboldt Current system has mainly been done by using methods that only disaggregate the community down to its component species. However, by doing so, important ecological features can be lost. Body size is a trait that captures a significant proportion of the ecologically relevant characteristics of organisms in an ecosystem. This chapter incorporates body size into modelling the dynamics of the pelagic fish community off Northern Chile. Using the framework of the observed scaling of abundance with body size in marine ecosystems known as size-spectrum a dynamic multispecies model is developed. The community model accounts for eight species which are ecologically and commercially important along with plankton community. In the mathematical model, the fish community arises from the combined size-based dynamics of each species. The energy flows in the system through the predation event and is transformed into process of somatic growth and reproduction. At the same time the death of prey gives rise to the mortality process. This process depends on the feeding behaviour of the species which are given as species-specific functions (feeding kernels) describing the relationship between a predator and prey. A novel feeding kernel is developed to describe the planktivorous feeding of anchovy and sardine. The results give estimates of the parameters of the model including feeding kernels, life history, allocation to reproduction and background mortality, derived from a variety of sources. The results also show initial densities of the pelagic community based on survey data to be used in numerical solutions of the model. The selection of species, feeding kernels and life history characteristic, difficulties in the parameterization of the interaction matrix, and the need for validation and further studies are discussed.

3.2 Introduction

The Humboldt Current System (HCS) extends along the coast of South America from 4°S off northern Perú to 40°S off central south of Chile. The ecosystem is widely known for its exceptionally high productivity of small pelagic fish (particularly anchovy), together with its interannual (every 5 to 7 years, El Niño), decadal and centennial climate variability and the large and dynamic oxygen minimum zone (Montecino and Lange 2009). The system encompasses three well-defined marine upwelling subsystems: a productive seasonal upwelling system off central-southern Chile; a lower productivity and rather large ''upwelling shadow" off northern Chile and southern Perú; and the highly productive year-round Perú upwelling system (Chavez and Messié 2009).

The most frequent approach to modelling the marine ecosystems along the HCS has been to use Ecopath with Ecosim (Christensen et al. 2005) to follow the flow of energy through trophic levels. Using this approach, the effects of fishing and environmental variability such as El Niño or regime shifts on the marine communities off Perú and Central South of Chile have been studied (Jarre et al. 1991, Jarre-Teichmann and Pauly 1993, Neira 2008, Guénette et al. 2008, Tam et al. 2008, Taylor et al. 2008). An individual-based size-structured model, OSMOSE (Shin and Cury 2004), has also been applied to study the effect of different management measures and scenarios on the hake population in the Peruvian system (Marzloff et al. 2009).

However, there has been relatively little attention given to the system shared between Chile and Perú at the level of the community. Studies on this system include a preliminary food web model (Ecopath) for the pelagic community (Medina et al. 2007) over the latitudes 18°20'S-24°00'S, and a simulation analysis (Ecosim) investigating the well-documented anchovy and sardine alternation using a more disaggregated model with 19 groups (Barros 2007). In common with other studies of upwelling systems, the authors describe the ecosystem as being immature, with low recycling of primary production and short trophic pathways. They also showed that organisms in the pelagic zone dominate the system in terms of biomass fluxes. The simulation analyses (Barros 2007) explored the effect of climate variability, fishing and vulnerability to predation (zooplankton) as drivers of anchovy-sardine

alternation and found that the fishing alone did not trigger the switch in dominance. The clearest alternation between the species took place when fishing was present, and physical forcing was modifying the size structure of the zooplankton community, together with an increase in the vulnerability of the zooplankton (top-down trophic control from anchovy and sardine).

The present study incorporates body size into modelling the dynamics of the Northern Chilean Marine Ecosystem (NCME) for the first time. Size-structured dynamics allow important ecological features to be included that are lost when aggregating from individuals to species (Woodward et al. 2005). For instance feeding interactions in aquatic ecosystems are strongly driven by body size with individuals progressively feeding on larger prey items as they grow (Scharf et al. 2000), as documented in HCS pelagic species such as sardine and anchovy (Van der Lingen et al. 2009). Thus a species can be both a prey and predator of another species, individuals changing status from one to the other as they grow. Furthermore, biological rates of growth, ingestion, metabolism, birth and death change with body size, and can be described by power law relationships of body mass m, of the form $Y = am^b$ (Peters 1983, Lorenzen 1996, Lewis et al. 2008). Partitioning organisms by body size rather than by species, reveals a remarkable empirical regularity in marine ecosystems that roughly equal amounts of biomass occur in logarithmic body size classes (Sheldon et al. 1972, 1973). At a community level, trophic dynamics are driven more by body size than species identity (Jennings et al. 2001).

Size-spectrum models were used (see Travers et al. 2007 for a review of a size-based and other ecosystem modelling approaches) to represent the density of the entire size structure of the pelagic system off North Chile from plankton to large fish predators. This framework draws on the observed scaling of abundance with body size in marine ecosystems (Sheldon et al. 1972, 1973). Early work showed that, if the standing stock in any size range is known, then the standing stock can be estimated at other sizes, and if the growth rate is known at that size, then production can be estimated (Sheldon et al. 1977). Platt and Denman (1977, 1978) calculated the steady state distribution of biomass as a function of body size in the pelagic ecosystem by introducing the concept of normalized spectrum, and established an empirical relationship describing the weight dependence on metabolism and growth. Silvert and Platt (1980) developed a continuous, non-linear model where the flux of energy

is governed by predation and the resulting growth and mortality, and predicting that the spectrum can be linear using a fixed predator-prey size ratio. More recently, this approach was extended by Benoît and Rochet (2004) by allowing predators to feed on a range of prey sizes.

Size-spectrum models of the kind above describe the dynamics at the level of the ecosystem, using densities of particles of different sizes, and do not differentiate between species, functional groups or spatially separated subcomponents. Species and other subgroups are important in practice, and there is increasing interest in disaggregating size spectra into their component parts. Andersen and Beyer (2006) derived the community power-law spectrum as the sum of the steady state spectra of a large number of species with different asymptotic masses. Blanchard et al. (2009) implemented a size-spectrum model to couple a pelagic and benthic community together with detritus. The spectrum of each community is the result of growth and mortality and the coupling between components is done through predation and production linkages. Using metabolic scaling theory, Hartvig et al. (2011) disaggregated the community size spectrum down to the level of individual species, allowing species to differ in reproduction and preferences for food, incorporating an interaction matrix to define the extent to which each species experiences its own size spectrum and that of other species.

Working from this multispecies approach a multispecies size-spectrum model (MSSM) for the NCME was implemented using three basic species-dependent processes: growth, mortality and reproduction. An advantage of this framework is that it requires a relatively small number of parameters, and can be used in data-poor conditions. The core of the approach is a preference for the size of food items, which is implemented by a kernel function for prey size relative to size of the predator as in previous dynamic size-spectrum models. However, a crucial difference from earlier work is that two of the most important species, anchovy and sardine retain the capacity for filter feeding on phytoplankton up to adult body sizes (Van der Lingen et al. 2009), and this calls for new assumptions about the kernel function for these species. The model incorporates a dynamic partitioning of the prey mass consumed. This requires a small proportion of the ingested mass being assimilated, some of which is transformed into body growth and some to reproduction once maturation has occurred. In the model, the extent to which species feed on their own size spectra

and those of other species is implemented by means of a community interaction matrix (Hartvig et al. 2011).

This chapter describes the development of the MSSM from a conceptual model of the community. First, I describe the system of study, location and species composition with their life history, trophic and distributional characteristics. Second the mathematical basis of the model in terms of the biological processes is presented. Third, I describe how parameters such as feeding traits, the life history and the plankton spectrum were obtained. Finally, the overall structure of the modelled pelagic community from plankton to large fish is discussed in the context of its consistency with empirical studies, future applications and limitations.

3.3   Methods

3.3.1   The system of study

NCME is part of the upwelling subsystem of northern Chile and southern Perú. This study takes the part under Chilean administration (**Figure 1.1**) which spans the latitudes from 18°20'S to 24°00'S and from the coast up to 200 nm corresponding to the limit of Exclusive Economic Zone (EEZ). The pelagic fish community that inhabits the area supports a purse seine fishery based successively on anchovy and sardine. Jack mackerel with mackerel as bycatch are also part of the catches in the area.

To model the pelagic fish community, the species were chosen according to (1) their ecological relevance in terms of their role in the ecosystem, and (2) fishery relevance in terms of biomass and catches levels. These criteria were balanced by availability of data. Three main sources of information were consulted: previous food web models (Ecopath with Ecosim) used in the NCME (Barros 2007, Medina et al. 2007), official landings (SERNAPESCA 1955-2008), and fleet logbooks (Institute of Fisheries Development-Chile). The species and/or groups selected are shown in **Figure 3.1** and comprise: mesopelagic fish, anchovy (*Engraulis ringens*), sardine (*Sardinops sagax)*, mackerel (*Scomber japonicus),* jack mackerel (*Trachurus*

murphyi), Eastern Pacific bonito *(Sarda chilensis)* (for simplicity it will be called 'bonito')*,* palm ruff (*Seriolella violacea*) and swordfish (*Xiphiaus gladius)*.

The mesopelagic group is an assemblage of species, the biomass of which has become important in the HCS since 1997 (Marzloff et al. 2009). More than 25 species belonging to more than 13 families have been described for the Peruvian and Northern Chilean systems (Sielfeld et al. 1995, Medina and Arancibia 1998, Cornejo and Koppelmann 2006). There is insufficient information to treat all these species separately, so I created a functional group to represent this assemblage in the pelagic environment. I parameterized the group based on the most abundant (96 % of the total relative abundance of mesopelagic fish) species in the NCME: *Cyclotone acclinidens, Diogenichthys atlanticus, Tripthoturus mexicanus* and *Vinceguerria lucetia* (Sielfeld et al. 1995). These species reach small asymptotic sizes, and are consumers of zooplankton, and early stage of fishes (eggs). Also they are part of the diet of mackerel, tuna, squid and mammals. One of remarkable characteristic of this group is their extensive diel vertical migration (Cornejo and Koppelmann 2006).

Anchovy and sardine are species that reach small to medium asymptotic size and dominate the pelagic system. They are mainly consumers of phytoplankton, zooplankton, itchyoplankton and small fish (Espinoza and Bertrand 2008a, Espinoza et al. 2009) and they have been described as prey of mackerels, hake, seabirds and mammals. Their spawning, nursery and feeding grounds overlap in HCS and therefore juveniles, adults and early life stages such as eggs and larvae can be found in the same areas (Checkley et al. 2009b). Mackerel and jack mackerel are pelagic species of medium asymptotic size and, although jack mackerel reach a larger size than mackerel, they have a similar size at maturity. Both species are consumers of zooplankton, mesopelagic fish, anchovy and fish in the NCME, although their diet may vary seasonally (Medina and Arancibia 1998, Bertrand et al. 2004a). Predators of mackerel and jack mackerel are not well identified, but they can be part of the diet of tuna, sharks and swordfish (Bayle 1987, Medina et al. 2007). Both species are widely distributed off the Peruvian and Chilean coasts (Serra 1983), and move in and out of the NCME. Their eggs and larvae are normally found in oceanic water off Perú and Chile (Checkley et al. 2009a). The jack mackerel population off Chile has been postulated to have different nursery, spawning and feeding grounds (Arcos et al. 2001). The mackerel spawning grounds could be found off Chilean and Peruvian

coasts (Checkley et al. 2009a), however it is not clear if a similar ground differentiation applies to mackerel.

Palm ruff and bonito in the HCS reach larger asymptotic sizes than the mackerels, but little is known about their diet composition or their selectivity for their prey off NCME. Part of the diet of palm ruff could be macrozooplankton (Wolff and Aron 1992, Trujillo 2006a) but it also can be a fish predator (Iannacone 2003, Trujillo 2006b). Bonito has been described as a piscivorous consumer of anchovy and mackerel (Ojeda and Jaksic 1979), and can be predated by sharks, seabird and mammals (Barros 2007, Medina et al. 2007). Swordfish reaches the largest size of the species modelled. Although information about its diet composition is quite scarce in HCS off Chile, swordfish has a trophic spectrum based on cephalopods (primarily jumbo squid, *Dosidicus gigas*), fishes (primarily jack mackerel) and crustaceans (Ibáñez et al. 2004, Castillo et al. 2007b, Yáñez et al. 2008b)
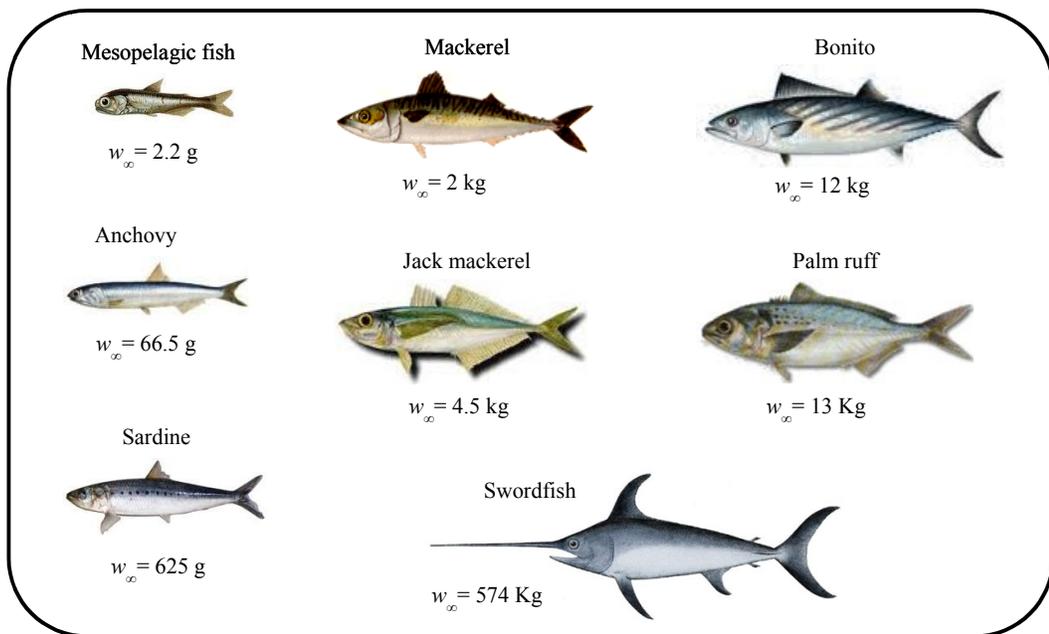
Figure 3.1. Fish species selected in the modelled pelagic community off Northern Chile and their asymptotic mass (w_∞).

3.3.2   Description of the Multispecies size-spectrum model

3.3.2.1 Multispecies size spectra

The primary state variable of the system is $N(w,t)$ (g^{-1} m^{-3}) which gives the number of individuals per unit of mass per unit of volume for organism of body mass w at time t. Ignoring species identity, the numerical density of organisms per unit volume in a range of body mass $[w_{min}, w_{max}]$ at time t is given by $N(t) = \int_{w_{min}}^{w_{max}} N(w,t)dw$. Size spectrum theory is usually developed in a logarithmic mass space owing to the scaling relationship between density and body mass in pelagic marine communities (Sheldon et al. 1972); I therefore replace w with $x = \ln(\frac{w}{w_0})$ where w_0 is an arbitrary value of mass assumed here to be 1 g. The numerical density $N(w,t)$ (g^{-1} m^{-3}) is then expressed as a function of the logarithmic mass as $U(x,t)$, here with units of m^{-3}.

A multispecies size spectrum disaggregates the community spectrum $U(x,t)$ down to smaller components. Typically these are species, although broader assemblages such as plankton and mesopelagic fish are sometimes used. These disaggregated spectra are here indexed $U_i(x,t)$, where $i=1,...n$ for fish, and $i=p$ for plankton.

The community size spectrum $U(x,t)$ is then the sum of all the disaggregated size spectra $U_i(x,t)$ given by

$$U(x,t) = \sum_i U_i(x,t) \qquad . \qquad \qquad \text{(3.1)}$$

The dynamics of the numerical density of each species $U_i(x,t)$ $i=1,...n$ in the system are governed by three continuous processes, somatic growth, mortality and reproduction. (The plankton class $i=p$ is treated separately below). To model growth and mortality, the equation of McKendrick (1926) and von Foerster (1959) is used (Blanchard et al. 2009, Law et al. 2009, Andersen and Pedersen 2010, Hartvig et al. 2011), giving the rate of change of density of class i at size x and time t as follows (arguments of the functions are omitted for simplicity):

$$\frac{\partial U_i}{\partial t} = -E_i \frac{\partial}{\partial x}(g_i U_i) - d_i U_i - \mu_i U_i \qquad \text{for } i=1,...n \qquad \text{(3.2)}$$

Here $g_i(x,t)$ is the average rate at which biomass from feeding is assimilated per unit mass of predator, for a predator of size x at time t; $d_i(x,t)$ is the per capita death rate caused by predation on size x at time t; $\mu_i(x,t)$ is the per capita death rate on size x at time t due to causes other than predation (intrinsic mortality). Following the approach of Law et al. (2012) mass assimilated from predation is partitioned so that a proportion $E_i(x)$ goes to growth, and a proportion $1-E_i(x)$ goes to reproduction. The dependence on x allows construction of a maturation schedule appropriate for each species i. The total rate at which reproductive mass is generated is transformed into a birth rate of eggs $b_i(t)$ at a fixed egg size $x_{i,\mathrm{egg}}$ for species i.

Thus, the dynamics are a consequence of the predation events that transport biomass from prey into somatic growth and reproduction of the predator, and at the same time generate predation mortality on the prey. Below I describe the functions $g_i(x,t)$, $d_i(x,t)$, $\mu_i(x,t)$, $E_i(x)$ and $b_i(t)$.

3.3.2.1.1 Biomass assimilation rate $g_i(x,t)$

Every time that a prey is consumed part of its mass is transformed into mass of the predator. Before this happens, the predator must encounter the prey. The approach here follows previous work on size-spectrum dynamics (Benoit and Rochet 2004, Blanchard et al. 2009, Andersen and Pedersen 2010, Hartvig et al. 2011), and assumes that the volume searched by a predator is an allometric function of the body mass, expressed as $A\mathrm{e}^{\alpha x}$ (Ware 1978). Here, x is the size of the predator, α is the allometric exponent, and A is a parameter describing the volume searched per unit time per unit size (raised to the power α). The encounter rate between a predator at size x and prey of type j at size x' depends on the prey density and is given by $A\mathrm{e}^{\alpha x} U_j(x',t)$. The consumption rate by a predator of type i and size x of prey of type j at size x' also depends on a dimensionless feeding preference function $\phi_{ij}(x,x')$, making the rate $A\mathrm{e}^{\alpha x}\phi_{ij}(x,x')\,U_j(x',t)$ with dimensions T^{-1}. The form of the feeding preference function $\phi_{ij}(x,x')$ is crucial, and is described below. The prey mass is converted into predator mass with a certain efficiency K, and the total assimilation rate for predator species i (per unit mass) at size x is obtained by integrating over all prey sizes x', and summing over all prey types j:

$$g_i(x,t) = KAe^{(\alpha-1)x} \sum_j \int_{x_{\min}}^{x_{max}} e^{x'} \phi_{ij}(x,x') U_j(x',t)dx' \qquad (3.3)$$

3.3.2.1.2 Predation death rate $d_i(x,t)$

The first source of mortality on species i at size x, comes from predation. Like the assimilation, this takes the encounter rate by predators of type j and size x' $Ae^{\alpha x'}$ $U_j(x',t)$, and multiplies by the feeding preference function $\phi_{ji}(x',x)$. The per capita death rate is then obtained by integrating over all predator sizes x', and sums over all predator types j, to get

$$d_i(x,t) = A\sum_j \int_{x_{\min}}^{x_{max}} e^{\alpha x'} \phi_{ji}(x',x) U_j(x',t)dx' \qquad (3.4)$$

3.3.2.1.3 Non-predation death rate $\mu_i(x,t)$

In general there are sources of mortality other than predation, such as parasitism, infections, starvation, hostile environmental conditions, which are greatest at small size and declining with body size (Lorenzen 1996). Moreover, there is likely to be some increase in death rate at large body sizes as a result of senescence. For instance, populations of guppy (*Poecilia reticulate)* exposed to high predation level shown a more rapid deterioration in physiological performance with age (Reznick et al. 2004). In addition, the senescence death in the MSSM helps to prevent the buildup of a high density of fish close to their asymptotic body sizes (Law et al. 2009). Thus non-predation death rate of species i is a U-shaped function (Hall et al. 2006) of body size x written here as:

$$\mu_i(x,t) = \begin{cases} \mu_0 e^{-0.25(x-x_0)} & \text{for } x < x_{i,s} \\ \mu_{x_{i,s}} e^{k_i(x-x_{i,s})} & \text{for } x \geq x_{i,s} \end{cases} \qquad (3.5)$$

For body sizes before the size at which senescence starts $x_{i,s}$, a standard function is set for all species such that the death rate is μ_0 at x_0, taking $\mu_0 = 0.2$ at $x_0 = 0.001$ g; the exponent -0.25 is a standard allometric scaling of the mortality rate to body mass (Brown et al. 2004). The death rate at the start of senescence $\mu_{i,s}=\mu_i(x_{i,s},t)$. From this

size onwards the death rate grows with an exponent $k_i=(\log\mu_\infty-\log\mu_{i,s})/(x_{i,\infty}-x_{i,s})$, where $x_{i,\infty}$ is the asymptotic body size to which type i grows, and μ_∞ is a maximum death rate, shared by all species and set here to have the value of 10. It is assumed that $x_{i,s}=x_{i,\infty}-1$ for all fish categories. In general, $\mu_i(x,t)$ can be a function of time, but is used in a time-independent form here.

3.3.2.1.4 Reproduction $E_i(x)$, $b_i(t)$

The function $1-E_i(x)$ describes the proportion of mass assimilated from prey allocated to reproduction in species i; this goes from 0 before maturation, and reaches a value 1 at an asymptotic body size $x_{i,\infty}$ at which point all incoming mass goes to reproduction. I follow Law et al. (2012) and Hartvig et al. (2011), defining the function as the product of two factors,

$$1-E_i(x)=\left[1+\exp(\beta_{i,0}-\beta_{i,1}\left(\frac{e^x}{a_i}\right)^{\frac{1}{b_i}})\right]^{-1}e^{\rho(x-x_{i,\infty})} \tag{3.6}$$

The first factor (in square brackets) corresponds to the maturity ogive, which accounts for the proportion of individuals at size x that have reached maturity. Parameters $\beta_{i,0}$ and $\beta_{i,1}$ describe the maturity based on the body length, and parameters a_i and b_i transform the length into mass using the allometric relationship for converting length (l) to body weight (w), as $w=a_i l^{b_i}$. The second factor (after the square brackets) describes the allocation to reproduction in a mature individual. It is assumed to be an exponentially increasing function of size that reaches 1 at an asymptotic size $x_{i,\infty}$ (Law et al. 2012). At this size, the entire biomass assimilated goes to reproduction and the somatic growth rate is zero. A value of the exponent ρ = 0.2 is thought to be appropriate in this function (see Law et al. 2012).

