TROPHIC MODELS OF THE BENGUELA UPWELLING SYSTEM: TOWARDS AN ECOSYSTEM APPROACH TO FISHERIES MANAGEMENT

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Thesis Presented for the Degree of
DOCTOR OF PHILOSOPHY
In the Department of Zoology
Faculty of Science
UNIVERSITY OF CAPE TOWN

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November 2000

ABSTRACT

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Using the trophic models, indices quantifying interactions between species and trophic groups were developed to provide useful measures for the comparison of marine ecosystem structure and function. A new trophic similarity index for anchovy and sardine explains the strong similarities in trophic functioning of the southern Benguela ecosystem in the 1980s and 1990s.

Modelling experiments using the dynamic ecosystem simulation tool *Ecosim*, suggest that observed changes in pelagic fish catches between the 1980s and 1990s are unlikely to have played a large role in driving changes in abundance of anchovy and sardine in the southern Benguela ecosystem. It is hypothesized that changed environmental conditions may have influenced the size composition of planktonic food of anchovy and sardine, thus changing their relative abundance, with some signs of a "regime shift' from anchovy to sardine dominance.

Steady-state models show that there are structural and functional differences between the northern and southern Benguela sub-systems. Dynamic simulations of altered fishing strategies show that in the south, heavy fishing on model hake and small pelagic fish has larger negative effects on horse mackerel and large pelagic fish respectively than in the north. There are large differences between the effects of altered fishing simulated under different assumptions of top-down and bottom-up flow control.

A new way of approaching fisheries management is proposed according to a 4-step plan using information from ecosystem modelling studies to address the call for "responsible fishing" and the need to take ecosystem effects into account in managing fisheries.

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ACKNOWLEDGEMENTS

This thesis would not have materialised without the support, encouragement, co-operation and advice of many people, and to each and every one I would like to express my most sincere thanks and appreciation. Many research staff unselfishly gave up their time and went to much trouble to give me their expert advice or to supply me with data and references. To all I say a big thank you, and in particular to Rob Crawford, Marc Griffiths, Hans Verheye, Carl van der Lingen, Chris Wilke, Larry Hutchings, Stan Pillar, Emmanuelle Beucher, Mark Gibbons, Cliffie Hart, Sharon Du Preez, Corne Erasmus, Manuel Barange, Francis Le Clus, Dave Japp and Jan van der Westhuizen. I especially thank Philippe Cury and Villy Christensen; Philippe, for the regular stimulating and informative discussions and emails, and for supervising two of my chapters, and Villy, for answering my many queries about the intricacies of *Ecopath with Ecosim* and providing me with early versions of the software. I thank Cathy Boucher for her patience and efforts with all the "spider plots", and Mark Prowse and Johann Rademan for solving my endless computer problems. Thank you to my close family and friends for listening attentively despite all the scientific details I insisted on providing! I am much indebted for the caring and kindness I could always rely upon. To my husband, Obie, thank you for your unfaltering belief in me and for silently suffering from "PhD" with me over the last year in particular. My sister, Debbie, kept me company by writing her PhD at the same time – thank you for commiserating along the way and for keeping me on track. Finally, I would like to express my most sincere thanks and gratitude to my three supervisors: John Field, Coleen Moloney and Astrid Jarre. I value your guidance, encouragement, supervision and inputs very highly. Thank you for the time and effort you put in to make this study possible and to provide me with such a valuable and enjoyable working experience.

CHAPTER ONE
INTRODUCTION

ABSTRACT

The main aim of this study is to explore the trophic functioning of the Benguela ecosystem during alternating periods of abundance of anchovy and sardine, with a view to providing insight into functioning of the Benguela ecosystem and ultimately to advising on multispecies management of marine resources in the region. The Benguela upwelling scene is set prior to laying out the key questions to be examined. An outline of the subsequent chapters follows.