The function $1-E_i(x)$ is used to obtain the total rate at which species i accumulates biomass for reproduction. This is achieved by multiplying it by the per capita assimilation rate and the density, and integrating over all sizes x:

$$R_i(t)=0.5\int_{x_{min}}^{x_{max}}(1-E_i(x))w_0e^x g_i(x,t)U_i(x,t)dx . \tag{3.7}$$

Here the value 0.5 reflects assumption that males and female are equally abundant at all size and species, and therefore the numbers of offspring only depend on females. The rate of egg production by species i at time t is the total rate at with the species is accumulating reproductive biomass divided by the egg mass $w_0 e^{x_{i,egg}}$

$$\hat{b}_i(t) = R_i(t) \Big/ w_0 e^{x_{i,egg}} \tag{3.8}$$

This expression is a rate of renewal of the size spectrum $U_i(x,t)$ of species i at its egg size $x_{i,egg}$.

The plankton spectrum is held at fixed values to correspond approximately to the state observed in the NCME (see below). To ensure that the densities of fish species cannot grow without limit, I introduced a density-dependent constraint in the egg production, drawing on the maximum density of eggs observed ($U_{i,megg}$) at sea during spring for each species from 2000 to 2006, and the density of eggs $U_i(x_{i,egg},t)$. I took

a ratio, $r_i = \dfrac{U_i(x_{i,egg},t)}{0.1U_{i,megg}}$ to construct a density dependent function:

$$b_i(t) = \hat{b}_i(t)e^{-cr_i} \tag{3.9}$$

The constant c decides how strongly density dependence operates The value of parameter c was chosen through numerical tests. Each test involved running the model with a value of c at a time. The range of values of c tested was from 6 up to 10 in steps of 1. The criterion of selection of c was to match the observed densities of egg of anchovy in the survey of 2008 at the NCME. The value selected was $c=10$ (a test of the sensitivity of the model to this parameter is provide in **Chapter 4**).

3.3.2.1.5 Feeding preference function

The rate at which prey biomass is assimilated (**Equation 3.3**), and the death rate due to predation (**Equation 3.4**) make use of a dimensionless function $\phi_{ij}(x,x')$ describing the preference of predators of type i and size x for feeding on prey of type j and size x'. Following Hartvig et al. (2011) this function is thought of in two parts

$$\phi_{ij}(x, x') = \theta_{ij}\phi_i(x - x') \qquad\qquad\qquad\qquad \textbf{(3.10)}$$

The scalar θ_{ij} provides a weight over a range 0 to 1 for the degree at which of type i consumes type j, with 0 indicating no feeding of i on j, and 1 indicating full feeding. This applies irrespective of the sizes of the predator and prey. The square matrix θ of order $(n+1)$ by $(n+1)$ with elements θ_{ij} thus captures some basic information about the food web. For instance, if the diagonal elements $(i=j)$ are 1, and off diagonal elements $(i \neq j)$ are 0, each type feeds on itself (cannibalism), with no feeding of different types on each other. Such a matrix would be possible if species were largely separated in space. If the column $j=p$ has all elements with value 1 (except $\theta_{i=p,j=p}=0$) and all other columns are zero, then all types i just feed on plankton.

The function $\phi_i(x\text{-}x')$ describes the size dependence of feeding by type i. In the absence of detailed information the function is assumed to be Gaussian (Ursin 1973) and normalized so that the integral is 1:

$$\phi_i(x - x') = \frac{1}{\sigma_i \sqrt{2\pi}} \exp\left(-\frac{\left((x - x') - \beta_i\right)^2}{2\sigma_i{}^2} \right) \qquad\qquad \textbf{(3.11)}$$

where x-x' is the log base e of the predator prey mass ratio (PPMR) with x-$x' > 0$ so that predators are always larger than prey. The parameter β_i is the preferred ratio of species i (mean value of the kernel function) and a large value means that the predator prefers prey x' a lot smaller than its own size. The parameter σ_i describes the diet breath with respect to body size. This feeding kernel 'moves' with the predator as it increases in size, such that the prey size distribution remains the same relative to the size of the predator. It was used for mesopelagic fish, mackerel, jack mackerel, palm ruff, bonito and swordfish.

However, it is well known (Van der Lingen et al. 2006) that sardine and anchovy retain a capacity for filter feeding on phytoplankton such as small diatoms and dinoflagellates, as well as feeding on larger particles, as they grow. Individuals of these species thus broaden their diets as they increase in size, and require assumptions about the feeding kernel different from those previously used in size-spectrum dynamics. To describe the feeding kernels of these species, I assumed that parameters β_i and σ_i vary with body size, while keeping the assumption of a gaussian

kernel function in place. For simplicity I refer to these species as 'planktivores' and the others as 'omnivores', although there is clearly some overlap in the diets of the two groups.

From sampling of stomach contents (Espinoza and Bertrand 2008b, Espinoza et al. 2009) the minimum prey sizes of sardine and anchovy can be defined, and was called the minimum prey size, $x'_{i,min}$, and write $x\text{-}x'_{i,min}$ as $(x\text{-}x')_{i,max}$ for the largest PPMR for type i at size x (for consistency with a PPMR notation). I assume that the minimum PPMR $(x\text{-}x')_{min}$, i.e. the largest prey body size x' relative to the predator body size x, is fixed and is the same both species having a value $\log_e 10$. The parameters of the gaussian feeding kernel are then

$$\beta_i(x) = \log_e 10 + \frac{(x - x')_{i,max} - \log_e 10}{2} \tag{3.12}$$

$$\sigma_i(x) = \frac{\beta_i(x) - \log_e 10}{3} \tag{3.13}$$

Thus, as the predator body size x increases, so do β_i and σ_i; the factor $1/3$ is chosen to ensure that almost all the feeding kernel is included (the kernel is then normalised to integrate to 1).

3.3.2.1.6 Parameterization of the multispecies size-spectrum model

Here the methods by which the parameters of the MSSM were estimated are described, together with the sources of information used.

3.3.2.2 Fish spectra: feeding traits and life history parameters

3.3.2.2.1 Feeding traits

In the case of the planktivores, the key parameter for the feeding kernel is the minimum prey size, $x'_{i,min}$. For anchovy this was taken from Espinoza and Bertrand (2008) and for sardine from Espinoza et al. (2009).

For fish species i other than the planktivores, the preferred PPMR (β_i) and the diet breath (σ_i) were calculated from predator and prey mass ratio (PPMR) in published

data or extracted directly from literature. In the cases where empirical PPMRs were calculated, the value of β_i and σ_i were obtained as mean and standard deviation of the $\log_e$ transformed ratios. A summary of how PPMR were calculated for each species is described below. To obtain this information a conversion from body length l to body mass w was sometimes needed; for this the allometric relationship $w = al^b$ was used, with parameters a_i and b_i taken from the literature.

Mesopelagic fish diet composition for the most abundant species off Northern Chile was obtained from (Oliva et al. 2006). Prey sizes were taken from (Espinoza and Bertrand 2008b) and from http://earth.leeds.ac.uk/cyclops/data/ncfs-zooplank.xls. For the allometric relationship between length and body mass, mean values for a_i and b_i of the four main species were obtained from Fishbase (Froese and Pauly 2000). Jack mackerel and mackerel feeding kernel functions were parameterized according to the study of Medina and Arancibia (1998). These authors calculated the predator prey mass ratio seasonally for both species. To obtain β_i and σ_i I took the mean value of the index for each species.

Palm ruff feeding traits were obtained from Aron et al. (1992) who reported the stomach contents of this species in the area of Coquimbo-Chile. This information of diet composition for predator size and prey size was combined with allometric function of length and mass to calculate the body weight of predator and prey. For each predator size the empirical ratio between its size and the size of its prey in $\log_e$ scale was calculated. The mean and standard deviation of these ratios corresponded to the preferred ratio (β_i) and diet breath (σ_i).

Information on PPMRs of bonito and swordfish had to be taken from outside the Humboldt Ecosystem. In the case of bonito, information on diet composition by predator size and their prey size was taken from Campo et al. (2006). This information was combined as the same as before with the allometric function to calculate the body mass of predator and prey and then the empirical PPMRs. In the case of swordfish, predator and prey body masses were taken from Barnes et al. (2008) to estimate the empirical PPMR. For both species the mean and standard deviation of the ratios in $\log_e$ scale corresponded to the preferred mass ratio and diet breath.

3.3.2.2.2 Life history parameters

Maturity ogive parameters were obtained from literature or estimated based on published data and/or from stock assessment reports. Thus, anchovy and swordfish maturity parameters were taken from Canales and Leal (2009) and Demartini et al. (2000) respectively.

Maturity parameters for all other groups were obtained by fitting empirical data (Black 1979, Pardo and Oliva 1992, Oliva et al. 1999, Canales et al. 2003, Stequert et al. 2003, Serra and Canales 2011) to a logistic function (Roa and Ernst 1999), of the form $P_i(l) = \dfrac{1}{1 + \exp(\beta_{i,0} + \beta_{i,1} l)}$, where $P_i(l)$ corresponds to the proportion of female mature at the body length (l) in species i, and $\beta_{i,0}$ and $\beta_{i,1}$ are parameters of the function to be estimated. As for the feeding traits, a conversion from body length l to body mass w was needed; this came from the allometric relationship $w = a_i l^{b_i}$, with parameters a_i and b_i taken from the literature. Sardine, anchovy, mackerel and jack mackerel parameters were obtained from fishery data (Institute of Fisheries Development-Chile). For mesopelagic fish, palm ruff, swordfish and bonito values of a_i and b_i were taken from Acuña et al. 1998, Marzloff et al. 2009, Cerna 2009 and Fishbase (Froese and Pauly 2000).

Equation 3.6 for the proportion of mass allocated to reproduction also requires the asymptotic size $x_{i,\infty}$ of each type i. Parameter values for mesopelagic fish and palm ruff came from Marzloff et al. (2009) and Acuña et al. (1998), respectively. For other species the allometric relationship $W_{i,\infty} = a_i L_{i,\infty}^{b_i}$ was used. In this relationship, L_∞ corresponds to asymptotic length taken from the von Bertalanffy growth equation, with the allometric parameters a_i and b_i as already described. For mesopelagic fish, anchovy, mackerel, jack mackerel, palm ruff and swordfish, von Bertalanffy growth parameters were taken from Aguayo and Steffens (1986), Cubillos (1991), Gili et al. (1995), Marzloff et al. (2009), Cerna (2009) respectively. Sardine and bonito growth parameters were taken from Fishbase (Froese and Pauly 2000). von Bertanffy growth equations parameterized for each species were also used to compare with somatic growth obtained from solving the size-spectrum model.

Weight of fish eggs were obtained directly from literature or calculated from information on egg diameter. Egg weight for mesopelagic fish, anchovy and jack mackerel were obtained from Helfman et al. (1997), Castro et al. (2009), and Santander and Castillo (1971) respectively. Egg weight for all others species were calculated by assuming a sphere of volume $V = \frac{4}{3}\pi\left[\frac{d}{2}\right]^3$ and transformed to weight assuming the density of water of 1 (g m^{-3}). Diameters (d) for sardine, mackerel, palm ruff, were obtained from Hunter and Kimbrell (1980), Herrera et al. (1987), Bustos and Silva (2011) respectively, and for bonito and swordfish from Fishbase (Froese and Pauly 2000).

3.3.2.2.3 Plankton spectrum

An empirically-derived baseline size-spectrum for plankton in the NCME was obtained according to a power law function $U_p(x) = U_{p,x_0}(x-x_0)^{-\lambda_p}$ with two parameters, U_{p,x_0}, the density of plankton at a chosen size x_0 (m^{-3}), and $-\lambda_p$, the slope of the spectrum. Using a fixed function, makes it possible to hold the plankton spectrum at a level similar to that observed in the NCME.

I parameterized the plankton spectrum according to the plankton size structure at NCME. Data from a monitoring survey carried in October 2008 in NCME were used (Braun et al. 2009). These data give the numerical density (m^{-3}) of the following plankton groups: picoplankton (0.2-2 μm), nanoplankton (2-20 μm), microphytoplankton (20-200 μm), microzooplankton (20-200 μm) and zooplankton (>200 μm). The density of each phytoplankton and zooplankton group was also available at different size subclasses. I selected the data for the area of study 18°20'-24°00' and from 0 to 50 m depth, in order to build the plankton spectrum for NCME. From this the slope ($-\lambda_p$) and density U_{p,x_0} at the particular size x_0 were obtained.

In building the empirical plankton spectrum several assumptions were needed to obtain the numerical density (m^{-3}) at particular body weight of plankton (g). Densities of the picoplankton and the five nanoplankton classes (2-4 μm, 4-8 μm, 8-12 μm, 12-16 μm and 16-20 μm) were assigned to the midpoint of the class. Cell

volume was found by assuming cells were spheres, with diameter (d) given by the midpoint size class. Thus volume was calculated as $V=4/3\pi r^3$ with $r=d/2$.

Microphytoplankton density was available fractioned for the dominant species. Body volume of each species was taken from Espinoza and Bertrand (2008). When cell volume of a genus was not available from literature an average volume was calculated by the group (diatoms or dinoflagellates) and assigned to the species. This was the case for two dinoflagellate species.

Microzooplankton densities were also available for the six main dominant groups in the community (ciliates, copepodites, nauplii, eggs, radiolarians and tintinnids). Body volume (um^3) for radiolarians and tintinids were taken Espinoza and Bertrand (2008). Body weight (g) of copepodites and nauplii were taken from http://earth.leeds.ac.uk/cyclops/data/ncfs-zooplank.xls. Ciliates and eggs were assumed to have a spherical form. Measures of body size (μm) for these two groups were available from the same source of data, and the average diameter for each group was taken.

Zooplankton densities were fractioned into twelve size classes. An ellipsoidal shape ($V=0.52\ d^2 D$) of their volume was assumed (Echevarria and Rodriguez 1994) where the D is the length of the longest axis in the ellipsoid and r is the width of mean cross section assumed as $D/3$.

The volumes calculated for all groups were transformed into weight (g) with standard value 1 (g cm^{-3}) for water density. Body weight class (g) and density (m^{-3}) were binned into $\log_e$ scales and the plankton spectrum obtained. Using linear regression analysis the slope ($-\lambda_p$) of plankton spectrum was estimated. From the predicted plankton spectrum U_{p,x_0} was obtained, where x_0 corresponded to the smallest size of plankton observed.

3.3.2.2.4 Fish spectrum

I also provide baseline spectra for fish categories, to provide initial conditions for numerical integration of the MSSM. As in the plankton spectrum, the spectra for each fish species were assumed to follow power law function of the form $U_i(x) = U_{i,egg}(x - x_{i,egg})^{-\lambda_i}$ where $U_{i,egg}$ is the numerical density of fish species i (m^{-3})

67

at the egg size $x_{i,egg}$. The slopes of the fish spectra ($-\lambda_i$) were all assumed to be -1 following the theory of size spectrum (Sheldon et al. 1972, Marquet et al. 2005) as no data were available to estimate the slope. Weights of fish eggs ($x_{i,egg}$) were obtained as described in **Section 3.3.2.2.2**

Ichthyoplankton data from Braun et al. (2009) were used to obtain numerical density (m^{-3}) at the egg size of each species. The total number of fish eggs in 10 m^2 was available by station. An averaged value for the area of study was estimated and expressed in m^{-3}. The arithmetic mean of density can be considered a good estimator to analyse changes with time on the variable. I tested this by resampling the total density of eggs estimated in 2008 equivalent to 23.88 [eggs/m^3]. After 10000 realizations of the data the final value was 23.81 [eggs/ m^3], similar to the averaged mean.

The species composition of the total egg density was taken from the observations made between 2000 to 2006 (Braun et al. 2009) owing to the low or lack representations of some species in the 2008 survey. Egg densities of sardine, anchovy, jack mackerel and mackerel were calculated for this period, based on their relative proportions. This period was considered a 'normal' condition in the system, which means an absence of strong of El Niño events. No information on egg density was available for the remaining species and the density of eggs for mesopelagic fish, palm ruff, bonito and swordfish were assumed to be contained in a group named 'other species' for the same period of time. The density of this last group was split into mesopelagic fish, palm ruff, bonito and swordfish. The first group was assumed to have a higher density of eggs because its high importance of biomass compared to the others. Equal proportions were kept for the remaining species palm ruff, bonito and swordfish.

3.4   Results

3.4.1   Feeding traits, life history and non-predation parameters

A summary of all feeding traits and life history parameters by species is provided in **Table 3.1.** The first set of parameters in the table and the smallest prey size of

sardine and anchovy together with their largest PPMR give the feeding kernel functions (**Equations 3.11, 3.12, 3.13**) shown in **Figure 3.2.** Anchovy and sardine functions are characterized by a variable β and σ that changed as function of the predator size. **Figure 3.2** shows an example at three predator weights 0.01, 1 and 60 (g). The heights and widths of their kernel become lower and wider respectively as anchovy and sardine increase in size. This is because the predator still consumes the smallest phytoplankton prey as it increases in body size, and therefore the ratio between a predator and prey becomes larger. In addition, the kernel functions of anchovy were narrower than sardine at all sizes, because anchovy predated on larger prey sizes than sardine.

The feeding kernel functions of the remaining fish categories were constant with size. Species of medium size such as mackerel and jack mackerel had greater diet breadths compared with those species that reach the largest size in the modelled community (palm ruff, bonito and swordfish). The difference was owing to mackerel consuming smaller sized prey such zooplankton at adult sizes, whereas the largest species fed mainly on fish.

At this stage, I do not provide estimates of θ_{ij}, describing the interactions between species. The effects of these parameters are investigated in the Chapter 4.

Table 3.1. Feeding traits and life history parameters of the each species i modelled in the MSSM of NCME. Feeding traits parameters, preferred PPMR ratio (β_i) and diet breath (σ_i). Maturation parameters $\beta_{i,0}$ and $\beta_{i,1}$, and $w_{i,\text{egg}}$ corresponds to the egg weight (g). $L_{i,\infty}$ (asymptotic length), k_i (growth rate), $t_{i,0}$ (age at minimum length), $w_{i,\infty}$ (asymptotic weight) are parameters from the von Bertalanffy somatic growth model. Parameters a_i and b_i correspond to allometric function between length (l) and weight (w) $w=a_il^{bi}$. (Highlighted values in grey are biological parameters **imported** from Eastern North Pacific Ocean, Eastern Atlantic Ocean and Mediterrean Sea).

Groups	Feeding parameters		Maturation parameters			Growth parameters				Allometric parameters	
	β_i	σ_i	$\beta_{i,0}$	$\beta_{i,1}$	$w_{i,\text{egg}}$	$L_{i,\infty}$ (cm)	k_i (y^{-1})	$t_{i,0}$ (y)	$w_{i,\infty}$ (g)	a_i (g cm^{-b})	b_i
Mesopelagic fish	6.57	2.054	9.78	3.20	0.0003	7.80	1.15	-0.06	2.20	0.0035	3.138
Anchovy	*	*	18.09	1.45	0.0003	20.25	0.88	-0.01	66.48	0.0048	3.160
Sardine	*	*	27.26	1.02	0.0035	38.60	0.21	-0.75	625.10	0.0068	3.129
Mackerel	9.36	3.067	19.91	0.74	0.0007	44.40	0.16	-1.54	2008.32	0.0090	3.246
Jack mackerel	7.57	2.395	19.88	0.76	0.0005	70.80	0.09	-0.90	4553.96	0.0100	3.058
Palm ruff	5.19	1.144	24.20	0.55	0.0005	82.00	0.52	0.00	12178.00	0.0134	3.071
Bonito	4.24	1.273	62.80	1.19	0.0001	101.0	0.15	0.02	13333.14	0.0118	3.020
Swordfish	7.71	1.646	14.90	0.10	0.0026	327.0	0.13	-2.59	573888.75	0.0034	3.272

*Anchovy and sardine smallest prey size were set at $x'_{min}=\log_e(10^{-8})$ and $x'_{min}=\log_e(10^{-10})$ respectively. The smallest PPMR for both species was set at $(x-x')=\log_e(10)$.
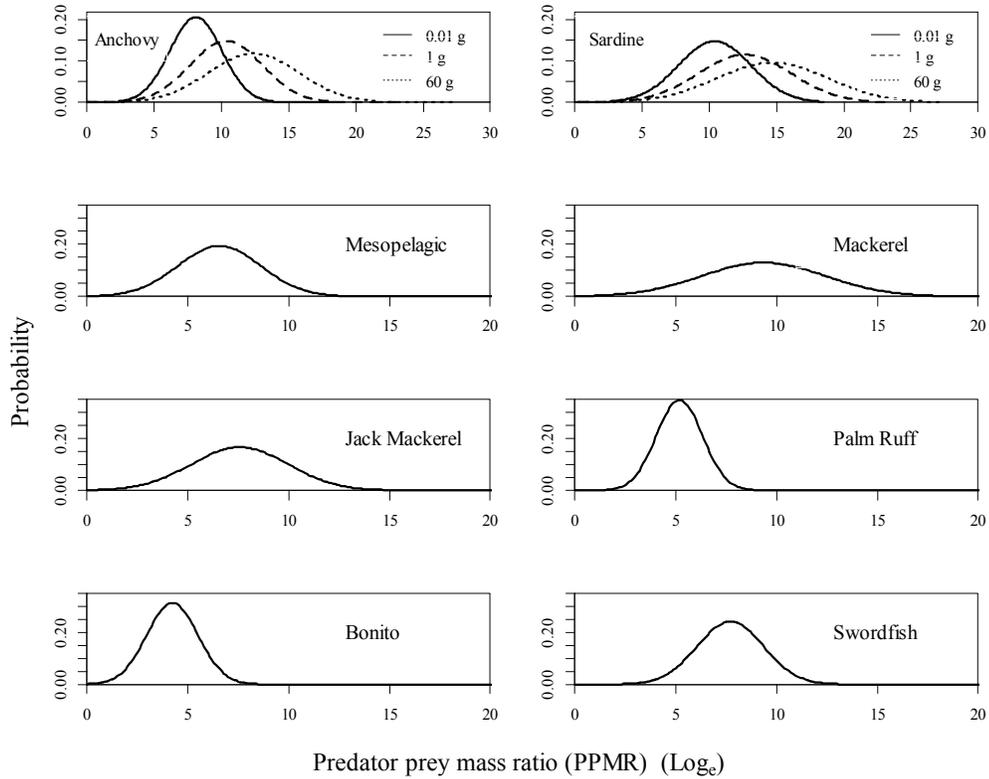
Figure 3.2. Feeding kernel functions of fish in the multispecies size-spectrum model of NCME.

Maturation parameters, allometric parameters, and asymptotic weight (**Table 3.1**) lead to the functions in **Figure 3.3** showing the proportion of mass assimilated from prey allocated to reproduction (**Equation 3.6**) as a function of body size. This proportion always increases with predator size, reaching value of 1 when the predator is at its asymptotic size ($x_{i,\infty}$) where all assimilated biomass goes to reproduction. Anchovy, sardine and mackerel invest rapidly the mass of prey into reproduction compared with palm ruff, bonito, swordfish and mesopelagic fish. Jack mackerel differs from the others in having a slower invest in reproduction after reached its maturity size because of its early maturity and large asymptotic size (Cubillos and Alarcón 2010), together with relatively fast growth before maturity (Serra, per comm).
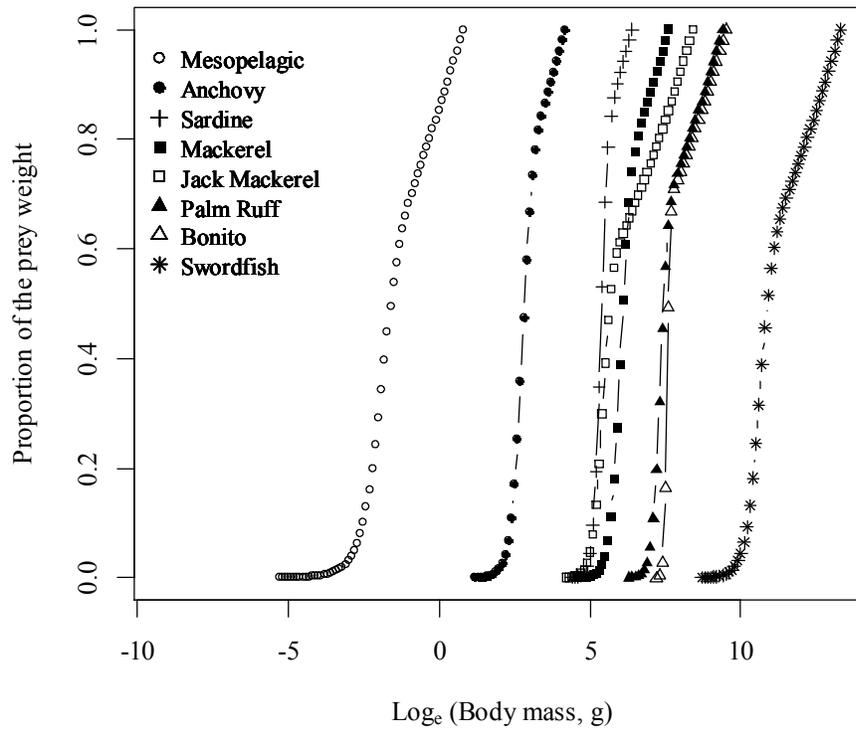
Figure 3.3. Proportion of mass assimilated from prey allocated to reproduction as a function of body size in fish groups.

Non-predation death rates of the fish groups are shown in **Figure 3.4**. Because of the assumptions in **Equation 3.5**, the curve are all near to a U-shaped, with a relatively high death rate for eggs and larvae. The death rate falls to lowest value before the onset of senescence, and then rising to a maximum of 10 at the asympotic size.
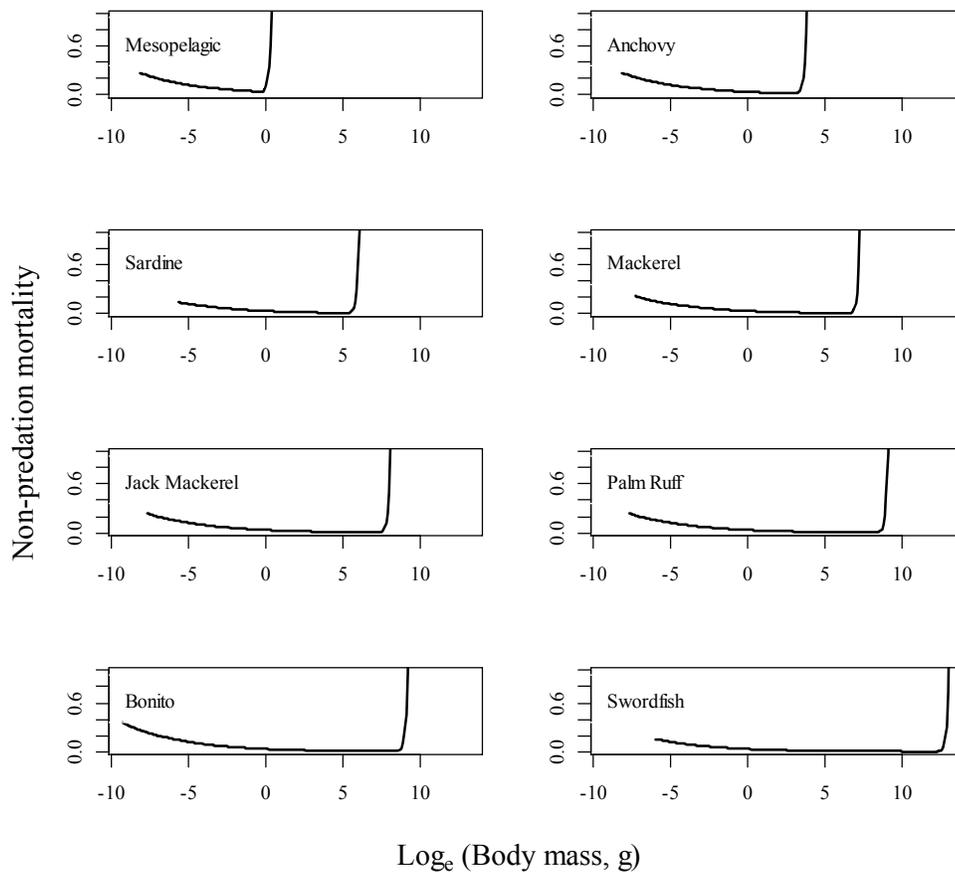
Figure 3.4. Non-predation mortality functions for each species in the multispecies size-spectrum model of NCME.

3.4.2   Multispecies size spectrum in NCME

Plankton and fish spectrum parameters together with parameters for body size (**Table 3.2**) lead to the representation of the multispecies size spectrum of NCME shown in **Figure 3.5.** The plankton spectrum spanned the logarithmic size range from -23 to -2.4 (10^{-10}-0.09 g) with density estimated from the regression model $U_p = -6.136 - 1.257 x_p$ (R^2=0.966, p-value <0.001, df=19) fitted to survey data. Largest size of the plankton community overlaps with the densities at small body sizes of the fish species. This is because the body sizes of the plankton community

can be similar to the sizes of the early stage of fish. The fish spectra are composed of eight categories with the highest numerical density corresponding to anchovy and the lowest to mackerel. The slope of the plankton spectrum is steeper than fish spectra because the fish spectra are assumed to have a slope value of -1.
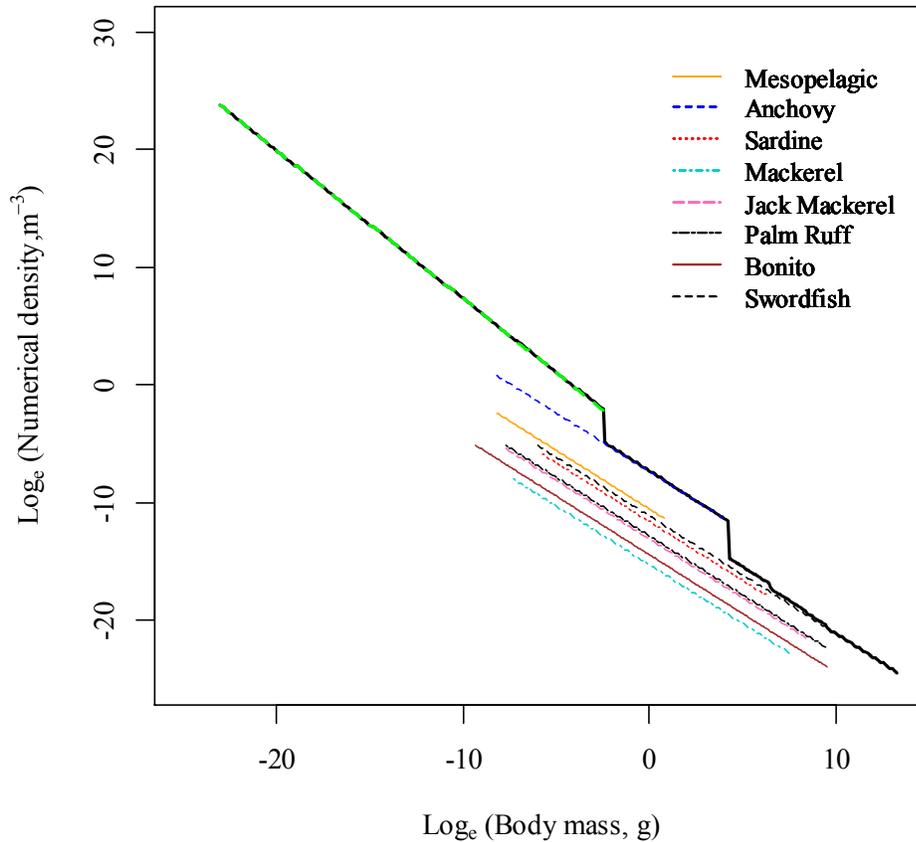
Figure 3.5. Multispecies size spectrum off Northern Chile. Initial conditions of the system. Plankton spectrum corresponds to the green dashed line extending from -23 up to -2.4 (**Table 3.2**) and the community spectrum is the black continuous line spanning from -23 up to 13.2 (**Table 3.2**). Fish size spectra extend from -9.3 up to 13.2 (**Table 3.2**). Species-specific size spectra are identified by different combinations of line types and colours.

Table 3.2. Symbol definitions, parameter values, units and sources for the dynamic community model of NCME. Note that $x = \ln(\frac{w}{w_0})$ with w_0=1g. All value are $\log_e$ scale.

Symbol	Description	Value		Unit	Source
Range of body mass pelagic community					
$[x_{min}, x_{max}]$	minimum and maximum size in the community	[-23, 13.2]			
dx	interval of size	0.1			
Plankton spectrum					
$[x_{pmin}, x_{pmax}]$	minimum and maximum values of the plankton size	[-23,-2.4]			
x_0	reference size plankton	-23			Braun et al. (2009)
U_{p,x_0}	numerical density of plankton at x_0	22.775		m^{-3}	Braun et al. (2009)
λ_p	exponent of phytoplankton spectrum	-1.257			Braun et al. (2009)
Fish spectra					
$[x_{fmin}, x_{fmax}]$	minimum and maximum values of the fish size	[-9.3,13.2]			
λ_f	exponent of fish spectrum	-1.0			
Initial densities					
	Species	$U_{i,egg}$	$x_{i,egg}$		Braun et al. (2009)
	Mesopelagic fish	-2.349	-8.2	m^{-3}	
	Anchovy	0.819	-8.2	m^{-3}	
	Sardine	-5.926	-5.7	m^{-3}	
	Mackerel	-7.987	-7.3	m^{-3}	
	Jack mackerel	-5.404	-7.7	m^{-3}	
	Palm ruff	-5.140	-7.7	m^{-3}	
	EP Bonito	-5.140	-9.3	m^{-3}	
	Swordfish	-5.140	-6.0	m^{-3}	

3.5 Discussion

The results given above summarize the extensive work in the development of a multispecies size-spectrum model for the NCME as a tool for future dynamical analysis of the pelagic fish community. This entails a definition of the system of study, species composition, a mathematical model for the processes that modulate the density of the populations and community, and estimation of parameters of the model.

The pelagic community in the model is composed of eight fish categories plus the plankton. Feeding mainly on the plankton are the mesopelagic fish, anchovy and sardine. The small pelagic fish provide food for large fish such jack mackerel, mackerel, bonito and palm ruff and also the top fish predator swordfish. In addition, large fish as jack mackerel and mackerel can also feed on zooplankton. The assemblage of species and their trophic relationship is similar to the conceptual model of food web in the Eastern Boundary Upwelling Ecosystems of Chavez and Messié (2009) and for HCS off Chile Thiel et al. (2007) which has at its centre the small pelagic fish population (anchovy and sardine) which provide food for a diverse community of large fish. Chavez and Messié (2009) also identify a second group of top predators composed by highly migratory fish such as swordfish and tunas that forage on small and medium size fish at the edges of system.

The trophic interactions in the model depended on the feeding kernel function $\phi_{ij}(x, x')$, which includes a function that depends on the predator size $\phi_i(x-x')$, and an interaction matrix $\theta_{i,j}$ (**Equation 3.10**). The function $\phi_i(x-x')$ has a preferred PPMR (β_i) and diet breath (σ_i), representing the different feeding habits of the fish species. Most fish pelagic predators in the HCS off Chile are recognized to be opportunistic on a wide range of different prey items (Thiel et al. 2007). It is important that the feeding kernels of sardine and anchovy should account for their capacity to continue filter feeding on small phytoplankton as the fish get larger, and this has required the development of a new type of feeding kernel function for these species. These kernels build in an important property of these planktivores that anchovy feeds on larger prey than sardine.

The interaction matrix $\theta_{i,j}$ accounts for the extent to experience the same prey at the same time and place. Parameter values for this matrix are not given in this Chapter. The lack of detailed information about the spatial overlap of the species to parameterize the model, called for further analysis. This will be addressed in Chapter 4 by exploring the complete range of values that the interaction matrix can take (i.e. from 0 up to 1). General knowledge about the distributions of the species indicates for instance, that anchovy and sardine may overlap in space over the full range of body sizes (Checkley et al. 2009b), but the remaining species may have wider distributions than the NCME. In addition, the exploration of values of interaction matrix may give a crude interpretation of the effect of predation in particular cannibalism and interspecific predation in term of strength of these processes and its effect on the dynamics of the populations and the community. Thiel et al. (2007) have emphasised the need for understanding of intra- and interspecific competition or intraguild predation in the pelagic food webs off Chile, the effects of the spatial segregation of predators and prey and the potential effect of the environment variability.

Life history parameters were collected to parameterize the reproduction process. They can also be used to compare individual growth of each species that emerges from the model with the growth describe by the von Bertalanffy model. This provides an independent check on whether the feeding as described by the model is consistent with the observed in the sea, and is investigated in the next chapter. Our collection of reproductive and growth parameters and in particular the values of L_∞ and L_m (length at maturity) of each species were close to the invariant value of the ratio $\frac{L_m}{L_\infty} = 0.66$ (Jensen 1996) in anchovy (0.62), sardine (0.67) and mackerel (0.60). Lower values were obtained for palm ruff (0.54), bonito (0.50) and swordfish (0.44) although still in the range of 0.4 to 0.8 reported for fish (Beverton and Holt 1959). However, the life history invariants calculated here were out of interval of confidence reported for the Chilean fish family (Araya and Pepe-Victoriano 2010) estimated through meta-analysis. In the particular case of jack mackerel the invariant (0.36) was distant from 0.66. It has been suggested that life strategy of this species not follow the theory of invariants (Cubillos and Alarcón 2010). Notice that in the MSSM I do not use explicitly L_∞ and L_m, but the asymptotic weight (w_∞) was

obtained from L_∞ and the ratio of the reproductive parameters $\beta_{i,0}/\beta_{i,1}$ is equivalent to L_m (Roa and Ernst 1999).

Combining intrinsic and senescence mortality results in type of U-shaped function for the non-predation mortality similar to that described Hall et al. (2006). Lacking information to parameterize these sources of mortality, I have used a standard values that applies to all species.

In gathering together the full set of parameters for MSSM off Northern Chile, some caveats need to be kept in mind: i) different sources information were combined to estimate values such as the feeding traits of mesopelagic fish, ii) there was an absence of data on the diet, prey size selectivity and maturity for anchovy, sardine, bonito, swordfish, and mesopelagic fish, iii) there may be bias in the sampling and temporal changes in the maturity and feeding traits of palm ruff. In addition, the estimation of plankton spectrum could have been biased in terms of the body size estimations of the different plankton fractions. Some caution is also needed because of the limited knowledge on basic biology of the commercial and non-commercial fish species in the NCME.

However, the MSSM was parameterized with the best information available. Furthermore, the absence of information on PPMR and diet composition is striking, but at the same time opens a door for empirical research on feeding behaviour. Most of life history parameters of maturity and growth are well known for the commercial species but almost no information exists for non-commercial species. I agree with previous works (Barros 2007, Medina et al. 2007, Thiel et al. 2007) that to move towards an ecosystem approach to fishery management of NCME, in which, where predation plays a fundamental role, improved understanding of the trophic ecology of commercial and non-commercial is required. By joining detailed information from the literature into a multispecies size-spectrum model framework, this study takes a few first steps towards that goal.

Chapter 4

Can cannibalism and interspecific predation promote sardine and anchovy coexistence in upwelling ecosystems?

4.1 Abstract

Large temporal oscillations in the population abundances of anchovy and sardine are a well-known and widespread phenomenon. Four mechanisms have been proposed as the drivers of anchovy and sardine alternations optimal temperature, trophic ecology, oxygen, and predation interactions. This chapter focuses on understanding the consequences of intraguild predation and cannibalism for a subset of the pelagic community: anchovy, sardine and the plankton community. Using chlorophyll-a data from satellite for the North Chilean Marine Ecosystem, the plankton size spectrum according to cool and warm condition was parameterized. The effects of predation interactions on anchovy and sardine abundance under cool and warm conditions predicted of the habitat and different levels of predation within and between species were studied. The results revealed that a change in the size-structure of the plankton spectrum between cool and warm conditions would not on its own lead to extinction or the alternation of these species. Warm conditions reduce the growth rates of both species, increasing their vulnerability to predation. Strong cannibalism could destabilize anchovy, and the interactions of cannibalism with intraguild predation buffered the species against extinction, and increased the stability of anchovy population. I concluded that neither is it enough to know the effect of the environmental conditions alone, nor is it enough to know the effect of predation alone: the environment and predation interact in their effects on the coexistence and extinction of these species.

4.2 Introduction

Large temporal alternating fluctuations in the population abundances of anchovy and sardine are a well-known and widespread phenomenon, having being observed in the

eastern Pacific (California and Humboldt system), northwestern Pacific (Japan), and southeastern Atlantic (e.g. Benguela) (Lluch-Belda et al. 1989, 1992, Schwartzlose et al. 1999). Most studies suggest that fishing cannot be sole driver of such large fluctuations; such variation must also be linked to large-scale atmospheric or oceanic forcing. Indeed, in the Pacific Ocean over the past 50 years, multiple influences affecting the population dynamics and fisheries of anchovy and sardine have been identified including: air and ocean temperatures; atmospheric carbon dioxide; and the productivity of coastal and open ecosystems (Chavez et al. 2003).

In general, four mechanisms have been proposed to advance understanding of the links between the physical forcing and sardine-anchovy variability. Firstly, from the view of trophic ecology, van der Lingen et al. (2006) carried out a comparison of the results of morphological, experimental field and modelling studies of the feeding behaviour of sardine and anchovy on plankton in the Benguela ecosystem. The comparison provided evidence that sardine and anchovy were trophically distinct. The authors suggested that sardine feeds on small copepods and phytoplankton in an environment dominated by small particles whereas anchovy feeds on larger copepods and phytoplankton in regions dominated by large particles. The different particle size distributions are thought to be triggered by different physical forcing, such as intermittent mixing (upwelling, cold) or more stable (warm) leading to different plankton spectra, ultimately providing more suitable prey availability for either anchovy in cold condition or sardine in warm condition.

Secondly, from the view of habitat suitability affecting population dynamics, Takasuka et al. (2007) proposed an 'optimal growth temperature' as a potential mechanism for alternations of sardine and anchovy in the north western Pacific Ocean. This mechanism assumes that even subtle growth variations driven by small temperature shifts could potentially cause drastic regime shifts in the fish community. The authors found a dome-shaped relationship between growth rates and the temperature of sardine and anchovy, with different optimal temperatures for growth at early life stages (eggs and larvae). For instance, around 22°C the growth rates of anchovy larvae would be at their maximum level, but growth rates of sardine would be low. Optimal temperatures for sardine larvae occurred at 16.2 °C. This simple mechanism could potentially cause the shifts between the warm anchovy regime and the cool sardine regime in the western North Pacific.

Thirdly, Irigoien and Roos (2011) argued in an extensive review that intraguild predation (IGP) could amplify small changes in species abundance caused by either the environment or by fishing. IGP operates when species from the same guild eat one another, as well as compete for the same resources (here plankton) (Polis et al. 1989). When IGP is present a reduction in abundance of one species impacts directly on the other through reduced predation, as well as through reduced competition for resources. Unlike the previous hypotheses (1 and 2), the deleterious effect of the external conditions on one species does not necessarily have to be mirrored by a positive effect on the other species for it to gain an advantage; the release from predation (e.g. from fishing effects alone) may be sufficient to allow the other species to increase in abundance.

Fourth, Bertrand et al. (2011) have proposed that oxygen could be a fundamental property regulating pelagic ecosystem structure in the south eastern Pacific. These authors argued that distribution and abundance of anchovy and sardine in the area are correlated to near-surface oxygen concentration/saturation and that anchovy and sardine respond in a different manner to the oxycline depth over a wide variety of scales.

Anchovy and sardine are generalist planktivorous, and their diets include fish eggs and larvae of both species, thus experiencing cannibalism as well as IGP. The combination of these two processes may have profound and intricate effects on the dynamics and interactions of fish populations. For example, Valdés-Szeinfeld (1991) suggested that the cannibalism and IGP are synergistic and could reinforce long-term shifts in the relative abundance of sardine and anchovy in the Benguela system. Alheit and Niquen (2004) proposed that warming and cooling trends in the Humboldt Current systems set in motion a number of changes in the trophic relationship of anchovy as both predator and prey also due to the combination of both cannibalism and IGP. Under warm conditions plankton food for anchovy changes in abundance and size structure, and their predation on eggs, larval, juveniles and adults increases. Also predation on anchovy by larger fish including sardine could increase because they move further southwest and overlap more with anchovy. In addition, cannibalism could reinforce IGP because anchovy concentrated near the coast.

Empirical evidence of cannibalism and IGP in anchovy and sardine has been reported in the upwelling ecosystems of Japan, California, Benguela and Perú (Hayasi 1961, Hunter and Kimbrell 1980, Alheit 1987, Valdés-Szeinfeld 1991), and off Argentina and Portuguese coasts (Pájaro et al. 2007, Garrido et al. 2008). For instance, cannibalism and IGP predation could account for mortality level in anchovy egg that varied between a 6% and 56% (Valdés-Szeinfeld 1991), and cannibalism in sardine could account for 81% of the egg mortality (Garrido et al. 2008).

The purpose of this chapter is to investigate numerically how the trophic interactions of anchovy and sardine affects the coexistence of the two species, when there is a shift between cool and warm conditions. The changes in trophic interactions when conditions become warm are potentially intricate due to the feedback mechanisms involved. For example, as the availability of plankton food changes, this could affect the body growth. Changes in growth subsequently could affect the strength of cannibalism and IGP by altering the abundance of predators and predation mortality rates on prey. Using the multispecies size-spectrum NCME model developed in Chapter 3 for the subset of the community that contains anchovy-sardine and plankton, the consequences of changing conditions across a wide range of IGP and cannibalism strengths is explored. The plankton community is parameterized for the NCME using satellite data (Chlorophyll-a), according to the normal-La Niña condition (cool, non-El Niño) and the contrasting El Niño (warm) condition. The model is solved numerically with different levels of cannibalism and IGP to see how the abundance of anchovy and sardine are affected in the long term by predation in cool and warm conditions.

In this chapter, the term 'cannibalism' is used (= intraspecific predation) for interactions where species A eats species A, and 'interspecific predation' for interactions where A eats species B. This is preferable to the term IGP here, because IGP has sometimes been used as a collective term covering both intra- and interspecific predation. In this chapter, the distinction is important.

4.3 Methods

4.3.1 The multispecies size spectrum model

The model developed in **Chapter 3** was used to test the effects of cannibalism, interspecific predation, and changes in the size structure of plankton community, on anchovy and sardine species. In this model the dynamics of the numerical density $U_i(x,t)$ of each species i in the ecosystem are governed by three continuous processes: somatic growth; mortality and reproduction. (For details about how each process is modelled see **Chapter 3.3.2**).