1.1. INTRODUCTION TO THE BENGUELA UPWELLING SYSTEM

There are four major upwelling regions of the world; the Benguela, California, Canary and Peruvian systems, associated with the four major eastern boundary currents (Fig. 1.1). The Benguela Current was first defined by Hart and Currie (1960) as the region of cool, upwelled water off the coast of south-western Africa. The Benguela system may be subdivided into two oceanographic sub-systems: northern and southern sub-systems. The northern Benguela is considered to extend south of the Angola-Benguela front, which is usually located between 14 and 16 °S (Meeuwis and Lutjeharms 1990). A permanent upwelling cell located in the vicinity of Lüderitz, Namibia (around 26°S) is believed to provide a barrier to the north-south migration of some fish stocks, such as anchovy and sardine. It is this upwelling cell that is often used to define the separation of northern from the southern Benguela sub-system. However, the conventional division between northern and southern sub-systems is the Namibian-South African border at the Orange River Mouth (about 29°S). Assuming the northern Benguela sub-system extends from 15 to 29°S, offshore to the 500-m depth contour, the northern Benguela sub-system covers 179 000 km^2 (Jarre-Teichmann *et al.* 1998). It is assumed that the southern Benguela sub-system extends from the Orange River Mouth (about 29°S) to East London (28°E),

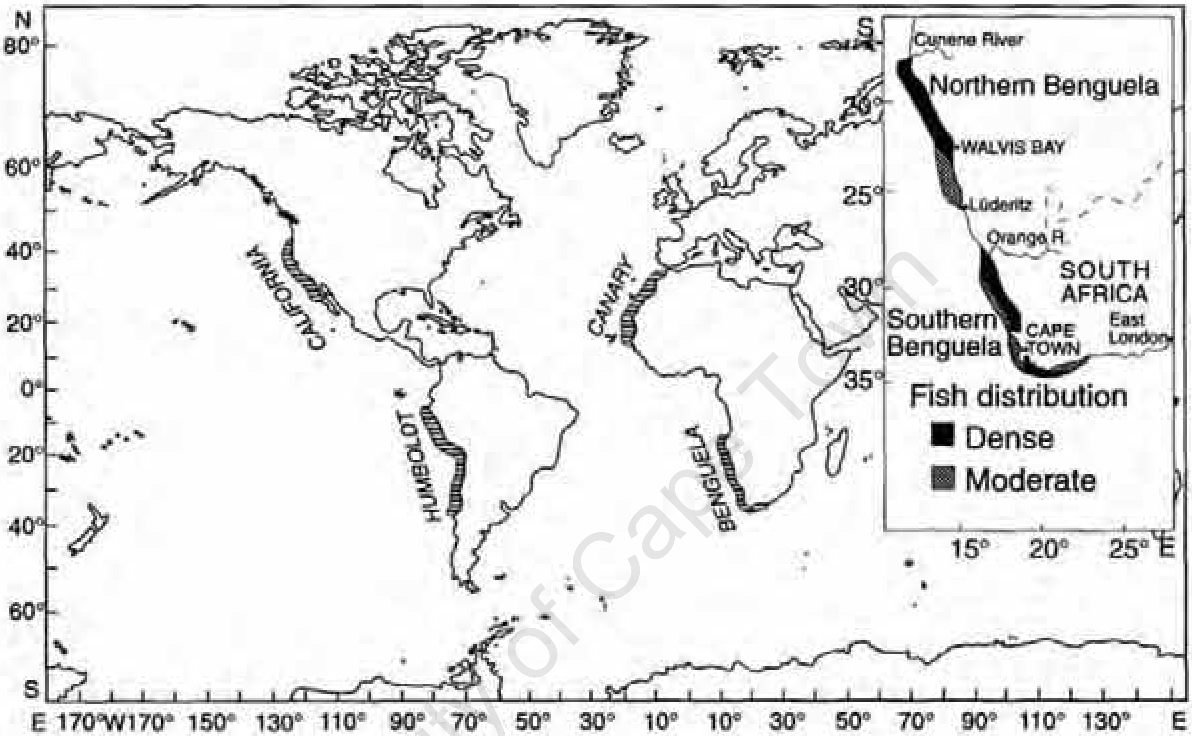


Fig.1.1 Map showing the four major upwelling areas of the world. Inset gives details of the Benguela upwelling system (after Jarre-Teichmann *et al.* 1998).