How a predator of type i and size x selects prey of type j and size x' is described by a feeding preference function and an interaction matrix (**Equation 3.10**). The model has a special feature of allowing sardine and anchovy to retain their capacity for filter feeding on phytoplankton, as well as feeding on larger particles as they grow, consistent with their biology as planktivores. Therefore assumptions about the feeding preferences function are different from those used in previous studies of size-spectrum dynamics (Blanchard et al. 2009, Law et al. 2009, Andersen and Pedersen 2010, Datta 2011, Hartvig et al. 2011). To describe the feeding kernels of these species, I assumed that parameters β (preferred prey) and σ (diet breadth) vary with body size while keeping the assumption of a Gaussian kernel function. Each species has a minimum prey size $x'_{i,min}$, and I write $x-x'_{i,min}$ as $(x-x')_{i,max}$ for the largest predator and prey mass ratio (PPMR) for type i at size x. I assume that the minimum PPMR $(x-x')_{min}$, i.e. the largest prey body size x' relative to the predator body size x, is fixed, and that is the same in both species having a value $\log_e 10$. The parameters of the Gaussian feeding kernel are then calculated following **Equations 3.12** and **3.13**.

Thus, as the predator body size x increases, so do β_i and σ_i; the factor 1/3 is chosen to ensure that the entire feeding kernel is included (the kernel is then normalised to integrate to 1). The smallest prey size of anchovy and sardine were set at $x'_{min}=\log_e(10^{-8})$ and $x'_{min}=\log_e(10^{-10})$ respectively (Espinoza and Bertrand 2008b, Espinoza et al. 2009). A summary of life history parameters used in this study for anchovy and sardine is shown in **Table 4.1**.

Table 4.1 Life history parameters of anchovy and sardine. Maturation parameters are $\beta_{i,0}$ and $\beta_{i,1}$, and $w_{i,\text{egg}}$ corresponds to the egg weight (g). $L_{i,\infty}$, k_i and $t_{i,0}$ are the asymptotic length, growth rate, and age at minimum length from the von Bertalanffy somatic growth model. Parameters a_i and b_i are from the allometric function between length (l) and weight (w) $w = a_i l^{bi}$ used to convert each species asymptotic length to asymptotic weight ($w_{i,\infty}$).

	Maturation parameters		Growth parameters				Allometric parameters	
	$\beta_{i,0}$	$\beta_{i,1}$	$w_{i,egg}$ (g)	$L_{i,\infty}$ (cm)	k_i (y^{-1})	$t_{i,0}$ (y)	$w_{i,\infty}$ (g)	a_i (g cm^{-b})	b_i
Anchovy	18.09	1.45	0.0003	20.25	0.88	-0.01	66.48	0.0048	3.16
Sardine	27.26	1.02	0.0035	38.60	0.21	-0.75	625.10	0.0068	3.13

*For the sources from which these parameters were taken, see **Chapter 3.3.2.2**

The initial conditions for anchovy and sardine were assumed to follow a power law function of the form $U_i(x) = U_{i,egg} \exp(-\lambda_i (x - x_{i,egg}))$ where $U_{i,egg}$ is the numerical density of fish species i (m^{-3}) at the egg size $x_{i,egg}$. The slopes of the fish spectra ($-\lambda_i$) were all assumed to be -1 following the theory of size spectra (Sheldon et al. 1972, Boudreau and Dickie 1992) as no data were available to estimate the slope. Weights of fish eggs ($x_{i,egg}$) and $U_{i,egg}$ were obtained as described in **Chapter 3.3.2.2**.

4.3.2 Size-structure of the plankton community under cool and warm conditions

To study the effect of the plankton community on anchovy and sardine dynamics, two fixed plankton size spectra were used, reflecting the physical forcing on the plankton community in the NCME of cool (non-El Niño) and warm (El Niño) conditions.

For cool conditions, I used (with one exception) the plankton spectrum shown in **Chapter 3.4.2**, obtained from a monitoring survey carried out in October 2008 (Braun et al. 2009), when the NCME was in a non-El Niño state. The exception was

the value $U_{p,x0}$= exp(22.275) (**Table 3.2**), which resulted in somatic growth of anchovy and sardine considerably slower than that found from von Bertalanffy growth equations parameterised for anchovy and sardine. The value was therefore adjusted to $U_{p,x0}$=exp(24.25), which resulted in growth trajectories close to those of the von Bertalanffy growth equations (**Figure 4.4**). This value of $U_{p,x0}$ still lies within the 95% confidence (corresponds to the 55 percentile) of predicted density at body size at x_0= -23, for the plankton size spectrum as estimated in **Chapter 3.3.2.2.3**

For warm conditions, a method suggested by Barnes et al. (2010a) for determining phytoplankton size spectrum parameters from satellite data was followed. Chlorophyll-a data from the sea-viewing Wide Field-of-View satellite sensor (SeaWiFS) http://oceancolor.gsfc.nasa.gov/ for NCME from 1997 to 2008 was used. Although, the direct relationship between the slope of plankton size spectra and chlorophyll-a concentration in Barnes et al. (2010a) is rather weak because of inherent variability in their global data (see their Figure 4a), there is a stronger relationship between chlorophyll-a concentration and the cumulative biomass of phytoplankton, expressed as a function of cell mass. In particular, the cell mass at which 50% of the biomass has been accumulated (M_{B50}) increases with chlorophyll-a concentration (see their Figure 2a), implying that biomass shifts to larger cell masses as the concentration of chorophyll-a increases. The method used here follows Barnes et al. (2010a Supplementary Material) and partitions the phytoplankton spectrum into three groups: pico-, nano- and micro-phytoplankton to make use of the sensitivity of (M_{B50}) to chlorophyll-a concentration.

Thus, the size structure of the plankton community for warm condition was predicted following the next steps. First, the empirical relationships between the chlorophyll-a data and the slope and intercept of the phytoplankton spectra were obtained for each year from 1997 to 2008 using the regression equations in Barnes et al. (2010a Table III). Second, with this information the corresponding values of M_{B50} and M_{B90-10} for each year were calculated using the equations S6, S7 (notation and equation numbers are as in Barnes et al. 2010a); M_{B90-10} is the range of cell masses that account for the 80% of the total biomass. Knowing these masses, the cell masses at 0% (M_{B0}), 10% (M_{B10}), 90% (M_{B90}) and 100% (M_{B100}) were calculated to account for the remaining 20% of the cumulative biomass; these came from equations S8, S9, S10, S11

(notation and equation numbers are as in Barnes et al. 2010a). Third, the biomass of the three phytoplankton groups (pico, nano, micro) was obtained from equation S12

$$\int_{M_1}^{M_n} b(M+a)dM = \frac{1}{2}bM_n^2 + aM_n - \frac{1}{2}bM_1^2 - aM_1$$, where M is cell mass, M_1, M_n are the lower

and upper boundaries of the pico, nano and micro groups, b and a are slope and intercept of the overall phytoplankton spectra. Following Barnes et al. (2010a), the integration limits were set at M_{B0} and the upper boundary (M_n) of the fraction size equivalent to and -0.08 ($\log_{10}$ pgC, picogram of carbon) for the pico group, -0.08 ($\log_{10}$ pgC) and 2.74 ($\log_{10}$ pgC) for the nano group, and 2.74 ($\log_{10}$ pgC) (M_1) and M_{B100} for the micro group. This information gave time series for the biomasses of pico-, nano- and microphytoplankton over the period 1997 to 2008.

Fourth, I then selected a warm year 1998 (strong El Niño event) from the time series of chlorophyll-a data, to compare with the cool (non-El Niño) year 2008. The shifts in densities of pico-, nano- and microplankton between 1998 and 2008 were assumed to be proportional to the shifts in the biomasses of these groups. These ratios (biomass 1998 divided by biomass in 2008 for each group) were then used to rescale the numerical density of phytoplankton fractions in the empirical size spectrum obtained from the survey data 2008 described in **Chapter 3.4.2**. A linear regression of the rescaled plankton spectrum was used to obtain the slope λ_p and intercept U_{p,x_0} to provide a plankton spectrum for warm conditions (El Niño). U_{p,x_0} was chosen at 55 percentile of the confidence interval of predicted plankton spectrum, the same percentile than in cool conditions.

Parameters, U_{p,x_0}, the density of plankton at a chosen size $x_0 = -23$ (m^{-3}), and $-\lambda_p$, the slope of the spectrum for cool and warm conditions were used to obtain an empirically-derived spectrum for plankton in the NCME based on a power law function $U_p(x) = U_{p,x_0}(x-x_0)^{-\lambda_p}$.

4.3.3 Predation experiments

A series of predation simulation experiments was carried out to investigate the response of anchovy and sardine to different plankton size spectrum conditions

broadly representative of cool and warm conditions and across a range of cannibalism and IP strengths. All experiments were run over 100 years with an integration step size $dt = 0.0001$ and a logarithmic body size step $dx = 0.1$.

Predation interactions (cannibalism and interspecific) are set in the multispecies size-spectrum model through an interaction matrix θ (**Chapter 3.3.2.1.5**). The elements of the matrix provide a weight over a range 0 to 1 for the degree to which of type of species i consumes type of species j, with 0 indicating no feeding of i on j, and 1 indicating full feeding. This applies irrespective of the sizes of the predator and prey. For instance, if for fish species the diagonal elements ($i=j$) are 1 and off- diagonal elements ($i{\neq}j$) are 0, each fish species feeds on itself (cannibalism present), but not on the other (interspecific predation absent). Because both anchovy and sardine are planktivorous, the column $j=p$ ($p=$plankton*)* has all elements with value 1 (except $\theta_{pp}=0$); if all other columns are zero, then both fish species just feed on plankton (the plankton do not feed on the fish).

Experiment 1 (**Figure 4.1a**) investigates the dynamics under pure planktivory, i.e. in the absence of any predation, to set a baseline to compare with effects of predation. Therefore, the column of θ with $j=p$ was set equal 1, and all others columns were zero. Experiment 2 (**Figure 4.1b**) adds on cannibalism in both species making the diagonal ($i=j$) elements of θ positive for both fish species. Experiment 3 (**Figure 4.1c**) examines asymmetric, interspecific predation, with sardine eating anchovy and not vice versa; this experiment is carried out with planktivory but not cannibalism. Experiment 4 (**Figure 4.1d**) is the reciprocal case of asymmetric, interspecific predation, with anchovy eating sardine and not vice versa. Experiment 5 (**Figure 4.1e**) combines planktivory, cannibalism and interspecific predation in a simple way, allowing cannibalism to vary, holding the level of cannibalism the same for both species, and allowing interspecific predation to vary holding this the same for both species.

$$\theta = \begin{bmatrix} 0 & 0 & 1 \\ 0 & 0 & 1 \\ 0 & 0 & 0 \end{bmatrix} \qquad \theta = \begin{bmatrix} a & 0 & 1 \\ 0 & a & 1 \\ 0 & 0 & 0 \end{bmatrix} \qquad \theta = \begin{bmatrix} 0 & 0 & 1 \\ a & 0 & 1 \\ 0 & 0 & 0 \end{bmatrix}$$

$$\theta = \begin{bmatrix} 0 & a & 1 \\ 0 & 0 & 1 \\ 0 & 0 & 0 \end{bmatrix} \qquad \theta = \begin{bmatrix} a_1 & a_2 & 1 \\ a_2 & a_1 & 1 \\ 0 & 0 & 0 \end{bmatrix}$$
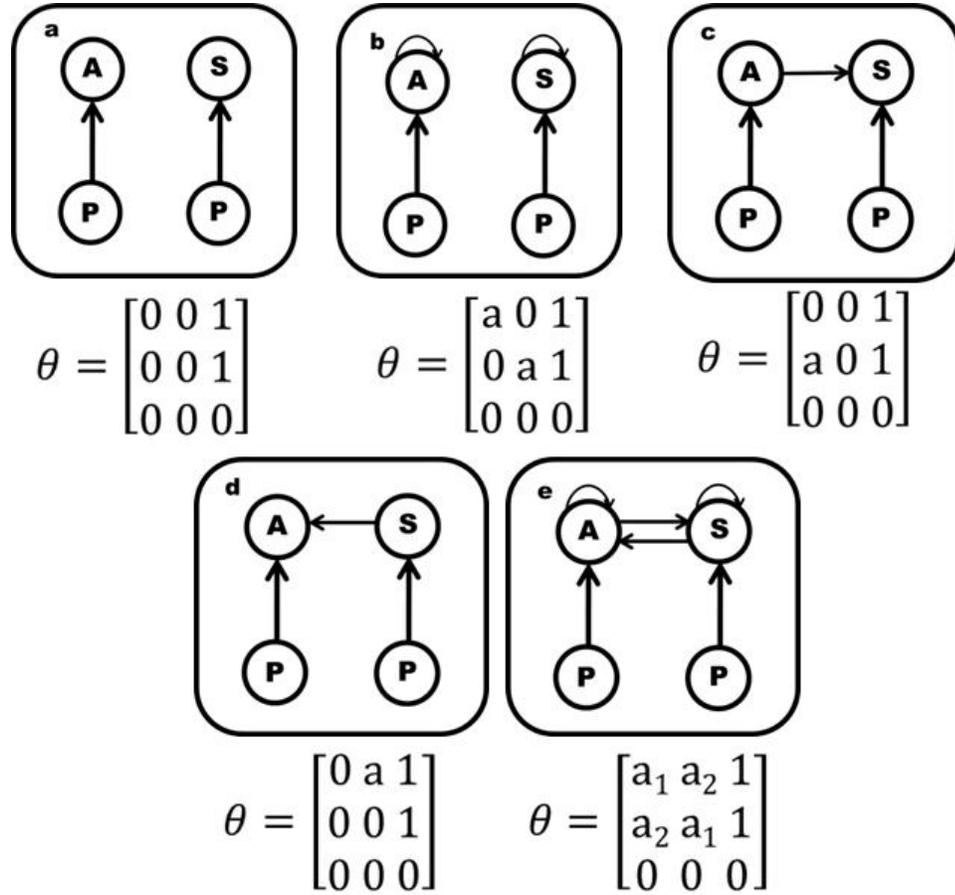
Figure 4.1. Summary of the simulation experiments (a-e) to study the effect of cannibalism and interspecific predation on anchovy and sardine dynamics under the two scenarios of the plankton spectrum. (a) Absence of cannibalism and interspecific predation, (b) cannibalism experiment, (c) predation by sardine, (d) predation by anchovy and (e) mutual interspecific predation and cannibalism. A denotes anchovy spectrum, S sardine spectrum and P the plankton spectrum. Arrows indicate the flow of mass from prey to predator. Elements a, a_1, a_2 in θ are variable, taking values from 0 to 1, in steps of 0.1.

4.3.4 Sensitivity analysis

A sensitivity analysis was carried out on the parameter K, A, $x'_{i,min}$, α, $U_{i,megg}$, c, μ_0, $x_{i,s}$ to explore their effect on the total numerical density of anchovy and sardine at the steady state. This was done changing the value of one parameter at a time from its

baseline value given in **Sections 4.3.1**, **4.3.2** and **4.3.3**, by a factor of 1.05. Denoting η as the baseline value of a parameter, the sensitivity analysis thus altered its value to $\eta'=1.05\eta$. This scales the parameter changes so that they are proportional to size of the parameters. The sensitivities of total density to changes in different parameters can then be compared.

The sensitivity $S_{i,n}$ of the total equilibrium density of species i to a change in parameter η is the partial derivative:

$$S_{i,\eta} = \frac{\int \hat{U}_{i,\eta'}(x)dx - \int \hat{U}_{i,\eta}(x)dx}{\eta'-\eta}$$

Here, $\hat{U}_{i,\eta}(x)$ is the equilibrium density of individuals of size x of species i with all parameters set to the baseline value, and the integral over x gives the total density. The term $\hat{U}_{i,\eta'}(x)$ is the corresponding equilibrium density when the parameter is altered to η', holding all other parameters at their baseline values. The integrals are over the range of body size from egg to the maximum body size of species i.

4.4   Results

4.4.1   Representing the size-structure of the plankton community under cool and warm conditions

Analysis of the satellite data on chlorophyll-a for NCME indicated that a decrease in the biomass of picoplankton occurred from 1997 to 2008, whereas an opposite trend in the biomass of nano- and microphytoplankton took place (**Figure 4.2**). The greatest biomass of the picoplankton occurred in the year 1998 and the lowest value in 2004. In contrast, the biomass of nano- and microplankton were at their greatest in the year 2004 and their lowest in 1998 and 1999 respectively. According to the index of sea surface temperature in the central Pacific (El Niño 3.4 Region) (**Chapter 2.4.1**) over the period of 1997 to 2008, several El Niño events of different intensities

occurred, the strongest being in 1997-1998. The system started to change to 'normal-cool' conditions in the years 1999 to 2001. **Figure 4.2** shows that the shift from warm (1997 and 1998) to cool conditions (1999 to 2001) is accompanied by transfer in biomass from pico- to nano- and microphytoplankton. This type of shift in the phytoplankton community between El Niño and non-El Niño conditions was also predicted from *in situ* values of chlorophyll-a from Iriarte and González (2004) off the North coast of Chile (23°S), supporting the results I shown here.
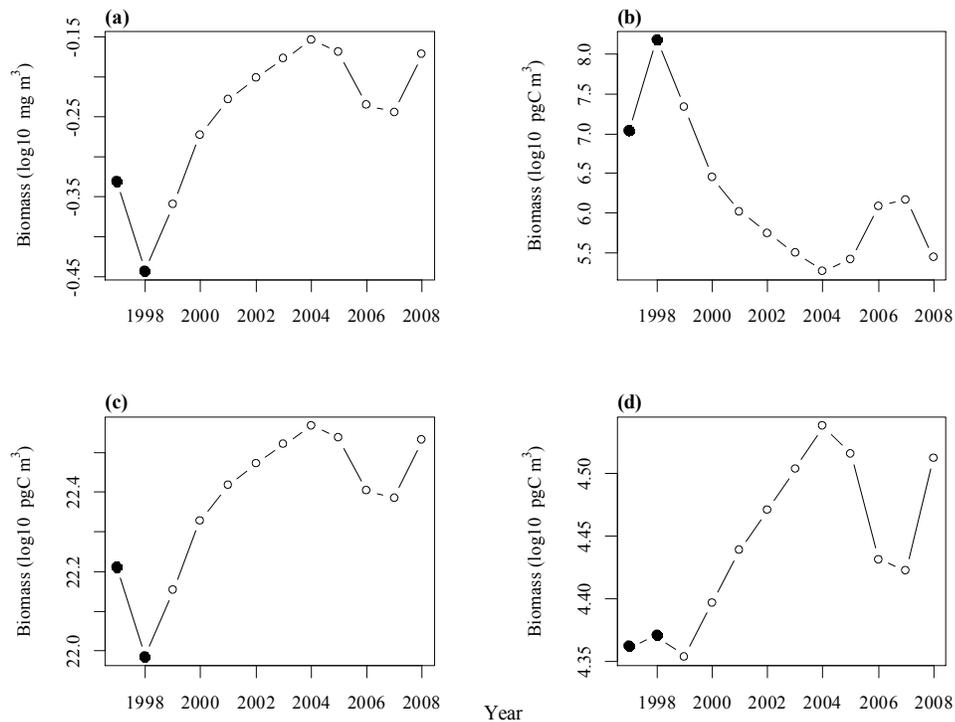
Figure 4.2. (a) Chlorophyll-a satellite data. Predicted biomass for (b) pico-, (c) nano- and (d) microphytoplankton in the NCME from 1997 to 2008. (Black dots indicate El Niño 1997-1998).

The values of the biomass in years 1998 and 2008 for the pico-, nano- and microplankton fractions were used to create the two scenarios for the plankton spectrum in the NCME under warm (El Niño) and cool (non-El Niño) conditions. The plankton spectrum for warm conditions (**Figure 4.3**) has a steeper slope of -1.628 with 95% confidence interval of [-1.515; -1.740] and for cool conditions a shallower slope of -1.257 with an interval of confidence of [-1.371; -1.143]. The

absence of overlap between the confidence intervals of the slopes indicates that they are significantly different. The two plankton size spectra intersect at a $\log_e$ body mass of -20. This means that in warm conditions body sizes x < -20 experience an increase in their densities, and sizes x > -20 a decrease. **Table 4.2** provides a summary of the parameters used in **Figure 4.3**, as well as the initial density for anchovy and sardine together with the range of body mass used in this study.
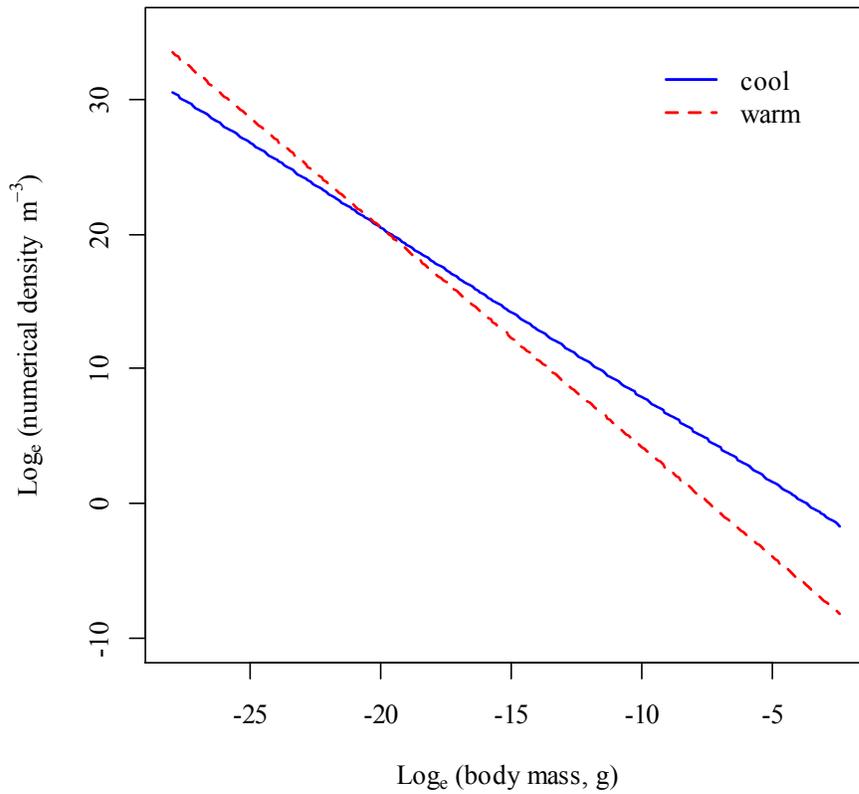
Figure 4.3. Predicted size-structure of the plankton community (plankton spectrum) in the NCME under warm (El Niño) conditions (dashed red line) and cool (non-El Niño) conditions (continuous blue line) using the power law relationship $U_p(x) = U_{p,x_0}(x - x_0)^{-\lambda_p}$. Parameters $U_{p,x0}$ and $-\lambda_p$ were obtained as described in **Section 4.3.2.**

Table 4.2. Symbol definitions, parameter values, units and sources for the dynamics community model of NCME. Note that $x = \ln(w/w_0)$ and w_0=1 g.