offshore to approximately the 500-m depth contour, and covers an area of 220 000 km^2 (Jarre-Teichmann *et al.* 1998). The southern Benguela sub-system is unique because it includes the upwelling region along the south-western coast of Africa, but also extends over the Agulhas Bank and along the south coast. For this reason, the demersal and benthic components of the southern Benguela ecosystem are more abundant and play a more important role than in most other upwelling systems. The upwelling and bank areas were not modelled separately owing to the complex life cycles of many species having spawning, nursery and feeding grounds in both areas and at different times of the year.

Work on the oceanography of the Benguela upwelling system began in the late 1800s (Muhry 1862, Petermann 1865). In 1895, Dr John Gilchrist was appointed as Government Marine Biologist. He held this position until 1926, and in that time undertook pioneering marine research, earning himself the title of the father of marine science in southern Africa. After World War II, detailed studies of the oceanography of the Benguela system were undertaken. These focussed on monitoring and were mainly descriptive (Shannon 1989). After 1970, more detailed, process-oriented studies were undertaken. The oceanography of the Benguela system has been well documented by Nelson and Hutchings (1983), Parrish *et al.* (1983) and Shannon (1985). Shannon and Nelson (1996) provided a comprehensive review of the subject, including previously unpublished information that has lead to the current understanding of the Benguela system.

Like all major upwelling systems (Ryther 1969, Cushing 1971), the Benguela system is productive and supports important pelagic and demersal fisheries. Purse seine nets are used to catch small shoaling fish such as anchovy and sardine, midwater trawls target larger fish like adult horse mackerel, and demersal trawls catch bottom-dwelling fish such as hakes (Payne and Crawford 1989). Fluctuations in the marine resources of the southern Benguela sub-system during the 20th century have been reviewed by Crawford *et al.* (1987). Changes in the marine environment have been shown to impact a range of species in the Benguela sub-systems simultaneously, with different lag periods being noted (Shannon *et al.* 1992). For example, the warm event that occurred during the mid-1980s has been linked to changes in resources such as anchovy, sardine, hake, rock lobster and squid (Shannon *et al.* 1992). Overall catches in the South-East Atlantic increased during the 1950s and 1960s, peaking at 3 million tons in 1968, and fluctuating at around 2 million tons thereafter (De Villiers 1985). The rapid increase in catches is attributed to the expansion of the purse seine fishery targeting pelagic fish. When these catches declined, there was an expansion of the demersal trawl fishery targeting hakes, and when hake catches decreased, horse mackerel were more heavily fished (De Villiers 1985).

At present in the southern Benguela sub-system, the most valuable commercial species are shallow- and deep-water hake, constituting 26% of the total catches in the region during the period 1990-1997, and 47% of the landed value. Hakes are caught in demersal trawls and by the line and the longline fisheries. There is little room for expansion of the demersal fishery above present levels, particularly the hake fishery for which production models suggest that exploitation is close to the optimal level (Punt 1994).

Most linefish stocks are currently overexploited and cause for recent concern (Griffiths 1999, Griffiths 2000). Owing to large fluctuations in anchovy and sardine stock sizes, the pelagic fishery is the most dynamic of all in this region. During the 1980s, anchovy was the dominant small pelagic fish in the southern Benguela sub-system. By the 1990s, anchovy biomass had declined and stocks of sardine, redeye, horse mackerel and both species of hake had increased in size. In the northern Benguela sub-system, there was heavy fishing on both sardine and hake during the 1970s. Sardine was the dominant pelagic species between 1971 and 1977 (Jarre-Teichmann and Christensen 1998a) but underwent a large decline during the 1980s. Anchovy abundance also decreased over this period and horse mackerel became the dominant pelagic species. Hakes and horse mackerel dominate catches in the northern Benguela sub-system.