Symbol	Description	Value	Unit	Source
Range of body mass pelagic community				
$[x_{\min}, x_{\max}]$	minimum and maximum size in the community	[-23, 6.4]		
Plankton spectrum - cool conditions				
$[x_{pmin}, x_{pmax}]$	minimum and maximum values of the plankton size spectrum	[-23,-2.4]		
x_0	reference size plankton	-23		
U_{p,x_0}	numerical density of plankton at x_0	$e^{24.25}$	m^{-3}	This study
λ_p	slope of the plankton spectrum	-1.257		Chapter 3
Plankton spectrum - warm conditions				
$[x_{pmin}, x_{pmax}]$	minimum and maximum values of the plankton size spectrum	[-23,-2.4]		
x_0	reference size plankton	-23		
U_{p,x_0}	numerical density of plankton at x_0	$e^{25.36}$	m^{-3}	This study
λ_p	slope of plankton spectrum	-1.628		This study
Fish spectra				
$[x_{fmin}, x_{fmax}]$	minimum and maximum of values of the fish size	[-9.3,6.4]		
$x_{i,egg}$	Species – Egg size			
	Anchovy	-8.2		
	Sardine	-5.7		
$U_{i,egg}$	Species – Initial density			Braun et al. (2009)
	Anchovy	$e^{0.819}$	m^{-3}	
	Sardine	$e^{-5.926}$	m^{-3}	
λ_f	exponent of fish spectrum	-1.0		

4.4.2   Effects of the plankton community on anchovy and sardine under cool and warm conditions

Figure 4.4 shows how the plankton size spectra under cool and warm conditions have different effects on growth of anchovy and sardine, mediated by the different feeding kernels of the fish species when the fish species are assumed to be pure planktivores with no predation on other fish (according to the model configuration show in **Figure 4.1a**).

In this model, sardine always grows faster in body mass than anchovy irrespective of whether the conditions are cool or warm (**Figure 4.4a, b**). The reason for this is that sardine can filter plankton down to a body mass of approximately 10^{-10} g (e^{-23}), in contrast to anchovy which can only filter plankton down to a mass of approximately 10^{-8} g ($e^{-18.4}$) (**Figure 4.4c, d**). Sardine therefore has an extra source of food unavailable to anchovy. Under cool conditions, the plankton spectrum is tilted more towards larger body sizes and, to the advantage of both, but this extra source of food is relatively small (see the consumption rates in **Figure 4.4e, f**). However, under warm conditions, the plankton spectrum is tilted more towards smaller body sizes. This is deleterious to the growth of both species (**Figure 4.4a, b**), but much more so to anchovy, because it is unable to take advantage of the increased density of the smallest plankton (**Figure 4.4e, f**).
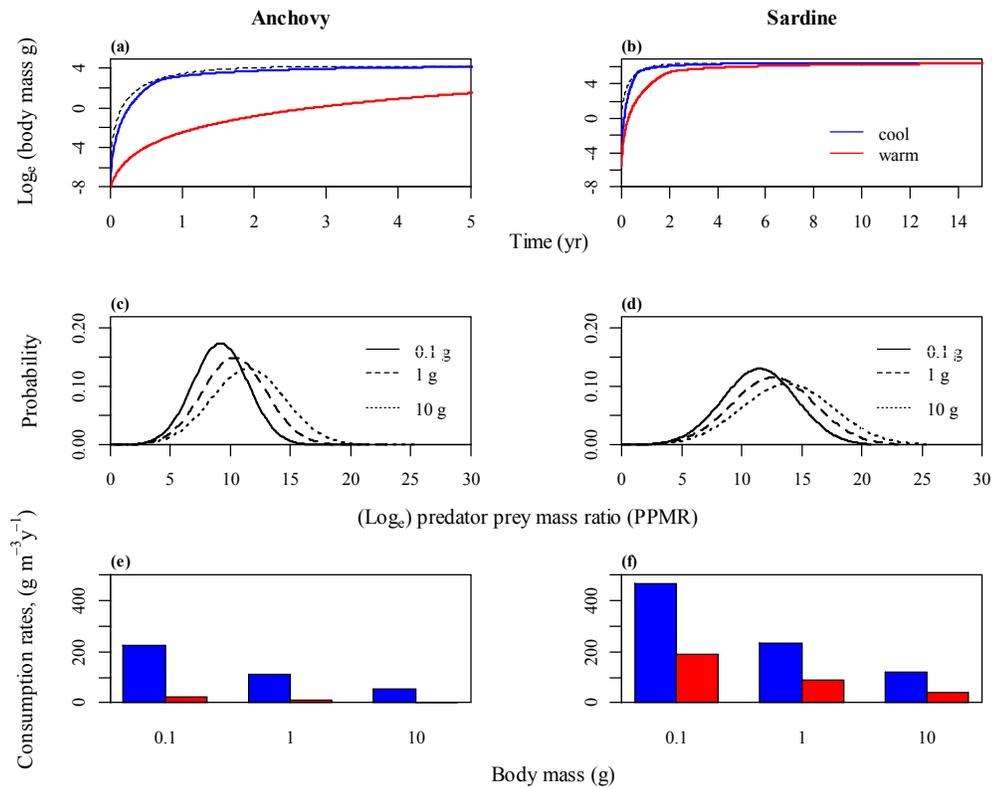
Figure 4.4. Somatic growth, feeding kernel and consumption rates by anchovy (column 1) and sardine (column 2). (a), (b) Growth trajectories from the MSSM at steady state for cool (or non-El Niño; blue line), warm (El Niño; red line) conditions and from the von Bertalanffy growth equation (dashed line) with parameters as in **Table 4.1**. (c), (d) Feeding preference functions at three predator body sizes. (**e**), (**f**). Consumption rates at the same three predator body masses under cool (blue bars) and warm (red bars) conditions.

The changes in somatic growth of anchovy and sardine from cool to warm conditions lead to changes in their size-structure, total density and biomass (**Figure 4.5**). Slow growth of anchovy in warm conditions increases the density at smaller body sizes and reduces the density at larger sizes, with a corresponding effect on the distribution of biomass over body size (**Figure 4.5a, e**). Overall the total density is increased, and the total biomass is increased slightly (**Figure 4.5c, g**). Although sardine experiences the same type of changes from cool to warm conditions, the effect on the larger body mass is smaller compared with anchovy (**Figure 4.5b, f**)

and the increment to the total biomass is greater (**Figure 4.5h**). In this way the shifting balance between anchovy and sardine under cool and warm conditions is mediated by the changing plankton spectrum and the different feeding behaviour of the two species.
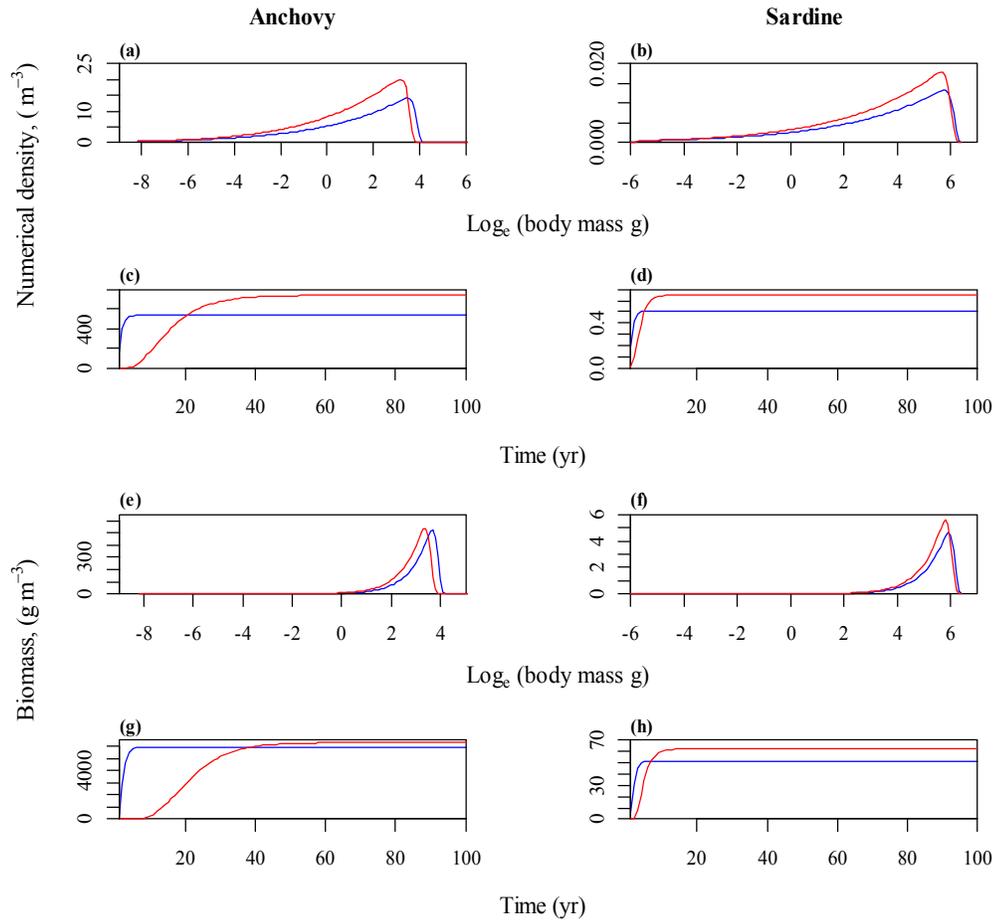
Figure 4.5. Size-structure, total density and biomass of anchovy (column 1) and sardine (column 2) under cool (non-El Niño; blue lines) and warm (El Niño; red lines) conditions. (a), (b) Size-structure of the density at 100 years or steady state. (c), (d) Time series of total density. (e), (f) size-structure of the biomass at 100 years or steady state. (g), (h) Time series of total biomass.

4.4.3 Effects of cannibalism on sardine and anchovy

Predation within species (**Figure 4.1b**), i.e. cannibalism, increases mortality for anchovy and sardine, and therefore causes a reduction in their densities (**Figure 4.6**) compared with non-predation conditions (**Figure 4.5c, d**).

Cannibalism acts as a negative feedback, operating with a time delay because it comes from larger fish eating smaller conspecific fish. It is well established in models aggregated to the community level that such feedback leads to oscillations in size spectra (Datta et al. 2011). The contrasting oscillations of the time series in **Figure 4.6** can be interpreted as an outcome of the relative importance of cannibalism and plankton feeding. First, the consumption rates in **Figure 4.4e, f** show that there is more plankton food consumed under cool as opposed to warm conditions. Correspondingly, the tendency for oscillation is weaker under cool (**Figure 4.6a, b**) than under warm conditions (**Figure 4.6c, d**). Second, compared with anchovy, sardine gets a greater proportion of its food from the plankton. In keeping with this, the tendency for oscillation is weaker in sardine (**Figure 4.6b, d**) than in anchovy (**Figure 4.6a, c**). Third, as the strength of cannibalism is increased, the tendency for oscillation gets greater. The lines within **Figure 4.6** panels (**a**) and (**d**) show this happening, although the oscillations in **Figure 4.6b** are too small and those within **Figure 4.6c** are too large to see this clearly.

It is also known that waves of high abundance move along size spectra more slowly as fish grow more slowly (Plank and Law 2011). After integrating over body size, the wavelengths in the time series of total abundance are expected to be longer. Both sardine and anchovy grow more slowly under warm than cool conditions (**Figure 4a, b**), and the wavelengths in the time series are also longer under warm than cool conditions, comparing **Figure 6a** with **c** and **Figure 6b** with **d**.
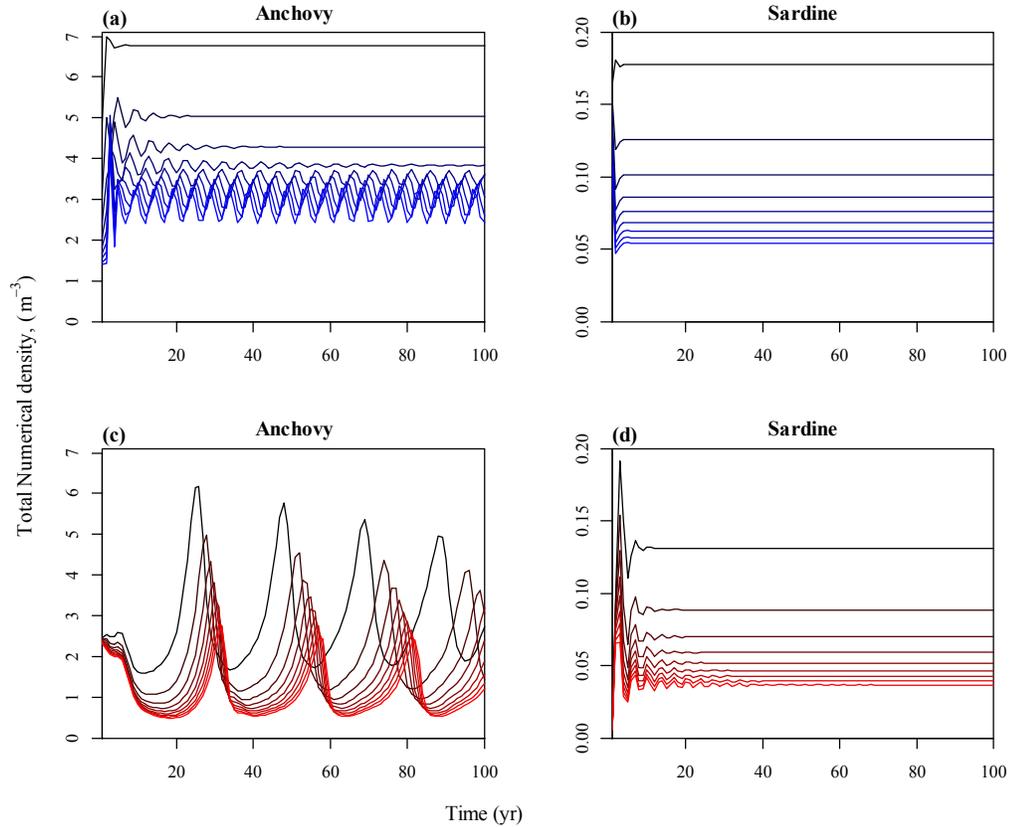
Figure 4.6. Effect of cannibalism on the total density of anchovy (a,c) and sardine (b,d) under cool (a), (b) and warm conditions (c), (d). Simulations were run for 100 years at different levels of cannibalism (elements on the diagonal of θ varied from 0.1 up to 1, in steps of 0.1. (The palette of colors from black to blue or red show the different levels of cannibalism, with black equivalent to the lowest values 0.1, and red or blue the maximum equal to 1).

4.4.4 Effects of the interspecific predation on sardine and anchovy

Figure 4.7 shows the sensitivity of sardine and anchovy to predation by the other species. In these experiments, cannibalism was absent, and interspecific predation was entirely asymmetric. In other words, the experiments examine just the effect of interspecific predation: (a) when sardine eats anchovy and anchovy does not eat sardine (**Figure 4.1c, Figure 4.7a, c**), and (b) when anchovy eats sardine and sardine

does not eat anchovy (**Figure 4.1d, Figure 4.7b, d**). This makes it possible to isolate the direct consequences of one species feeding on the other.

Predation was highly deleterious to the prey species; the prey species was almost always driven to extinction by the predator, leaving an ecosystem reduced to the plankton-predator subsystem described in **Section 4.3.2**. Extinction occurred even when the predation interaction term $\theta_{i,j}$ was small. Over the range of $\theta_{i,j}$ values used, the only case in which the prey species survived was when predation on anchovy by sardine had a value $\theta_{i,j} = 0.1$; all values $\theta_{i,j} \geq 0.2$ led to extinction. The mechanisms driving the prey species to extinction however are not the same. In the case of predation by sardine on anchovy, the sardine reaches a larger body size and the fraction of anchovy in its diet increases as it does so. This effect is amplified under warm conditions because the density of small anchovy increases (**Figure 4.5.c**) and anchovy becomes more vulnerable to sardine. It is known that fast growth is necessary to reduce the time spent at vulnerable sizes and therefore the risk of being consumed (Werner and Gilliam 1984). In the case of predation by anchovy on sardine, the high density anchovy achieves under cool and warm conditions, together with the fact that it can consume small sardine, drives the sardine density down.

Overall the path to extinction was slower under warm than under cool conditions (**Figure 4.7**). The dynamics are slowed down at higher temperature because body growth of the fish species is slowed down due to the poorer supply of plankton food.
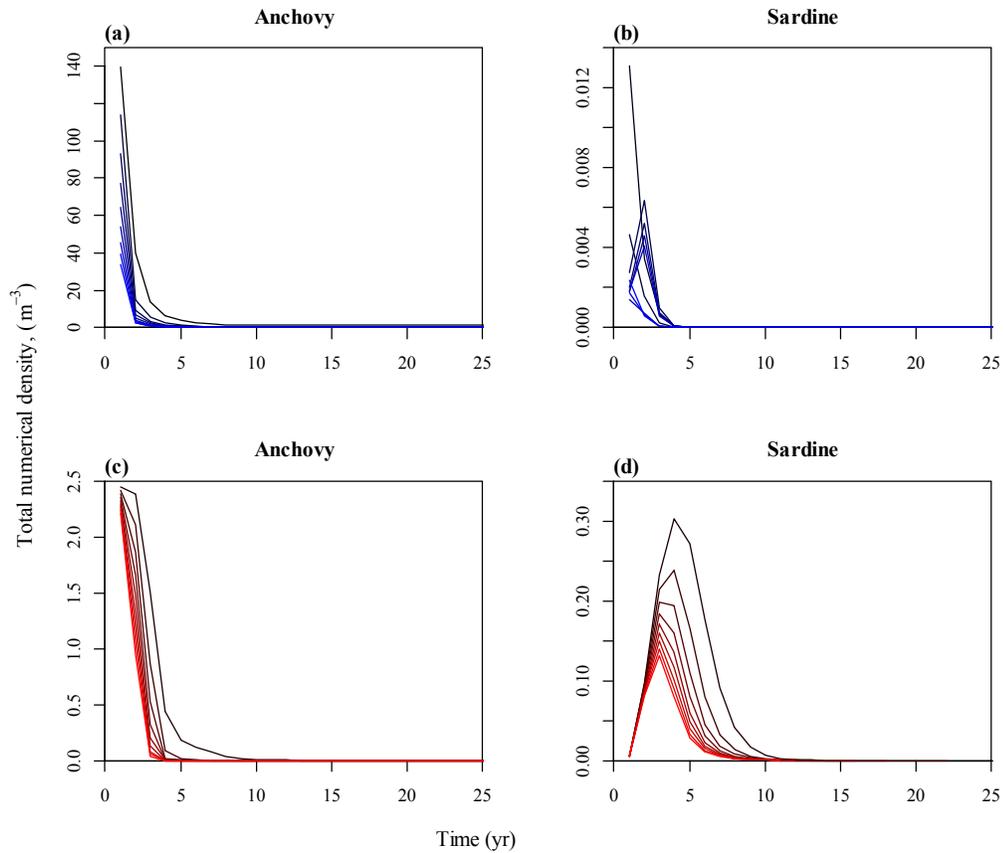
Figure 4.7. Effect of predation by sardine on the total density of anchovy (a,c) and predation by anchovy on the total density of sardine (b,d). Cool conditions (a), (b) and warm conditions (c), (d). Simulations were run for 100 years at different levels of predation (the non-zero, off-diagonal element of θ varied from 0.1 up to 1, in steps of 0.1); for graphical purposes 25 years only were plotted. The palette of colors from black to blue or red show the different levels of predation, with black equivalent to the lowest values 0.1 and red or blue the maximum equal to 1.

4.4.5 Combined effects of cannibalism and interspecific predation on sardine and anchovy

Figure 4.8 combines all of the processes above (e.g. model configuration shown in **Figure 4.1e**): (a) the contrast between cool and warm conditions as determined by the plankton spectrum, (b) cannibalism, and (c) interspecific predation. This is done using the same value of θ_{ij} for interspecific predation for anchovy and sardine, and the same value of θ_{ii} for cannibalism. With this symmetry, neither species has an inherent advantage over the other species through predation.

Under these combined processes, **Figure 4.8** makes the following points. First, anchovy remains in the ecosystem under cool conditions irrespective of cannibalism and interspecific predation, but is driven to extinction under warm conditions for most combinations of predation (**Figure 4.8a, c**). Predation does not usually compensate for the major loss of planktonic food experienced by anchovy when conditions are warm (**Figure 4.4**). However, it is possible for anchovy to remain under warm conditions if cannibalism of sardine is sufficiently large, and interspecific predation is low. In other words, the existence of anchovy in the ecosystem is determined by an interaction between: (a) the external conditions operating through the plankton spectrum, (b) cannibalism, and (c) interspecific predation.

Second, sardine remains in the ecosystem under warm conditions irrespective of cannibalism and interspecific predation, and also under cool conditions for most combinations of predation (**Figure 4.8b, d**). This is consistent with the fact that the switch from cool to warm conditions has less effect on the supply of plankton food for sardine than for anchovy (**Figure 4.4**). However, sardine can be driven to extinction under cool conditions, if cannibalism is low, and interspecific predation is sufficiently large. Thus, like anchovy, the existence of sardine in the ecosystem depends on cannibalism and interspecific predation, as well as on the external conditions.

Third, interspecific predation usually dampens the oscillations in anchovy generated by cannibalism (**Figure 4.6**); in the presence of low interspecific predation these oscillations were only observed when cannibalism in anchovy reached a value of 0.9 (**Figure 4.8a, c**). However, an additional region of oscillation arose from an

interaction between the species at a moderate level of cannibalism, and a high level of interspecific predation. These oscillations appear from the predator and prey cycle between anchovy and sardine, in particular when large anchovy follows density of small sardine.

Fourth, although sardine is driven to extinction by anchovy under fully asymmetric interspecific predation (**Figure 4.7**), there is a large region of parameter space under which sardine coexists with anchovy when interspecific predation is reciprocal, cannibalism is present, and when conditions are cool (**Figure 4.8b**).

4.4.6   Sensitivity Analysis

The results from the sensitivity analysis are summarized in **Table 4.3.** The total density at steady state is relatively insensitive to changes in most parameters, i.e. the absolute values of the sensitivities are usually considerably less than one. The results are therefore robust to moderate uncertainty in these parameters close to the values used. However, the parameters K and α do have a relatively large effect on the total density, consistent with results reported previously (Law et al. 2012). The values for K and α used in this analysis are within the range of the values used in others size-spectrum model (Benoit and Rochet 2004).

Table 4.3. Sensitivity analysis of the total density of anchovy ($S_{anchovy,\eta}$) and sardine ($S_{sardine,\eta}$) to changes in the value of parameter of the baseline. η is the value of the parameters in the baseline, and η' is the value of parameter from $\eta'=1.05\ \eta$.

Parameter	η	η'	$S_{anchovy,\eta}$	$S_{sardine,\eta}$
K	0.1	0.105	16.600	0.200
A	640	672	-3.12E-05	0
$x'_{anchovy,\ min}$	-18.421	-19.342	-0.443	---
$x'_{sardine,min}$	-23.026	-24.177	---	-0.008
α	0.8	0.840	-15.508	-0.278
$U_{anchovy,megg}$	40.194	42.204	0.060	---
$U_{sardine,megg}$	0.047	0.050	---	0.845
c	10	10.5	-0.235	-0.004
μ_0	0.2	0.21	0.060	0.010
$x_{anchovy,s}$	3.2	3.36	-0.063	---
$x_{sardine,s}$	5.4	5.67	---	0
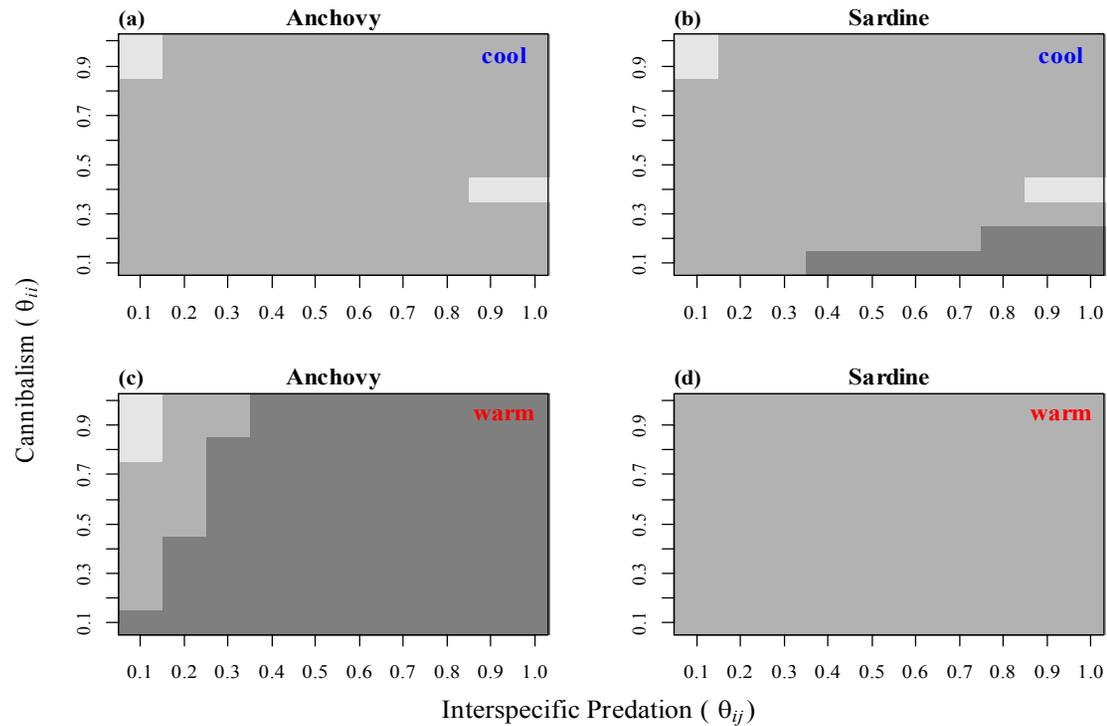
Figure 4.8. Combined effects of interspecific predation and cannibalism on anchovy (a, c) and sardine (b, d) coexistence, under cool (a), (b) and warm conditions (c), (d). Simulations were run for 100 years at different levels of cannibalism and interspecific predation, with the symmetry that the species have the same values of θ_{ij} (interspecific predation) and θ_{ii} (cannibalism). Shading indicates the state at the end of the simulation: medium gray= species present and at steady state, light gray = species present and oscillating, dark gray = species extinct. Elements off (θ_{ij}) and on (θ_{ii}) the diagonal varied from 0.1 to 1, in steps of 0.1 for each species.

4.5 Discussion

Using a multispecies size-spectrum model, I assessed for the first time the effects of two different and major environmental conditions and hypotheses about the relative role of IGP and cannibalism on the long-term size-based dynamics and coexistence of anchovy and sardine off northern Chile. The model incorporates cannibalism and interspecific predation in the dynamics of the abundance of anchovy and sardine and, by assuming that a persistent condition such as El Niño in the North Chilean Marine Ecosystem is analogous to climate regime shift towards a warm condition, differences between cool warm conditions on the equilibrium states were analysed. Our findings revealed that change in the size-structure of the plankton between cool and warm conditions would not on its own lead to extinction or the alternation of these species, but that warm conditions reduce the growth rates of both species (especially anchovy), increasing their vulnerability to predation. I also found that cannibalism on its own would decrease the abundance of both species and could destabilize anchovy species at high values, and that asymmetric interspecific predation would lead to extinction of the prey species. However, putting cannibalism and mutual interspecific predation together buffered the species against extinction, and increased the stability of anchovy. Importantly, the results show that neither is enough to know the effect of the environmental conditions alone, nor is it enough to know the effect of predation alone: the environment and predation interact in their effects on coexistence and extinction of these species in the NCME.

The dynamics of these two species anchovy and sardine have been previously studied in the NCME. Barros (2007) tested the effect of changes in the sea surface temperature, fishing and top down effects (both species feeding on the zooplankton) on the alternation of sardine and anchovy in NCME using the Ecopath with Ecosim (EwE) model (Christensen et al. 2005). A comparison between their results and those found in this work is difficult since cannibalism and intraguild predation were not taken into account in the EwE model. Moreover, the model incorporated large predators and discretized groups of plankton (phytoplankton, micro-, meso-, and macrozooplankton) with both species feeding mainly in mesozooplankton (higher proportion in their diet composition). Nonetheless, results from the EwE model indicate that alternation between these species could be promoted by changes in the

size-structure of the zooplankton community alone, and also by fishing and the top-down effects of these species on zooplankton. In our case, extinction of sardine took place in cool conditions when mutual interspecific predation was high and cannibalism was low. Anchovy extinction took place in warm conditions when less food was available and therefore the reduction in growth made its individuals more vulnerable to predation. Thus, our findings suggest that an alternation in anchovy and sardine dominance could follow from changes in the somatic growth arising from the environmental variability coupled to cannibalism and interspecific predation.

In agreement with Irigoien and Roos (2011), IP can limit the coexistence of anchovy and sardine. When IP applied to both species (**Figure 4.8**), anchovy went to extinction under warm conditions unless IP was weak, and sardine could be driven to extinction under cool condition, if cannibalism was sufficiently strong. Irigoien and Roos (2011) were not explicit about how cannibalism would affect anchovy and sardine coexistence; the work here shows that cannibalism can act as a buffer against interspecific predation, extending the conditions under which coexistence is possible. Our results are consistent with the earlier work by Valdés-Szeinfeld (1991) in the sense that mechanism such as cannibalism and interspecific predation could trigger the alternation of anchovy and sardine. I show that the combined effect of intraspecific and mutual interspecific predation on anchovy and sardine could cause extinction depending on the environmental conditions. However, whether or not the effect of both sources of predation is synergistic on the eggs mortality of anchovy and sardine is difficult to establish from these results. This is because in the model intra- and interspecific predation were associated with a range of body size for each species rather than a particular body size (e.g egg), and therefore the response of anchovy in warm conditions to predation was related with to a higher mortality in a range of body sizes of anchovy rather than a particular body size (e.g. egg). In addition, owing to that cannibalism and interspecific predation affected simultaneously anchovy and sardine abundances, it is difficult to establish if cannibalism and IGP predation were synergistic on one particular species.

I made a link between the climate variability and the pelagic system of NCME through changes in the size-structure of the phytoplankton community contrasting cool and warm conditions. The most direct way of making this link would be

through direct measurement of phytoplankton size spectrum under different environmental conditions, but this was not available. I characterized the expected differences in the phytoplankton size-structure under contrasting conditions using empirical relationships linking chlorophyll-a with phytoplankton median cell mass and size spectrum metrics, as a simple first step. However, the steepening of the phytoplankton spectrum detected here under warm conditions is consistent with previous *in-situ* observations of the phytoplankton community in NCME (Iriarte and González 2004). Moreover, several studies report shifts towards smaller zooplankton in the NCME during the El Niño event 1997-1998. For instance, Hidalgo and Escribano (2001) observed a decrease in the abundance of copepods in the coastal water (Mejillones) off northern Chile from non-El Niño conditions (1996) to El Niño (1997). González et al. (2000) mentioned a gradual decrease of large zooplankton such euphausiids from non-El Niño to El Niño 1997-98 in the areas off northern Chile. Ulloa et al. (2001) found that the endemic species of copepod *Calanus chilensis* changed its size structure becoming more abundant small body size than larger one when the system move from non-El Niño to El Niño conditions. Nonetheless, uncertainty about the exact change in the phytoplankton spectrum during a shift from cool to warm conditions exists, and our results would benefit from future validation with observational data.

The planktivorous feeding kernels of anchovy and sardine are crucial features of the model. Sardine is able to filter smaller phytoplankton than anchovy, with the result that it suffers less when the plankton spectrum steepens under warm conditions. In the absence of information for NCME, I based the feeding kernels on the largest and smallest prey items in the diet of anchovy and sardine in the Northern Peruvian ecosystem, as reported in Espinoza and Bertrand (2008) and Espinoza et al. (2009). It should be noted that most of this information came from adult anchovy and sardine. Since the dynamics of NCME are sensitive to assumptions about the feeding kernels of anchovy and sardine, there clearly is a need for basic research on their trophic ecology. In doing this, it would be necessary to take into account not only the diet composition of the species, but also other variable such body size, season, and location (Espinoza et al. 2009, Barnes et al. 2010b).

Another caveat of this study is that the plankton spectrum was held fixed with a shape consistent with either cool or warm conditions, whereas in reality the plankton

community experiences its own complex dynamics of growth, mortality and reproduction causing changes through time. Fixed conditions were used here for simplicity, although empirical information was used as much as possible to support how these differences were represented, including ensuring that the average growth of anchovy and sardine in the model were consistent with observed von Bertanlanffy growth curves. However, it should be noted that this approach simplifies a food web that is, in reality, much more complicated. Missing feedbacks include, for instance, large zooplankton (euphausiids) that are known to consume anchovy eggs in the Humboldt Current ecosystem there is evidence that large zooplankton (euphaussiids) would consume anchovy eggs (Krautz et al. 2003).

The work was based on a simple food web (plankton community + anchovy + sardine) and therefore the sources of predation mortality were limited to cannibalism and interspecific predation across the two fish species. This subsystem of the larger community in Chapter 3 was chosen because of its special interest in upwelling systems (Schwartzlose et al. 1999). Minimum realistic models are useful tools to answer specific questions (Plagányi et al. 2012) like the one explored here. Also anchovy and sardine are keystone species in the transfer of the energy from plankton to top predators in upwelling ecosystems, as the prey of large resident fish species (e.g. jack mackerel) and migratory ones (e.g. swordfish) (Chavez and Messié 2009). It remains to be seen how such predators would affect the dynamics of anchovy and sardine in different environmental conditions, and or how the reduction in the growth rate of anchovy and sardine would propagate through the pelagic food web. These are important matters to explore, especially in the context of the fishing mortality.

Anchovy and sardine in the NCME maintain the main fishery of small pelagic fish in Chile, however, how the fishing effects on these species propagate throughout the fish community is still poorly understood. Some efforts such as Barros (2007) had found that although fishing mortality itself cannot explain the fluctuations of anchovy and sardine in the NCME, its interaction with other factors such as zooplankton availability could trigger their alternations. Recently the impacts of fishing low trophic level, or "forage fish" such as anchovy, on the structure and dynamics of ecosystems have been hotly debated. Smith et al. (2011) found for several upwelling marine ecosystems (including the Peruvian system) that fishing on low trophic level species could produce several negative impacts in other

commercial fish species, mammals and seabirds. Changes in their biomass above a 60% could be observed even at depletion level of a 25% on low trophic level species, and fishing on abundant species consistently have large impacts (e. g. Peruvian anchovy) calling for a reduction in the exploitation rates of these species. However, it has been stated that in addition to lower exploitation rate, it is also important to have a more balanced exploitation of marine communities (Garcia et al. 2012) which involve trying avoid the disruption on the size distribution of commercial species which could be destabilizing. For instance, Law et al. (2012) found that harvesting according to the productivity (rate at which biomass flow, dimensions: mass, volume^{-1}, time^{-1}) at body size allows a greater sustainable biomass yield than harvesting selectively on large fish, and in addition improve the resilience of the ecosystem and reduced the disruption of size distribution of fish. The consequences of fishing at different levels of organization as well as resolving more sustainable ways of fishing are important aspects to explore in NCME and they are calling for further research.

Overall, I suggest that warm conditions that persist off northern Chile and suppress coastal upwelling, could trigger the following changes: 1) low biomass and low primary productivity of the phytoplankton community, associated with a shift towards picoplankton and also accompanied by a shift towards smaller body size in the zooplankton community; 2) reduced growth rates of sardine and anchovy, and with shifts toward smaller body sizes of both species; 3) greater deleterious effect for anchovy than sardine, because anchovy is unable to feed on smaller size of phytoplankton to the same extent as sardine. In contrast, cool conditions which strengthen upwelling would trigger: 1) an increase in biomass and productivity and shift towards large body size in the plankton community; 2) these changes cause an increase in the consumption of plankton food by both species, giving them greater rates of growth, and shifting their size-distributions towards larger body sizes. This makes both species less vulnerable to predation, and increases their capacity to coexist, although sardine may be driven down by anchovy if cannibalism by sardine is very low. This suite of predictions has implications for determining the levels of exploitation that are considered to be sustainable for sardine and anchovy, particularly in light of climate variation and climate change. These model predictions

could also be tested empirically using observational data alongside existing hypotheses that offer alternative explanations for sardine and anchovy fluctuations.

Chapter 5

Effect of the selective and balanced harvest strategies on anchovy dynamics off Northern Chile

5.1 Abstract

Low-trophic level species such as anchovy are key species in marine food webs and are economically important. It has been proved that not only does exploitation level have negative impacts in marine population and communities but also the practice of selective fishing. Fishing regulations on the anchovy fishery in the North Chilean Marine Ecosystem indirectly generate size selection. This Chapter presents an initial analysis on the effect of fishing mortality on the pelagic community off Northern Chile. The model developed in Chapter 3 was adapted to investigate anchovy only, with fishing added as an extra source of mortality to the model. The effects of two fishing strategies, traditional size-at-entry and balanced harvest on anchovy dynamics and fishery were assessed. Four indicators: variability in abundance, disruption of size structure, yield and mean length were calculated to assess the effect on anchovy dynamics. The findings show that fishing anchovy with traditional size-at-entry of 1 g had less negative impacts on anchovy dynamics than any other harvesting strategies explored. Balanced harvest strategy based on productivity became more disruptive for anchovy dynamics but fishing in proportion to relative growth rate seemed to be more beneficial for anchovy dynamics than any other strategies tested, because the first remove a higher proportion of adult individuals from the population Assumptions made in the anchovy size-spectrum model, indicators used, the implications of current fishing strategies, and further step of work are discussed.

5.2 Introduction

Low-trophic level (LTL) species (e.g. anchovy, sardine, and herring) are generally plankton feeders and are present at high abundance in many marine ecosystems. They play an important role in marine food webs because they transfer energy production from plankton to larger omnivorous predator fish, marine mammals and birds (Smith et al. 2011). Besides being keystone species, especially in upwelling ecosystems, they are economically important accounting for 30% of global fish landings used mainly in the production of fishmeal, fish-oil and animal feeding. Although human consumption is a minor use of these species (0.73% of Peruvian anchovy landings), in some developing countries they are a source of high quality protein at low cost that feed poor human communities (Tacon and Metian 2009). Thus, overfishing of these species can have a negative impact not only on fish populations, communities and marine ecosystems, but also on the economy and on the food security of human communities.

Recently, it has been argued that it is not only the intensity of the exploitation that can trigger the collapse of the fishery resources, but also the practice of fishing selectively. Zhou et al. (2010) suggested that, in trying to reduce the fishing exploitation of marine ecosystem, fisheries managers use one or more of the "6-S" selection strategies (species, stock, size, sex, season and space) exacerbating rather than reducing the impact of fisheries on marine ecosystems, and in turn negatively affecting the capacity of such systems to sustain catches. For instance, Hsieh et al. (2006) showed evidence that exploited species exhibit higher temporal variability in abundance than unexploited species. This is probably caused by fishery-induced truncation of the age structure when fishing selectively removes the larger individuals in a population, which reduces the capacity of the population to buffer environmental fluctuations, so that it becomes more variable over time. Similar findings were reported by Anderson et al. (2008) who observed changes in demographic parameters such as intrinsic growth rate, in addition to the age truncation effect and unstable population dynamics. These authors called not only for protection against depletion of the fish stock but also for protection against the age truncation effect, because even low levels of exploitation can have a negative impact in fish species and communities owing to the selective fishing. Indeed, Zhou et al.

(2010) proposed a combination of low fishing rate and a less selective fishing to maintain catches without compromising the functioning and structure of the ecosystem.

One alternative way of fishing marine populations to accomplish the goal of a less selective fishing would be to use balanced harvesting. Recently, Garcia et al. (2012) suggested this strategy as an alternative to selective harvesting to mitigate adverse ecological effects of fishing while supporting sustainable fisheries. This strategy is based on the distribution of a moderate mortality from fishing across the widest possible range of species, stocks and sizes in an ecosystem in proportion to their natural productivity, so that the relative size and species composition could be maintained. For instance, modelling a marine ecosystem, Law et al. (2012) found that fishing a life history similar to mackerel in proportion to the size-based productivity could lead to a larger sustainable biomass yield, with greater resilience to environmental change and less disruption to the size structure of the population.

The North Chilean Marine Ecosystem (NCME) provides an interesting case of exploitation of pelagic fish communities. Exploitation of this ecosystem started in the middle of 1950s (with anchovy and sardine) with its greatest development in the middle of 1970s and early 1980s when the landings reached 3.3 million tonnes (SERNAPESCA, 1955-2008). Since then and until 2008 a sustained decay of the landings has been reported, due to the collapse of the sardine fishery, and a decrease of jack mackerel catches and adult individuals caught. Nowadays, the pelagic fishery is mainly sustained by anchovy (see **Chapter 2.4.2**).

The fishery management of these pelagic species in the north of Chile has followed traditional approaches with changes in the access to the fishery (from open to closed access) and technical fishing regulations. Open access was changed to the state of closed in 1986 and in 2001 a TAC (total allowable catch) system was introduced to control the level fishing mortality (Peña-Torres 1997). Technical regulations on the industrial fleet aim to protect recruits and spawners and also to preserve some areas for an artisanal fleet. The regulations include: (i) a fixed size-at-entry fishery for some species, sardine (21 cm) and jack mackerel (26 cm until 2000, after was reduced to 21 cm), (ii) seasonal closures (summer and late winter), and (iii) fishing ban within the first five nautical miles from coast line for industrial vessels. The combinations of these technical regulations with the TAC have the final aims of

control exploitation (fishing mortality), protect small individuals and catch the largest ones within the range of biological references points for the spawning biomass.

However, in spite of the good aims of the current fishery management towards controlling the level of fishing mortality on the pelagic species, the management does not take into account the potential effects that implementation of regulations could have on the age- or size-structure of the stocks. Neither does it account for the effect on structure and function of the ecosystem, and threats to the stability of the system. For instance, the anchovy TAC involves splitting the catch according to the size of the fishing vessel and dividing the complete fleet in two categories artisanal and industrial. The fishing fleet that operates in the north of Chile is essentially an industrial fleet and therefore most of TAC is taking by this type of vessel. The fishing ban that regulates the areas where the industrial can operate concentrates fishing mortality on mature or adult individuals. The risk of size truncation seems clearer in sardine and jack mackerel which size-at-entry is regulated through the mesh-size (21 and 26 cm respectively).

This Chapter presents work currently in progress on the effect of fishing mortality on the fish pelagic community off Northern Chile. In Chapter 4, I observed that predation mortality (cannibalism and interspecific predation) in an unexploited system could significantly affect the stability and numerical density of anchovy and sardine. Implications of the combined effect of fishing mortality with predation in the context of climate variability would help understanding of the extent to which current levels of fishing mortality and fishing strategies on anchovy can be sustainable for the pelagic ecosystem and in addition the implications for the structure and functioning of the pelagic community. These aspects as was mentioned before are not taken into account by the current fishery management in NCME. As work in progress, the chapter concentrates initially on anchovy, and analyses the effect of different fishing strategies on size-based dynamics of anchovy and on fishery indicators. The effect of two types of fishing strategies, traditional size-at-entry and balanced harvest was studied. The effects of both strategies on the dynamics of anchovy were compared in terms of anchovy stability and disruption of its size structure, and the effect on the fishery were analysed through yield and the

mean length of anchovy catches. The implications for anchovy dynamics and fishery of the two types of fishing practised are discussed.

5.3 Methods

5.3.1 The size-spectrum model

The multispecies size-spectrum model (MSSM) (**Chapter 3.3.2**) was used to test the effects of different fishing mortality strategies on anchovy size-based dynamics. In the following description unless is stated parameters values were as **Chapter 3**. The MSSM the dynamics of the numerical density $U_i(x,t)$ of each fish species i in the ecosystem are governed by three continuous processes, somatic growth, reproduction and mortality. (For the details about reproduction and growth processes see **Chapter 3.3.2.1**). For simplicity in the initial analysis given here, the MSSM was parameterized for just one fish species, anchovy, plus the plankton community (**Table 5.1**). Since there was only one fish species, the species index i is omitted in this chapter and $U(x,t)$ describes the density of anchovy of size x at time t.

The plankton spectrum was chosen to represent cool conditions in the NCME because anchovy has been shown to be more successful in this condition (see **Chapter 4.4.5**). Parameters of the plankton spectrum in cool conditions are shown in **Table 5.1**. The initial condition of anchovy was set as follows. The spectra for the anchovy was assumed to follow a power law function of the form $U(x) = U_{egg} \exp(-\lambda(x - x_{egg}))$ where U_{egg} is the numerical density of anchovy (m^{-3}) at the egg size x_{egg}. The slope of the anchovy spectrum $(-\lambda)$ were assumed to be -1 following the theory of size spectra (Sheldon et al. 1972, Boudreau and Dickie 1992) as no data were available to estimate the slope. Weights of anchovy egg (x_{egg}) were obtained as described in **Chapter 3.3.2.2** and U_{egg} was taken from survey data (Braun et al. 2009).

Table 5.1. Symbol definitions, parameter values, units and sources for the size-spectrum model. Note that $x = \ln(w/w_0)$ and $w_0 = 1$ g.

Symbol	Description	Value	Unit	Source
Range of body mass in the ecosystem				
$[x_{min}, x_{max}]$	minimum and maximum body mass	[-23, 4.2]		
Plankton spectrum - cool conditions				
$[x_{pmin}, x_{pmax}]$	minimum and maximum size in the plankton community	[-23,-2.4]		
x_0	reference size plankton	-23		
U_{p,x_0}	numerical density of plankton at x_0	$e^{24.25}$	m^{-3}	Chapter 4
λ_p	slope of the plankton spectrum	-1.257		Chapter 4
Fish spectra				
$[x_{fmin}, x_{fmax}]$	minimum and maximum size of anchovy spectrum	[-8.2,4.2]		
x_{egg}	Anchovy egg size	-8.2		
U_{egg}	Anchovy initial density	$e^{0.819}$	m^{-3}	(Braun et al. 2009)
λ_f	exponent of anchovy spectrum	-1.0		

Because the analysis dealt only with anchovy and the plankton spectrum, there was no predation on large anchovy by other species, which would lead to unrealistically high densities of anchovy at large body size. Yields from fishing would have been rather sensitive to the absence of this predation as well, so the mortality rate on large anchovy was increased to compensate for this. This was done by reducing the body size x_s at which extra mortality started (previously referred to as senescent mortality in **Chapter 3.3.2.1.4**). In addition, the truncation of the size structure caused by fishing tended to destabilize the steady state. For the initial analysis given here, it was helpful to work with steady-state results, so the $(x-x')_{min}$ the minimum predator and prey mass ratio (PPMR) (**Chapter 3.3.2.1.5**), i.e. the largest prey size relative to

the predator size, was changed to ensure stability of the steady state. Parameter values were chosen such that, at steady state, the size-structure was close to that observed in the anchovy surveys from 2007 to 2010 (Castillo et al. 2007a, 2008, 2009, 2010). The values chosen were $\log_e 2$ for $(x-x')_{min}$ (previously, $\log_e 10$), and 1.2 for x_s (previously, 3.2).