Only a few attempts have been made to model the Benguela upwelling system as an ecosystem in which interactions between species are defined. Shannon and Field (1985) examined phytoplankton standing stock size and estimated the consumption of phytoplankton and zooplankton by fish stocks in the southern Benguela sub-system. Using a particle-size model, Moloney and Field (1985) predicted standing stock and yield of pelagic fish from phytoplankton standing stocks in four areas off southern

Africa, including the southern and northern Benguela sub-systems. Bergh *et al.* (1985) constructed a preliminary carbon budget for the southern Benguela pelagic ecosystem. Baird *et al.* (1991) used network analysis of the carbon flows in the southern Benguela sub-system to compare the ecology of the sub-system to five other marine ecosystems. Moloney (1992) modelled the trophic flows and nutrient cycles in the planktonic food web of the southern Benguela sub-system. In this dissertation, trophic flows from phytoplankton through to top predators are examined in the southern and northern Benguela sub-systems, and interactions between species are explored to provide insight into the functioning of the Benguela ecosystem. This is necessary if we are to move towards managing our fisheries from an ecosystem perspective.

1.2. OBJECTIVES OF THE THESIS AND KEY QUESTIONS ADDRESSED

The aim of the thesis is to compare the functioning of the Benguela ecosystem during alternating periods of abundance of anchovy and sardine, with a view to advising on multispecies management of marine resources in the region. Although the focus of this research is on the pelagic fish resources of the southern Benguela sub-system (Fig. 1.1), it is useful to include similar work on the northern Benguela sub-system for comparative purposes.

Key questions addressed in the thesis are grouped into three categories:

1. **Trophic flows in anchovy- versus sardine-dominated periods in the southern Benguela ecosystem:**

a) What are the biomass, production, consumption and catches of the components of the southern Benguela ecosystem during periods of a) anchovy dominance (1980s) and b) sardine dominance (1990s)?

b) How do mass-balanced models of these two regimes compare? How do the following compare: trophic flow diagrams, total system throughput, mean transfer efficiency, primary production required to sustain catches, trophic pyramids, and mixed trophic impacts of various groups? (These terms are described in Chapter Three, sections 3.3 and 3.4).

c) When ranges of input parameters (biomass, catches, production/biomass ratios, etc.) are considered as opposed to means, what can be learnt of the southern Benguela ecosystem in different periods?

d) How do the trophodynamics of the southern Benguela ecosystem change as there is a shift in dominance of pelagic species? Is it possible to develop quantitative indices of species interactions in ecosystems (e.g. keystone species and redundancy)?

e) Is there a trophic mechanism capable of sustaining regimes over extended periods or precipitating a switch between dominant species?

2. Comparing the trophic functioning of the southern and northern Benguela ecosystems:

Models of the 1980s serve as a basis for this comparison.

a) What are the biomass, production, consumption and catches of the components of the northern Benguela ecosystem during the 1980s?

b) How do mass-balanced models of the northern and southern Benguela sub-systems compare during the 1980s? How do the following compare: trophic flow diagrams, total system throughput, mean transfer efficiency, primary production required to sustain catches and mixed trophic impacts of various groups?

3. Towards multispecies approaches for management of resources in the Benguela upwelling region:

a) What are the short- and long-term effects of different harvesting strategies during periods of anchovy and sardine dominance in the southern Benguela ecosystem?

b) How does our understanding of the way in which species interact influence the potential effects of altered fishing?

c) How do the southern and northern Benguela sub-systems respond to similar fishing strategies?

d) What can be learnt from the trophic models with regard to development of a multispecies approach to management of the Benguela ecosystem? What management advice can be given and how can this be improved upon in the future?