5.3.2   Fishing mortality

Fishing mortality was included in the model as an extra death term in the McKendrick von Foerster equation (**Equation 3.2**) in addition to the non-predation death rate $\mu(x,t)$ and the predation death rate $d(x,t)$. This led to a new flux term fU in the equation, where f is the per capita rate of fishing mortality,

$$\frac{\partial U}{\partial t} = -E\frac{\partial}{\partial x}(gU) - dU - \mu U - fU \; ; \tag{5.1}$$

all terms are described in **Chapter 3.3.2.1.**

The fishing death rate f changes with body size x, and is a function of fishing intensity (F) (y^{-1}) and the proportion $s(x)$ of individuals caught at body size x,

$$f(x) = Fs(x) \tag{5.2}$$

The proportion of individuals caught at body size $s(x)$ depends on the strategy chosen to catch the fish. In this work I tested two types of fishing strategy, the traditional size-at-entry strategy and balanced harvesting. The first strategy, most widely used, protects juvenile individuals and fishing effort is concentrated on catching adult individuals. The second strategy, balanced harvesting, targets individuals of each body size in proportion to their productivity at their current body size. Balanced harvesting therefore tries to reduce disruption of the size-structure of the fish population by preferentially removing body sizes that are most productive. A related pattern of harvesting, also considered here, is to remove body sizes in proportion to the rate of somatic growth at each size.

The traditional size-at-entry strategy was modelled with a logistic curve following the assumption of the stock assessment of anchovy in the NCME (Serra and Canales 2009). This function represented a gradual recruitment of fish to the fishery, with

small individuals almost absent from the fishery and large ones fully recruited. The traditional harvest function $s(x)$ is described by the following function (Sparre and Venema 1998),

$$s(x) = \left[1 + \exp(s_0 - s_1 \left(\frac{e^x}{a} \right)^{\frac{1}{b}} \right]^{-1}, \tag{5.3}$$

where parameters s_0 and s_1 describe the selectivity based on the body length, and parameters a=0.005 and b=3.17 transform length into mass using the allometric relationship for converting length (l) to body weight (w), as $w = al^b$. Parameters s_0 and s_1 were chosen according to the size-at-entry to the fishery. Here, three scenarios of size-at-entry were studied: (i) size-at-entry of 1 g, (ii) at maturity 15 g and (iii) large body size 40 g. Since the logistic curve represents a gradual entry to the fishery at body size, here was assumed that size-at-entry was interpreted as the body size at which 50% of the fish were vulnerable to capture. To compare this size-at-entry with the current fishing activity in the NCME, the size structure of the catches of anchovy used in **Chapter 2** (for details of data source an estimation of the size structure see **Chapter 2.3.3**) were used to estimate the exploitation pattern of the fishing fleet. The period from 1999 to 2008 was chosen based on the absence of strong El Niño events in the NCME, and therefore cool conditions prevail in the system consistent with the plankton spectrum used in the size spectrum model.

The balanced harvest strategy depends on the shape of the productivity curve as a function of body size. This was obtained from productivity at body size under unexploited steady state conditions following Law et al. (2012). Anchovy productivity, $P(x)$ ($gm^{-3}y^{-1}$) at body size x was calculated as

$$P(x) = w_0 e^x E(x) g(x) U(x), \tag{5.4}$$

where w_0 corresponds to 1 g, and $U(x)$ and $g(x)$ are respectively the numerical density and relative rate of biomass assimilation at body size x at the steady state of the unexploited ecosystem. The term $E(x)$ is the fraction of incoming prey mass allocated to somatic growth as opposed to reproduction at body size x. The exploitation pattern based on $P(x)$ was then obtained as

$$s(x) = \frac{P(x)}{P_0},$$
(5.5)

where P_0 is the productivity at the smallest size of capture.

The exploitation pattern based on the relative growth rate in the steady state unexploited system was obtained in a similar way to the one based on productivity $\frac{E(x)g(x)}{g_0}$, where g_0 is the growth rate at the smallest size of capture. In this study the size for P_0 and g_0 was set at 1g.

5.3.3 Simulation experiments

Two types of experiments were carrying using the size-spectrum model to study the effect of the different fishing strategies on anchovy size-based dynamics. Experiment 1, corresponded to the traditional size-at-entry. This experiment involved three scenarios depending on the size-at-entry fishery, (a) 1 g, (b) 15 g and (c) 40 g. Experiment 2, involved two scenarios depending on whether the pattern $s(x)$ was based on productivity or on the relative growth rate. All experiments were run with different levels of fishing mortality (F) from 0.1 up to 1.5 (y^{-1}) in steps of 0.1. Values of F were taken from anchovy stock assessment at NCME (Serra and Canales 2009). Simulation experiments of fishing strategies and for each level of F were run for 100 years with an integration step size $dt= 0.0001$, a logarithmic body size step $dx=0.1$ and cannibalism level 0.5. The level of cannibalism was chosen based on the results of Chapter 4. The value of 0.5 allows anchovy to survive in conditions of predation by sardine and also if the system is warm or cold (**Figure 4.8**).

5.3.4 Indicators

To compare the effect of the two types of fishing strategies on anchovy dynamics, four indicators were calculated from the outcome of the simulation experiments. Two indicators summarized the effect of fishing on anchovy dynamics. These were the level of disruption of anchovy size-spectrum from the unexploited conditions and the coefficient of variation to assess the effect on anchovy stability. The other two

indicators described the effect on the fishery. These were the mean length of the catches and yield.

Disruption of the anchovy size structure caused by fishing was measured as a deviation from the unexploited steady state condition, using the logarithm of the harvested steady state, i.e. $\log U(x)$, and the logarithm of the unharvested steady state, i.e. $\log U'(x)$ at each log body mass x (Law et al. 2012). Overall deviation here is given by integrating over all body size x.

$$\Delta U = \int \left| \log U(x) - \log U'(x) \right| dx \qquad (5.6)$$

The stability of the total numerical density of anchovy for all fishing strategy was measured as the coefficient of variation (CV) of the total density, as

$$CV = \frac{\sigma}{\overline{U}}, \qquad (5.7)$$

where $\overline{U}$ corresponds to the mean value of the total density of anchovy, and σ to its standard deviation. Note that each experiment was run for 100 year.

The mean length $\overline{L}$ (cm) of the catches of anchovy at the beginning of year and at the steady state condition was obtained as

$$\overline{w} = \frac{\int U(x)\exp(x)s(x)dx}{\int U(x)s(x)dx}, \qquad (5.8)$$

with $\overline{w}$ identifying the mean weight of the vulnerable range, $U(x)$ corresponding to total numerical density at steady state, $s(x)$ being the selection pattern, and dx being logarithmic body size step. The $\overline{w}$ was transformed to length ($\overline{L}$) using the allometric relationship for length and body weight, as $\overline{L} = \left[\dfrac{\overline{w}}{a} \right]^{1/b}$. Parameters a and b were the same as those used in **Equation 5.3**.

The yield Y (g m^{-3}y^{-1}), obtained at steady state, was calculated for all scenarios of fishing strategy as

$$Y = \int w_0 e^x f(x) U(x) dx,$$

(5.9)

where w_0 corresponds to 1 g, $f(x)$ is the fishing death rate, and $U(x)$ is the numerical density.

5.4   Results

5.4.1   Parameterization of the fishing strategies

Parameters and exploitation patterns of the traditional size-at-entry and balanced harvest strategies are summarized in **Table 5.2** and **Figure 5.1**. Three scenarios of traditional size-at-entry fishery were considered: 1 g, 15 g and 40 g. (**Figure 5.1.a**). Size-at-entry of 1 g removed immature and mature fish; 15 g targeted individuals around the size at maturity and larger, small fish being less vulnerable; 40 g concentrated on removing mature long-lived fish which are at low density in the system. **Figure 5.1.a** also shows the selective pattern from the fishery in the NCME (1999-2008). The pattern is close to the selective pattern with size-at-entry at maturity showing that the fishery at the NCME removes mainly mature fish.

Table 5.2 Traditional size-at-entry fishing strategy. Parameters s_0 and s_1, correspond to the intercept and slope of selectivity curve of anchovy describe by the **Equation 5.3**, for each traditional size-at-entry. Mass at 19 g represents the average size-at-entry to the fishery in the NCME (1999-2008).

	Size-at-entry fishery			
	1 g	15 g	40 g	19 g
s_0	15	18.1	33	23.6
s_1	2.82	1.45	1.94	1.74

The parameterization of the exploitation patterns in the balanced harvest strategy was based on the productivity of anchovy in unexploited steady state conditions (**Figure 5.1.b**). The shape of anchovy productivity function depends on its biomass density and also on the relative growth rate, expressed as functions of body size in

unexploited steady-state conditions (**Figure 5.1.c**). The productivity curve (**Figure 5.1.b**) reaches a maximum at a body size of x=2.4 (11 g). This is in contrast to the findings of Law et al. (2012), where productivity peaked at a much smaller body size (less than 1 g). The main reason for this difference was a high density of large individual at the steady state of anchovy (see the Discussion section for further explanation). The exploitation pattern arising from productivity therefore concentrates the removal of fish around their maturity size. In contrast, the relative growth rate (**Figure 5.1.b**) decreases with increasing body size, thus a harvest pattern set in proportion to growth rate corresponds to removing at a high rate the individuals located at small body size and decreasing the intensity of fishing as individuals get larger.
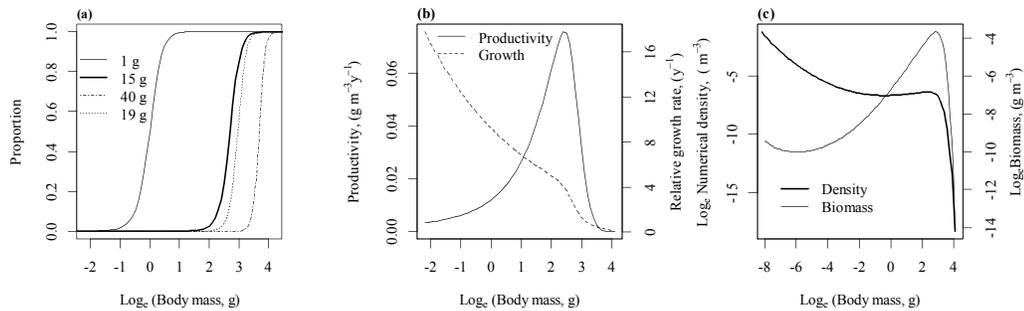
Figure 5.1. Patterns of size-selective fishing. a) Traditional size-at-entry fishing strategy using at 1, 15 and 40 g with parameter values as in **Table 5.2**; the size-at-entry 19 g represents the selection pattern from the anchovy fishery. b) Productivity and relative growth rate at body size at unexploited steady state conditions used for balanced harvesting calculations. c) Numerical and biomass density at body size at unexploited steady state conditions.

5.4.2   Indicators

Anchovy numerical density reached a constant steady state in all fishing strategies and at all levels of fishing mortality. Outcomes from all simulation experiments were summarized in the indicators shown in **Figure 5.2**.

5.4.2.1 Disruption of the size structure (ΔU)

ΔU in both traditional size-at-entry and balanced harvest strategies increased linearly with the level of fishing mortality (**Figure 5.2**). The largest disruption to anchovy size spectrum was observed in the presence of balanced harvesting when productivity was used as a selective pattern (c.f. Law et al. 2012) (**Figure 5.1.b**). This disruption was due in part to the productivity being greatest near the size at maturation, as a result of which balanced harvesting led to the greatest removal of fish around maturity. As the level of F increased, large fish decreased in density and so did smaller fish. The loss of small fish comes from the reduction in egg production caused by the loss of mature fish. As a consequence, the size-structure became distant from the one observed under unexploited conditions.

In the traditional size-at-entry strategies, disruption decreased as the size-at-entry increased. This is because, the later the size-at-entry, the smaller the impacts on the population. For instance, there were relatively few fish remaining available to be caught in a fishery with a size at entry of 40 g (**Figure 5.1.a**), so the disruption caused by fishing would be small. The disruption caused by fishing in proportion to growth rate was also relatively small, because removing fish at small size more heavily than those at largest size helped to maintain the proportion of densities between body sizes and therefore the size structure is closer to the one observed at unexploited steady state condition.

5.4.2.2 Coefficient of variation (*CV*)

CV of the anchovy numerical density shows that traditional size-at-entry of 15 g or 40 g produced the highest variability in anchovy density over the time period of simulation with little variation between the levels of fishing mortality (**Figure 5.2**). The CV of the balanced harvest strategy using productivity showed a non-linear trend with the level of F. The minimum value of CV was observed at a value of F = 0.6 y^{-1} with an increasing trend on the CV for values of F above 0.6. The decreasing trend on the CV values (F≤0.6) was consequence of the removal of fish, which decrease the variability at beginning of the simulated time series. For values of F>0.6 the egg production is negatively affected by fishing mature individuals and also

smaller ones, decreasing the egg density at the beginning of simulation period leading to large fluctuations and as consequence larger values of CV.

Harvesting in proportion to growth rate led to a high CV although with a slightly downward trend as F increased. Size-at-entry of 1 g shown the lowest variability and as the same as the previous scenario, the CV decreased with the level of fishing mortality. It is important to mention that $\overline{U}$ numerical density always decreased with the increase in F, and therefore σ was influenced for the magnitude of fluctuation of $\overline{U}$ at the beginning of the simulated period.

5.4.2.3 Mean length ($\overline{L}$)

The $\overline{L}$ of size range of the catches of anchovy in all scenarios showed low variation with the level of fishing mortality (CV≤ 0.02) (**Figure 5.2**). Under selective fishing the lowest $\overline{L}$ was observed at a size-at-entry of 1 g. Entering at a size of 15 and 40 g give values for $\overline{L}$ of 13.7 (±0.09 cm) and 16.1 (±0.04 cm) taking into account all level of F respectively. An extra experiment was run with a size-at-entry of 19 g (value for the fishery in the NCME between 1990 and 2008) and the value of the $\overline{L}$ was 14.5 similar to $\overline{L}$ reported for catches at NCME of 14.7 cm excluding El Niño years (see **Chapter 2.4.2**). $\overline{L}$ under balanced harvesting were smaller than traditional size-at-entry strategy. In the productivity scenario $\overline{L}$ was around 9.6 (±0.5 cm) and relative to the growth was even lower 8.7 (±0.07 cm).

5.4.2.4 Yield (*Y*)

In all strategies, yields increased as the level of the fishing increased over the range value of F from 0.1 up to 1.5 (**Figure 5.2**). Balanced harvest produced the highest yield and selective fishing at size-at-entry of 40 g the lowest ones. Within the traditional size-at-entry strategies, the highest yields were observed at a size entry of 1 g. In the balanced harvest case the highest yields were obtained with exploitation pattern based on productivity.

Overall, comparing all indicators, the results show that fishing anchovy selectively at a size-at-entry of 1g would have the best outcome for anchovy dynamics and fishery. Fishing with a size-at-entry of 15 g or 40 g produced higher variability in anchovy dynamics and the lowest yield. Balanced harvesting in proportion to productivity had a strong deleterious effect on anchovy size structure. Harvesting in proportion to the growth rate was less disruptive for anchovy, but the mean length and yields were the lowest values found.
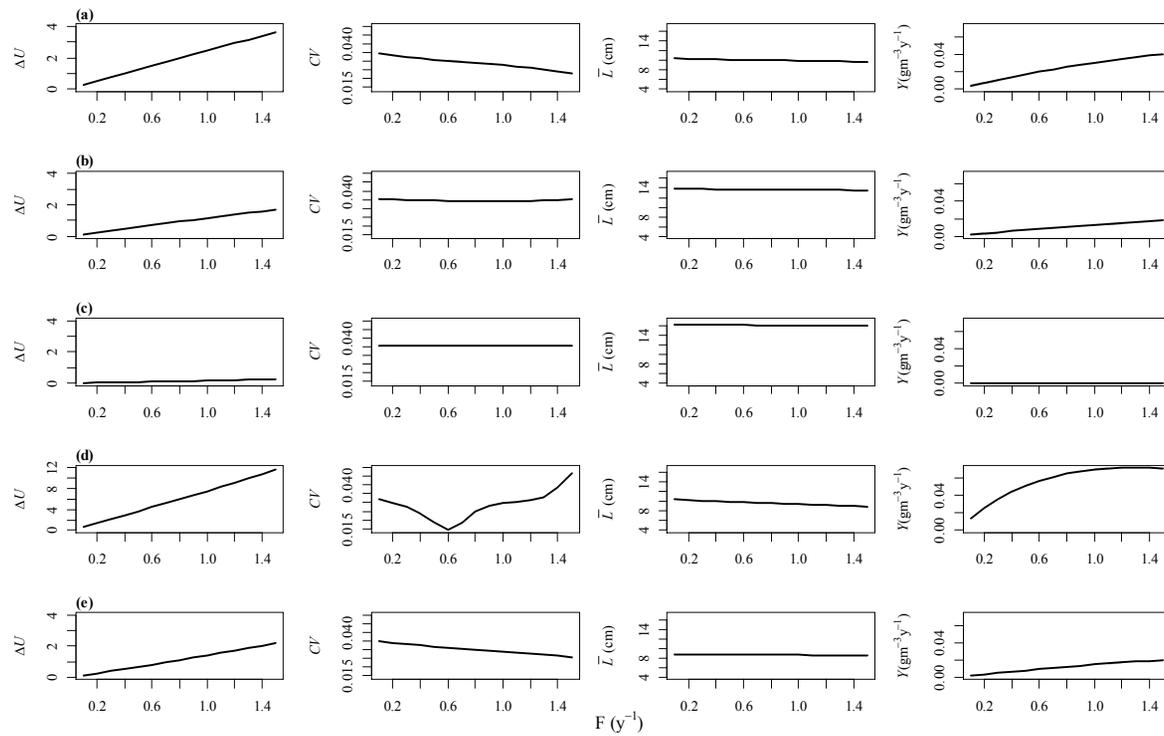
Figure 5.2. Indicators of the effect of fishing on anchovy size based dynamics and fishery. ΔU=disruption of the size structure, *CV*=coefficient of variation, $\overline{L}$ = mean length, *Y*=yield and *F*=fishing death rate. Rows are harvest strategies with size-at-entry: (a) 1g, (b) 15 g, (c) 40 g, (d) balanced harvesting based on productivity, (e) balanced harvesting based on growth rate. ΔU, $\overline{L}$ and *Y* were all obtained at steady state. Note that in (d) the scale of the y-axis of ΔU is different from other fishing scenarios.

125

5.5 Discussion

The present study shows initial results of a more long term study on the effects of the fishing on the size-based dynamics of the pelagic fish community of the NCME. To this end just one keystone species, anchovy was chosen from the ecosystem for this study. The findings show that fishing anchovy with traditional size-at-entry of 1 g had less negative impacts on anchovy dynamics and fishery than other harvesting strategies explored. Balanced harvest strategy, which is thought to be promising in other contexts (Zhou et al. 2010, Garcia et al. 2012), became more disruptive for the anchovy dynamics than fishing by traditional size-at-entry methods. However, balanced fishing in proportion to relative growth rate seemed to be beneficial for anchovy dynamics even compared with the traditional size-at-entry of 1 g, although with lower yields and mean length.

The difference between the effect of balanced harvesting found here and that found in previous work (Law et al. 2012) is related to the different shape of the productivity function used and the selective pattern calculated from it. In previous work the peak of the productivity occurred at a body size less than 1 g, and productivity decreased with increasing body size over the full range of sizes harvested. In this study, the slope of the anchovy size spectrum was flatter (close to zero over part of the range of body size) when I tried to match the shape of the anchovy spectra with the size structure of anchovy observed by survey in the NCME (Castillo et al. 2007a, 2008, 2009, 2010). The peak of the productivity function from the anchovy model was at a large body size and as a result the greatest rates of fishing mortality were close to the size at maturity. However, it is possible that predation mortality rate on large anchovy was still too low in the present study in spite of the use of survey data as reference. A caveat about the size structure obtained from the survey is that it could be biased because it came from observing the same fraction of the population every year in the same period of time; information from smaller body sizes such those below to size $x=1$ (2.7 g) is incomplete as well as long-lived individuals.

Nevertheless, balanced harvest in proportion to the relative growth rate shows similar effect on the anchovy size spectrum dynamics than to those reported by Law et al. (2012) in terms of a lower disruption to the size structure. The exploitation

pattern that arises from productivity in Law et al. (2012) has a similar shape to the one arising from the relative growth rate of anchovy in this study. Therefore, low removals of fish larger that the size-at-maturity could take place following the relative growth rate which could lead to low disruption level of anchovy size structure.

The initial results from traditional size-at-entry close to the size at maturity carry a warning about the effects on the anchovy dynamics when fishing mortality remove mostly mature anchovies without leading to the highest yield. Predictions from this work would indicate high variability of the anchovy at all level of fishing mortality when selection is close to maturity. The selective pattern of anchovy fishery at the NCME (size-at-entry 19 g) is placed near to the maturity ogive (exploitation pattern with a traditional size-at-entry of 15 g is equivalent to the maturity ogive) indicate that anchovy stability could be affected by the current fishing activity in the NCME. Moreover, initial results also indicate that a reduction of the traditional size-at-entry could benefit anchovy stability and produce higher yields.

These initial results show that the effects of fishing on anchovy dynamics depend on its size spectra. However, the existence of caveats about its size structure shows the importance of taking further steps in this work, such as adding other species (e.g. sardine, jack mackerel) to the system and see if less of a build-up in density is shown, and then explore the effect of different fishing strategies on anchovy dynamics in a community context.

In this work, I used four indicators to compare the effect of fishing on anchovy dynamics when different fishing strategies and sizes-at-entry were applied. Further work is needed on the coefficient of variation. The CV was calculated to measure the stability of the total density of anchovy, over the complete time period of simulation. Because of this, some of the variation was caused by the initial conditions, which were not set to be close to the steady state. Starting from a size spectrum close to the steady state could give different results because initial condition influence is damped. Alternatively, using a conventional stability analysis to get information on the dominant eigenvalue, as in Law et al. (2012) could be helpful in assessing the stability of the system.

In addition to the indicators used here, it is also important to assess the biological reference points for forage species, such as anchovy. This is a particularly interesting topic in the context of the single species model used on stock assessment (Tyrrell et al. 2011). Single species models assume that natural mortality (which includes predation mortality) is constant over size, age, and time, whereas in reality predation mortality varies explicitly over time, space and developmental stage of the fish. This applies as much in the case of the NCME as in the other ecosystems. Variability of the predation mortality on species such as anchovy, or forages species in general is important owing to the ecological role that they play in transferring energy from low trophic levels up to different large fish predators, availability of energy that also changes in the context of climate variability, especially in upwelling marine ecosystems.

In conclusion, further steps mentioned above need to be addressed to confirm the implications of current fishing strategies on the anchovy size-dynamics, the potential positive effect of new strategies for the fishery and anchovy, and the implications for the pelagic community. The effect of fishing mortality in the context of predation mortality and climate variability, and strategies to produce higher yields while maintaining the size structure of population, could have serious implications for the future fishery management of the pelagic fish community of NCME.

Chapter 6

General Discussion

Humans and their societies depend on marine systems for a wide range of goods and services that are essential for their well-being (Link 2005, Levin and Lubchenco 2008, Halpern et al. 2008, Kershner et al. 2011). The use of these goods and services generate anthropogenic impacts that frequently affect function and integrity of the marine system (Kershner et al. 2011). Although for most of human history these goods and services have been readily available, today most marine ecosystems are severely degraded and stressed as result of overfishing, bycatch, habitat destruction, pollution, selective fishing, ocean warming and acidification and therefore their ability to supply the goods and services required or desired by humans is threatened (Myers and Worm 2003, Pauly and Palomares 2005, Orr et al. 2005, Levin and Lubchenco 2008, Levin et al. 2009). Marine ecosystems are complex adaptive systems in which the dynamics of interactions at small scales permeate up to large system dynamics, which then feedback to influence the smaller scale. Therefore, it is important to understand the linkage between these scales and incorporated that knowledge into public awareness, management actions, and policy decisions (Levin and Lubchenco 2008). Ecosystem based fisheries management (EBFM) has been widely proposed as a useful approach to account for these complexities, to protect ecosystem structure and function, and to maintain ecosystem resources and services Although there is a general consensus that ecosystem based management is the framework for marine and coastal decision-making, the major challenge lies its implementation (Kershner et al. 2011).

The current fishery management of Chilean marine ecosystems is still based on the goal of sustainability of single-species stock in the medium- to long-term without accounting for the impacts of these removals on the ecosystem. The Chilean government has joined international agreements to move towards ecosystem based fishery management, but the problem remains a to how to it is to be implemented (Pitcher et al. 2009). The general aim of this thesis was to contribute to the understanding of the dynamics of the pelagic community off northern Chile and in doing so, to work towards the implementation of the ecosystem approach to fishery

in the NCME. To accomplish this goal I chose to follow empirical and theoretical approaches based on body size. The reason for doing this is that body size is a trait that captures a significant proportion of the ecologically relevant characteristics of organisms in an ecosystem (Woodward et al. 2005). Moreover, most fishing process are size selective (Link 2005, Shin et al. 2005) and body size is also sensitive to climate variability and climate change (Daufresne et al. 2009, Shackell et al. 2010).

6.1   Size-based indicators, climate variability and fishing

In the implementation and framework of EBFM, indicators play a central role because they provide the basis for the diagnosis of status and trends in populations, communities and ecosystems (Rochet and Trenkel 2003, Levin et al. 2009, Ye et al. 2011). Thus managers can evaluate current and past policy decisions, as well as plans for the future according to certain target or references points (Levin et al. 2009, Kershner et al. 2011, Ye et al. 2011). In **Chapter 2** of this thesis, I created a set of size-based indicators on fishery data from NCME to look for persistent trends at the species level (including anchovy, sardine, jack mackerel and mackerel), and at the assemblage level, and investigated whether these indicators were related to the climate variability (e.g. El Niño event or Regime shift). Thus, I find downward trends in the size-based indicators of the catches of sardine, jack mackerel and in the slope of the size spectrum of catches, indicating that from 1990 to 2008 the catches of industrial fleet had been maintained by increasingly catching small individuals especially anchovy. Although, no long-term relationships were found with environmental indicators (SST, CHL) and fishing was not taken into account, interpretation of the size-based indicators case-by-case suggested that the trends could have emerged from the combined effect of fishing and of climate variability. There was evidence of overfishing of sardine and changes in the selectivity of fishing on jack mackerel. However, climate variability and in particular the onset of a cold regime in the NCME at the end of 1980s beginning of 1990s (Yáñez et al. 2008a), could have influenced the ratio anchovy:sardine in the HCS (Gutiérrez et al. 2007). Therefore anchovy became the dominant forage species in the NCME and more available to be caught. Climate variability such as El Niño was also present from 1990 to 2008 producing temporary disruption in the size-structure of anchovy,

but the fishery activity seemed to return to its previous state after the event. The finding of this chapter on fishery-dependent data is in line with previous findings in upwelling ecosystem. For instance, comparisons of ecological indicators across upwelling and non-upwelling ecosystems explicitly recognize that fishing in upwelling marine system is modulated by climate variability (Mackinson et al. 2009, Link et al. 2010), and Shannon et al. (2010) explicitly recognize the need include climate variability in the analysis of the effect of fishing on ecosystem state and trends. The findings are also in line with the previous conclusions about how population, community and fishery changes with the climate variability in the Northern Peruvian Marine Ecosystem (Bertrand et al. 2004, Alheit and Niquen 2004, Ñiquen and Bouchon 2004, Gutiérrez et al. 2007). Results in **Chapter 2** also call for attention to the implications for the pelagic community on fishing largely on planktivorous pelagic fish. It has been shown theoretically that fishing on planktivorous species could slow down the growth rate of predators (Andersen and Pedersen 2010), and it has been postulated as a mechanism that could delay the recovery of collapsed stocks (Heath and Speirs 2012).

6.2   Basis of an operating model of pelagic system off Northern Chile

Understanding how fish community interacts with fishing, climate variability and climate change is not a trivial task. Populations, communities and ecosystems vary at different temporal and spatial scales, making it difficult and expensive to do the sampling needed, or to run controlled biological experiments. Thus, models constitute excellent tools to run controlled simulation experiments to test hypotheses about the dynamics of fish communities and their interactions with climate variability and human pressures. In a fishery-management context, models (referred to as operating models) are key tools either for single-species or ecosystem based management. For instance, through models the effect on the biological system of different management strategies can be assessed (Ye et al. 2011, Plagányi et al. 2012). In **Chapter 3**, I developed a multispecies size-spectrum model (MSSM) for the pelagic community off northern Chile, the eventual aim of which is to become a tool for dynamical analysis of the pelagic fish community off northern Chile. The

MSSM focuses on a limited number of fish species (eight) some of which play key ecological roles in the NCME (e.g. anchovy, sardine), and with others of which such as, jack mackerel, mackerel, swordfish, and bonito and palm ruff constitute fisheries resources. The model also includes as a functional group, the community of mesopelagic fish which has become important over the last decade or so in NCME and in the HCS. The fish community extends towards the plankton community also represented as size-structured functional group (no species distinction). These set of species plus the plankton represented in simplified way the structure of a typical pelagic food web of an upwelling system (Chavez and Messié 2009).

In the mathematical model, the fish community arises as a result of the combined size-based dynamics of each species. Fish lifespans encompass a range of body sizes from that of an egg up to their maximum size, and species interact through predation events (on individuals from other species and on conspecifics). In this way fish transport energy through the community, from which somatic growth, reproduction and predation mortality emerge. The McKendrick (1926), von Foerster (1959) equation is used to model each species' dynamics. In models of this kind, feeding preferences of predators are usually described by a feeding kernel which assumes that logarithm of the predator and prey mass ratio follows a Gaussian distribution and that larger fish only eat small fish. However, the assumption of a feeding kernel based on predator-prey body size ratios is not appropriate for planktivores fish, as these continue to filter very small plankton particles as they grow large. Thus this chapter introduced a novel kind of feeding kernel to match the diet composition of anchovy and sardine.

The model structure has several advantages. (i) It extends towards the plankton community allowing a direct link to be established between the lower trophic levels (plankton) and the physical forcing, so that effects of climate variability or change can be scaled up to the fish community. (ii) Anthropogenic effects such as fishing mortality can be easily incorporated because they are size-based processes as well (e.g. different types of fishing fleet, industrial and artisanal). (iii) It can be used to assess the effect at community and population level of different fishery management strategies. (iv) It accounts for interspecific predation and cannibalism, so depensatory effects (Allie effect) can be explored especially in the context of rebuilding stocks and species predation interactions. (v) The number of parameters

needed is relatively small, so it is not too hard to parameterize the model, making it a good candidate for use in poor-data conditions. The model could be seen as a minimally realistic model Plagányi et al. (2012). Although models of this type are not used for tactical purposes (short-term decision, e.g. how much to catch), I believe the model given in this thesis could be the basis of an operating model that can be used within strategic studies (long-term decision making). These studies include, for instance, questions about how different management strategies influence the state of fish populations and community.

6.3 Cannibalism and intraguild predation matter in anchovy-sardine coexistence

In **Chapter 4** using the MSSM, I focused on analysing the consequences of intraguild predation and cannibalism for a subset of the pelagic fish community, that comprising anchovy, sardine and the plankton community. Using satellite data for NCME, the plankton size spectrum was parameterized according to the normal-La Niña condition (cool) and the contrasting El Niño (warm) condition establishing in this way a link between physical forcing and the pelagic community. The findings revealed a change in the size-structure in the plankton spectrum between cool and warm conditions would not on its own lead to extinction or the alternation of these species, but that warm conditions reduce the growth rates of both species (especially anchovy) increasing their vulnerability to predation. Strong cannibalism could destabilize anchovy, and the interactions of cannibalism with intraguild predation buffered the species against extinction, and increased the stability of anchovy. I concluded that climate variability and predation interactions are both needed to understand the coexistence and extinction of anchovy and sardine.

Thus, the research in this chapter supports the role of predation mechanisms as drivers of anchovy-sardine alternations earlier proposed by Valdés-Szeinfeld (1991). Recently, Irigoien and Roos (2011) argued that environmental conditions on their own cannot trigger an alternation between anchovy and sardine, but that predation interactions between species could amplify small changes in species abundance caused by either the environment or by fishing. The authors called for more attention in these processes, in keeping with van der Lingen et al. (2009) who noted in a

global synthesis that they had been given little attention in the context of understanding the dynamics of small pelagic fish populations in upwelling ecosystems. The findings show another important environmental effect that has not been taken in consideration in anchovy-sardine dynamics. This is the decrease in the somatic growth rate of anchovy during warm conditions, as well as in sardine, which also amplifies the effect of predation between species. The reduction on fish somatic growth rate can have implications at individual level such increasing its vulnerability to predator and therefore higher mortality (Werner and Gilliam 1984). In a community context this effect can also propagate to the predators populations affecting differentially the size-structure of predators. For instance, Olson (1996) found a differential effect on predator body size when the prey decreased its growth rate. Small predators grow slowly due to the small size of the prey, but growth rates increase substantially as predators get larger because they are able to feed on old/larger age classes of the prey, in addition to the small and young prey. The changes in growth rate leading to changes in mortality can also have important implications for sustainable fishing as well as for the references points (Tyrrell et al. 2011) especially for these heavily fished species (Smith et al. 2011).

6.4   Effect of different fishing strategies on anchovy dynamics and fishery

To understand how fishing mortality interacts with predation mortality under different environmental conditions, **Chapter 5** started an investigation of the effect of different fishing strategies on the fish pelagic community off Northern Chile. As the first step, this study focused just on the effect of fishing on anchovy under cool conditions. I study in particular the effect of two types of fishing strategies, traditional size-at-entry and balanced harvest. Initial results showed that fishing anchovy under traditional size-at-entry strategies, with fish entry to fishery at body size below size at maturity (e.g. 1 g), would have relatively low negative impacts on anchovy dynamics. However, a size-at-entry near maturity, as is the case of the current exploitation pattern of the industrial fleet in NCME, would lead to a higher variability. A promising new fishing strategy was explored, balanced harvest (Zhou et al. 2010, Garcia et al. 2012); this was beneficial for anchovy dynamics and fishery

yield, but only when the selection pattern followed the relative growth rate of anchovy. The findings, although depending on anchovy size-structure, revealed interesting aspect of the effect that management strategies can have on the dynamics of anchovy species in the NCME. Further work is needed to give more support towards these results. Studies of these impacts on population and community are not currently taking place in NCME.

6.5   Limitations and projections of this thesis

This thesis has taken a 'holistic' view of the pelagic marine ecosystem off Northern Chile and its main drivers. By calculating size-based indicators from fishery data an state of the commercial fish assembly of species and its fishery was identified. Following the size-spectrum theory, a mathematical model that includes fish species (commercial and non-commercial) and plankton was created. The dynamics of the community then emerge from the interaction between the species and with the plankton influenced by fishing, climate variability and fishery management decisions (**Figure 6.1**). Using this framework (size-based indicators and MSSM), it has been possible to study different hypotheses about the dynamics of the pelagic community and its interaction with the environment and human pressures. In doing so, caveats, gaps in basic research, ways to improve the model have become evident, together with projections for future work.
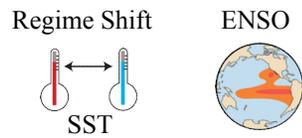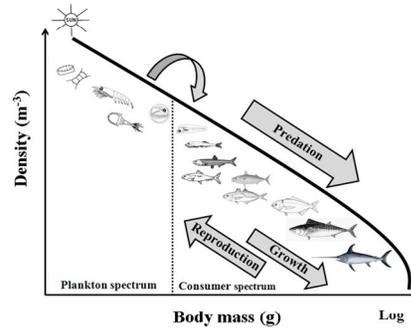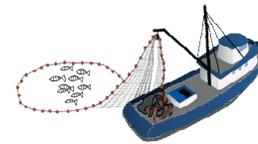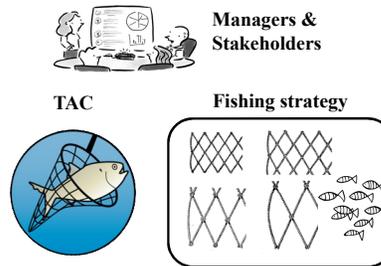
Figure 6.1. Diagram of the processes that MSSM could address to study the dynamics of the pelagic marine ecosystem off Northern Chile. (a) Climate variability such as El Niño/La Niña (ENSO) and Regime shift (SST: Sea surface temperature), (b) Ecological system: pelagic community off northern Chile (operating model), (c) Human pressure is incorporated in the MSSM via mortality term and (d) Fishery management such effect of total allowable catch (TAC) and fishing strategies can be explored.

The set of size-based indicators created in **Chapter 2,** although showing interesting findings about changes in the size-structured of catches in the NCME over time, turned out to be limited in their correlations with environmental variables. Although, the number of data points is a key aspect in the identification of trends, the results found here clearly cannot be explained exclusively by the climate variability. Other variables, such as fishing need to be taken into account. It is possible that fishing in combination with environmental variable may explain the variability observed in the size-structured.

This type of study can be complemented by fishery-independent data to create the same set of size-based indicators and maybe others (e.g. diversity indices, trophic links, size spectra). The advantage of using survey data is that the relationship between the population and community and climate variability is not masked by other variables such as fishing; instead fishing mortality can be added as another explanatory variable (e.g. Blanchard et al. 2005). This set of size-based indicators complements other indicators could be used in the management process to check whether fishing mortality levels are sustainable at the population and community level. These imply identify threshold for the populations and the community (reference points).

Another limitation of the work is that it concentrated on a limited number of species, those with the greatest economic importance. However there other commercial species in the system for which detailed information did not exist, as well as non-targeted species. It is possible that lack of information will prevent indicators of the type used here from being used on these species, although, in the absence of detailed information, there are alternative ways to detect trends, such as the one shown by Godoy et al. (2010). The thesis deals with fishing by the industrial fleet, but there is also an artisanal fleet that operates in NCME. This operates in different areas and, although the removals by artisanal activity are far lower than those by the industrial fleet in the NCME, it is believed that the size-structure of the catch is different, and the importance of the fleet has gradually increased since 2001 (Castilla 2010).

The MSSM developed in **Chapter 3,** although it accounts for many of key aspects of the pelagic system off northern Chile, does still have some limitations. For simplicity, the size-structured of the plankton community was assumed to be

constant over time. In reality, this community has its own dynamics and at the same time interacts with fish spectrum. For instance, off southern California euphausiid appear to be significant predators on the early stages of northern anchovy (*Engraulis mordax*) accounting for a 47 and 78 % of the natural mortality of eggs and yolk-sac larvae (Theilacker et al. 1993). Therefore, future work should incorporate approximations to account for plankton dynamics. A simple approach for instance would be to model the resource spectrum (plankton) by using a semi-chemostatic model (Hartvig et al. 2011)

An aspect of the environment that was not considered in this work was seasonality. Although considered to be weak process in the context of climate variability off northern Chile compared with other systems (e.g. central-south of Chile) (Montecino and Lange 2009), should be taken into account so that its effect on the dynamics of fish community can be assessed. Even a 'weak' seasonal forcing can cause variation in the carrying capacity of the system (intercept of the plankton spectrum), which will propagate into the fish spectrum affecting the processes of growth and reproduction. Datta (2011) implemented seasonality in a size-spectrum model following the approach of Pope et al. (1994) showing for instance that growth rate of newborn larvae is high around the plankton bloom.

The MSSM developed here also assumed homogeneous space, whereas in reality distribution and abundance of fish species varies also in space. Physical processes in the HCS modify the three-dimensional distribution of physical (e.g. temperature), chemical (e.g. oxygen) and biological (e.g. plankton) parameters of the so-called oceanic landscape. Then, mobile predators such as anchovy and fishers respond to these spatial perturbations (Bertrand et al. 2008a). Castle et al. (2011) developed a spatially explicit size-spectrum model, with individuals moving locally towards areas with high concentrations of favoured prey, and moving away from areas of high predator density. They also incorporate passive transport for the smallest size classes to represent the effects of turbulent mixing of plankton. This approach also can account for competition process do not considered in the MSSM implemented here.

The parameterization of the MSSM identified gaps in basic knowledge of the feeding traits on the majority of the species in the model. Feeding traits of the target species

are less well documented than other relevant aspects of their biology and feeding traits of non-target species are almost completely undocumented for the NCME. The majority of the studies normally refer to diet composition without for instance considering how diet changes with body size. Almost totally absent for all species are diet studies for fish of small body size (pre-recruit and larvae). Basic research on trophic ecology of the pelagic community off northern Chile is an urgent need especially in the context EBFM. In the process of doing such work, it would be helpful to have a better understanding of how diet changes with body size, with space and with time, because the predation changes within, as well as between species (Barnes et al. 2010b, Hunsicker et al. 2011). Irigoien and Roos (2011) mention a series of techniques that could be applied to study the diet at small body size such as in larvae. Life history information on non-target or less important commercially species is also scarce.

Parameterization of plankton spectrum would also require further validation since a number of assumptions about its size-structure had to be made. Research on the MSSM model has so far been restricted two species (anchovy and sardine) plus the plankton community. This is because early explorations of the model showed it was difficult to achieve coexistence of several species and there was uncertainty about the parameter values to use in the interaction matrix. However, a recent exploration of the model has shown that up to five species can coexist at equilibrium. This was accomplished with the assumptions taken in **Chapter 4**, where the model was anchored to anchovy growth rate in cool conditions, and interaction matrix was assumed to take values around 0.1. Future work, should consider how to parameterize the interaction matrix according to level of spatially overlap of these species in NCME. To incorporate species with distribution beyond the NCME (e.g. jack mackerel) an external resource spectrum could be added to model (as simple way approach); this has been also informally explored.

From a fishery management perspective aspect such as quantification of the uncertainty and statistical comparison with observation at sea (monitoring: community and/or fishery) are also matter of future work. However, Law et al. (2009) reported a match of the deterministic results from the size spectrum model with those arisen from studying stochastic size spectra, indicating that the

deterministic approximation of size spectrum model is reasonable and therefore the results presented here.

In **Chapter 4** I demonstrated that IP and cannibalism are as important as the climate variability in anchovy-sardine alternation in the upwelling ecosystem. To test this I linked the climate variability to the plankton spectrum by changing the size-structure of the plankton spectrum as function of environmental data. However, the alternation of these two species is also thought to be triggered by changes in temperature (Takasuka et al. 2007). The optimal range of temperature for the growth of the early life stages of anchovy and sardine is likely to be different. Recently, Bertrand et al. (2011) have proposed that oxygen would be a fundamental property regulating pelagic ecosystem structure in the southeastern Pacific. These authors proposed that distribution and abundance of fish in the area is correlated to near-surface oxygen concentration/saturation and that anchovy and sardine respond in a different manner to the oxycline depth over a wide variety of scales. Anchovy does not seem to be affected by a very shallow oxycline (<10 m), and can use it as a refuge from predators, but sardine avoids such areas. Furthermore, sardine has a higher respiration rate than anchovy (Van der Lingen et al. 2006). These observations can be investigated if the space dimension is introduced in the model, or alternatively explored through changes in physiological rates. Temperature is directly linked to these rates (Brown et al. 2004) and its effects on size spectra have been previously shown by Maury et al. (2007). Oxygen consumption rate per unit of mass has been shown decrease as individuals increase in body mass (Seibel and Drazen 2007). How the anchovy-sardine alternations are affected by large fish predators (e.g. jack mackerel, mackerel), and how the effect on anchovy and sardine growth propagates under different environmental conditions are also questions that can investigated with the model.

Chapter 5 of this thesis showed work in progress, and from this perspective several steps need still to be taken. Key points here are to incorporate more species into the analysis, to see if the size-structure of anchovy then shows less of a build-up in density at large body sizes, and to investigate further some of the indicators calculated. From the point of view of fishery management, the stability of community and populations based conventional stability analysis (Law et al. 2012) can be a tool to be incorporated in future analyses. One aspect not considered in this

study and previously mentioned is that the pelagic fishery off northern Chile is composed by two fleets, industrial and artisanal. Although, historically the industrial fleet has been the main source of fishing mortality would be interesting to compare the effect to both exploitation pattern on anchovy population as well as at community level. Reference points for forage species also need to be explore, especially in context of variation of predation in time and body size (Tyrrell et al. 2011). Today the fishing activity is maintained almost only on anchovy and assumptions such as constant predation mortality over time and body size could be overestimating the reference points of the species.

In closing this thesis, Watson et al. (2012) reported that global catches have now generally stagnated or declined, and that most of biomass that supported the global fisheries has been substantially reduced in the last few decades. Although, this trend could be debated (Hilborn 2007b, Worm et al. 2009), the study also showed that fishing fleets have increased in power by an average of 10-fold since the 1950s. The majority of the 18 regions of world considered in the study had an overall reduction in CPUE in recent years following some relative maximum in the 1970s or 1980s; the Pacific Southeast (location of HCS) is one of three exceptions of this global trend in the CPUE and therefore its conservation need to be seriously considered.

This thesis has attempted to develop a basic framework on which to work towards an ecosystem based management for pelagic system off northern Chile, the system that accounts for about 30% of all Chilean pelagic landings. It is not the first contribution in this direction in the NCME (Barros 2007, Medina et al. 2007) and this thesis took into account their observations and findings. The novelty here is that the system has been seen from the perspective of body size and species, following the evidence that size matters in marine ecosystems, and that when is not taken into account a wide range of biological process that scale up to ecosystem level can be missed (e.g. growth). In addition, size is a trait in which underlying processes can be intuitively understood by non-scientists (from fishers to managers). Empirically and theoretically, the analysis has been carried out with the size-based dynamics of pelagic community of NCME in mind. However, the interesting findings are not only a contribution to NCME, but also to the understanding of fish community dynamics of upwelling ecosystems in general. The study has also identified gaps of basic research, limitations of the approach, but most of all exciting possibilities for

future work!. Finally, the knowledge and experience that I have accumulated over these last four years, following several years of using only single species stock assessments to diagnose the state of pelagic populations of the Chilean marine ecosystems, has made me realize that there is not just a way to the ecosystem based management, for ecosystem based management is the way.

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