1.3. THESIS OUTLINE

In Chapter 2, the concept of shifting regimes of pelagic fish species is introduced. The chapter provides a background to regime shifts, considers some reasons for shifts in dominance of pelagic fish, and discusses some of the processes involved. The progression in fisheries science from traditional single-species management techniques to the incorporation of ecosystem considerations is introduced.

In Chapter 3, the *Ecopath* modelling tool is described. The dynamic simulation tool *Ecosim* is also outlined. Underlying assumptions and limitations of this approach to ecosystem modelling are discussed. The key questions outlined in section 1.2 are addressed in Chapters 3-13 (Table 1.1).

In Chapter 4, collated data are presented for the southern Benguela ecosystem during the 1980s and 1990s. Included are biomass estimates and other parameters used as model input, diet data and catches. Techniques used in balancing the *Ecopath* models for the two periods are documented.

In Chapter 5, results of *Ecopath* models of the southern Benguela sub-system during the 1980s and 1990s are presented. Summary statistics, trophic flow diagrams, mixed trophic impact assessment and primary production required to sustain the fisheries are among those results compared between decades, and discussed with reference to results of similar studies in other systems.

In Chapter 6, the sensitivity of input model parameters is investigated using a simple sensitivity analysis routine and *Ecoranger*, which incorporates variability about input parameters. In addition, selected scenarios were modelled so that the effects of alternative estimates of some of the lesser known parameters could be examined.

Chapter 7 presents a model of the northern Benguela ecosystem during the 1980s.

In Chapter 8, trophic flows through the northern Benguela and southern Benguela sub-systems are compared. A preliminary comparison is made of potential effects of altered fishing scenarios in the two ecosystems.

In Chapter 9, the effects of altered harvesting strategies for the three most abundant pelagic species (anchovy, sardine and redeye) as well as the commercially most important fish species (hake) on the southern Benguela ecosystem are investigated. Underlying assumptions about the way in which ecosystem components interact are explored. Differences between altered harvesting strategies of these fish species are investigated assuming top-down, bottom-up and wasp-waist control in the southern Benguela ecosystem.

In Chapter 10, the effects of altered harvesting regimes in the southern Benguela sub-system are further explored. Refined models of the southern Benguela ecosystem are used and catches are specified by gear type. Responses of the ecosystem to fishing are examined. The ecosystem effects of fishing are compared between "regimes" of pelagic fish dominance in the southern Benguela ecosystem.

In Chapter 11, results from mass-balanced models (Chapters 4 and 5) and dynamic simulations (Chapter 10) are used in the development of indices quantifying species interactions in ecosystems.

In Chapter 12, simulations of the anchovy-sardine dominated shifts in the southern Benguela ecosystem are explored. Firstly, the change in the pelagic fisheries between the 1980s and 1990s is examined for its possible role in the observed "regime shift". Secondly, the change in zooplankton available to anchovy and sardine is investigated as a mechanism through which regime shifts may be mediated.

In Chapter 13, the work presented in the previous chapters is drawn upon to develop the first ecosystem-based method for fisheries management in the southern Benguela sub-system.

A summary of the main results and conclusions of the thesis is given in Chapter 14.

Table 1.1 Key questions (columns) addressed by Chapters 4-13 (rows)

Key Question/ Chapter	1a	1b	1c	1d	1e	2a	2b	3a	3b	3c	3d
Four	X										
Five		X		X							
Six			X								
Seven						X					
Eight							X			X	
Nine								X	X		
Ten								X			
Eleven				X							
Twelve					X						
Thirteen											X

Summary of main objectives underlying key questions:

1 SOUTHERN BENGUELA ECOSYSTEM MODELS

1a Estimating parameters as input to models of the southern Benguela ecosystem
1b Comparing mass-balanced models of the southern Benguela ecosystem for 1980s and 1990s
1c Incorporating variability about input parameters in southern Benguela ecosystem models
1d Developing ecosystem indices
1e Trophic mechanism sustaining regimes

2 NORTHERN BENGUELA ECOSYSTEM MODEL

2a Estimating parameters as input to model of the northern Benguela ecosystem
2b Comparing mass-balanced models of the southern and northern Benguela ecosystems during the 1980s

3 TOWARDS MULTISPECIES APPROACHES FOR MANAGEMENT

3a Simulating effects of altered harvesting strategies in the southern Benguela ecosystem
3b Investigating assumptions about top-down, bottom-up control and their effects on simulations of altered harvesting strategies
3c Comparing modelled effects of altered harvesting strategies between the southern and northern Benguela ecosystems
3d Developing a multispecies approach to fisheries management for the southern Benguela ecosystem

CHAPTER TWO

REGIME SHIFTS AND WHY ECOSYSTEM MODELLING CAN HELP FISHERIES MANAGEMENT IN UPWELLING SYSTEMS

ABSTRACT

Fisheries management is complicated by large fluctuations in fisheries stock sizes in relation to changes in temperature, currents, fishing, food and other factors. In upwelling areas, periods of great abundance of anchovy alternate with periods in which sardine is dominant. Regime shifts have implications for the management of fisheries in these areas. Multispecies models build on single-species approaches by considering both the direct and indirect effects of fishing in an ecosystem context. If fisheries management is to be improved, it will be necessary to consider ecosystem structure and function. *Ecopath* models are used to explore these aspects in the Benguela upwelling system.

2.1. INTRODUCTION

Worldwide, fisheries management is made difficult by large fluctuations in abundance of fish stocks. Variables thought to account for most of the observed variability of exploited fish stocks and that cause regime shifts are temperature, turbulence, transport, food, predation and population density (Parrish *et al.* 1983). In addition, fishing may play a major role. A single environmental variable does not necessarily limit all stocks of a given species group. Rather, stocks have similar functional relationships to each environmental variable, but variability within a species group can be a function of any or all of the variables proposed (Parrish *et al.* 1983, Bakun 1996).

Regimes are defined as large ecosystems that are climate-ocean linked, undergo shifts in states over 10-30 year periods and to which fish and other marine biota respond by changing their dynamics (Beamish and Mahnken 1999). In most upwelling regions where anchovy and sardine co-exist, there has been alternation between regimes of high sardine and anchovy abundance (Lluch-Belda *et al.* 1992a). There are two main hypotheses regarding regime shifts: i) continuous environmental change such as a prolonged period of warming, which may permit an expanded spawning range and increased egg production, and ii) episodic environmental events, which may result in formation of powerful year-classes (Schwartzlose *et al.* 1999). Altered circulation, altered wind patterns and therefore intensity of upwelling, availability and access by larvae to food (related to turbulence), temperature and changes in suitable habitat are believed to operate during regime shifts (Lluch-Belda *et al.* 1992b). Other factors include predation (Crawford 1989), fishing effort (e.g. Silvert and Crawford 1988, Korrubel 1992), preferred mode of feeding (van der Lingen and Hutchings 1995) and the influence of temperature on egg and larval development (Butler *et al.* 1993), on spawning (Lluch-Belda *et al.* 1991) and on the distribution, density and availability of fish to fisheries (e.g. Muck *et al.* 1989a).

In this chapter, the subject of alternating periods of dominant pelagic fish will be introduced. First, some of the factors causing variability in fish stocks will be discussed, with a view to identifying some of the mechanisms responsible for driving and sustaining regime shifts. This is not intended to be a comprehensive review of all literature on fluctuations in pelagic fish dominance. Rather, the chapter aims to provide some background to the leading research on regime shifts between anchovy and sardine in the major regions of the world where both species co-occur. The chapter continues by introducing the concept of managing fisheries from an ecosystem perspective. Various multispecies modelling techniques are mentioned, putting into context the model (*Ecopath*) used in this thesis to explore ecosystem management in the Benguela upwelling system. The chapter outlines why ecosystem management is a pressing issue, and how addressing ecosystem functioning in different regimes of pelagic fish dominance can assist in the development of an ecosystem approach to fisheries management in upwelling regions.

2.2. WHAT MAKES FISH STOCKS FLUCTUATE?

2.2.1. Temperature

In their review, Lluch-Belda *et al.* (1992b) discuss possible mechanisms that govern the success of fish stocks. They suggest that if fish abundance is determined by survival of eggs to the late larval stage, and if this is also linked to temperature regimes, then eggs-to-larvae ratios should differ between high and low abundance phases. However, they show that for sardine in the region of the southern California Bight, this ratio is constant from year to year, supporting the hypothesis previously proposed by Lluch-Belda *et al.* (1991) that spawning itself is variable, depending on the environment. In the California Current system, sardine are eurythermic (spawn over a wide temperature range) and spawn at intermediate levels of upwelling activity (Lluch-Belda *et al.* 1991). By contrast, anchovy are stenothermic and spawn at low and high levels of upwelling. The authors suggest that these differences could imply the existence of competitive exclusion between anchovy and sardine off California, but warn that further analysis is required.

Lluch-Belda *et al.* (1992b) stress that in the southern Californian Bight, sardine abundance may be determined by egg production and survival, with both dependent on environmental conditions. In fact, other authors have shown that survival of early life stages of small pelagic fish is responsible for fluctuations in their population sizes; Butler *et al.* (1993) used a stage-based model of northern anchovy *E. mordax* and Pacific sardine *S. sagax* to compare the life history stages that accounted for the greatest changes in population growth of the two species. They showed that for sardine the greatest changes resulted from natural variability in duration and instantaneous mortality of the late larval stage, but in anchovy both the early and late larval stages were important. Temperature determines the duration of egg and yolk-sac larval stages as well as the rate at which larvae mature (Butler *et al.* 1993).

2.2.2. Currents

Transport of fish eggs and larvae has been a topic of much discussion (e.g. the review of Norcross and Shaw, 1984), and has been shown to affect recruitment of many fish species (e.g. Bartsch *et al.* 1989, Kasai *et al.* 1992, Werner *et al.* 1993, Bernsten *et al.* 1994, Bjørke and Sætre 1994, Bakun 1995, Shannon *et al.* 1996, Shannon 1998). Shifts in oceanic circulation, associated with shifts between cool and warm regimes (Lluch-Belda *et al.* 1992b), have implications for pelagic fish stocks. For example, favourable conditions for the survival of post larvae are caused by a shift in the Kuroshio Current, a key factor in the rapid increase in the Japanese sardine stock after 1970 (Kondo 1980). Similarly, there are indications that in recent years the California Current has weakened and upwelling and mixing has been reduced (Lange *et al.* 1990). It was postulated that this could lead to enhanced spawning activity by sardine, but it was not certain whether conditions would be more favourable for the survival of larval sardine (Lluch-Belda *et al.* 1992b). It has since been concluded that sardine abundance off California is rapidly increasing, although future trends are uncertain (Arenas *et al.* 1996, Butler *et al.* 1996). In his discussion of low frequency variability in fish populations off California, MacCall (1996) predicted a peak in California's sardine abundance some time around 1998, a decade after Japanese sardine catches peaked. Based on biological indicators, he forecasted a transition to a cool regime between 1996 and 2006. Parrish *et al.* (1981) show how both short and long-term environmental changes affect the transport processes of pelagic fish in the California Current system.

2.2.3. Fishing

It is now generally believed that collapses of pelagic fish stocks and subsequent replacement of dominant species are primarily environmentally linked, with fisheries usually serving to hasten and intensify the collapse rather than driving the regime shift (Jennings and Kaiser 1998). The extent to which a possible "replacement species" is exploited immediately following the collapse of another species can determine whether the replacement is successful (Crawford *et al.* 1987). Silvert and Crawford (1988) modelled the replacement of one pelagic fish stock by another in five upwelling regions, finding that species replacements are attributed to a combination of fishing and competition between predatory species for forage fish. Cisneros-Mata *et al.* (1996) modelled fluctuations of sardine in the Gulf of California, concluding that fishing has large effects on a modelled sardine stock undergoing long-term environmental forcing, and that recovery is slow (20-40 years) after modelled fishing is stopped. However, the model showed that the sardine stock in the Gulf of California shows resilience; it is able to recover after a near collapse.

Fisheries are subjected to a combination of biological, economic and political influences (May *et al.* 1979). This is well illustrated in the California system. Off California, anchovy and sardine compete for zooplankton prey. There have been researchers who have recommended heavy fishing on anchovy to allow sardine, of greater commercial value, to increase. This is unacceptable to sports fishers, who realise the importance of anchovy as prey for sports fish (May *et al.* 1979).

During the 1970s, fisheries off Namibia operated in a similar manner to that recommended in the California system. Commercially valuable sardine began to show signs of collapse. The fisheries targeted heavily on anchovy, with the view that reducing anchovy would benefit its competitor, viz. sardine (Butterworth 1983). However, sediment core analysis (Shackleton 1987, 1988) suggests that the two species did not compete. The attempt to enhance sardine abundance failed, and both anchovy and sardine underwent major declines in the late 1970s. By comparison, off South Africa, anchovy were conservatively managed when sardine collapsed in the late 1960s, allowing anchovy to reach large biomasses and support a large fishery during the 1980s. Using an age-structured model to investigate alternation between anchovy and sardine populations in the southern Benguela system, Korrubel (1992) found harvesting was important in determining the dominance of stocks.

Management options for the Peruvian system considered the potential for anchoveta to recover following a collapse, if fishing and predation pressures are light (Muck 1989). This would require heavy fishing on important predators of anchoveta (Muck 1989), namely horse mackerel and mackerel (Muck and Sanchez 1987), with no guarantees for a successful outcome for anchoveta.

Working on the Chilean system, Yanez *et al.* (1992) used a multiple regression model to explain the observed variability of sardine *Clupea benticki* and anchovy *E. ringens* and found fishing effort, sea surface temperature and turbulence to be explanatory variables. For example, during El Niño periods, sea temperatures in spring are unusually warm and do not favour spawning or the development of eggs and larvae of pelagic clupeoids off the Chilean coast.

The effects of fishing extend beyond the target species themselves. Seabirds and other predators of fish are affected, both in abundance and distribution (Crawford 1987, Crawford *et al.* 1987, Crawford *et al.* 1989). Peaks in handline catches of the predatory fish, snoek *Thyrsites atun*, were linked to abundance of pelagic fish species and their predators off the west coast of southern Africa (Crawford and De Villiers 1985). In the Benguela system, guano harvests were related to trends in the abundance of breeding seabirds, which in turn reflected the abundance of forage fish (Crawford and Shelton 1978). Shifts in the dominance of anchovy and sardine off southern Africa strongly influence the distribution and abundance of the African Penguins (Crawford 1998). The collapses of penguin colonies along the west coast of southern Africa, and an overall decline of 25% in the African Penguin population coincided with a decrease of sardine during the 1980s (Crawford 1998). When the sardine stock began to increase in size in the 1990s, west coast colonies stabilised and new colonies were formed near Cape Town. However, a major decrease in number of penguins at Dyer Island on the south coast, associated with reduced availability of small pelagic fish in this vicinity, accounted for a further reduction of 19% in the overall African Penguin population (Crawford 1998).

Fishing can affect both exploited and unexploited species that compete with exploited species for food, for example hake and horse mackerel (Crawford *et al.* 1987). Adult horse mackerel *Trachurus trachurus capensis* and juvenile hake *Merluccius* spp. have similar diets and feeding grounds, so that a decrease in one of these species can improve feeding conditions for the other (Krzeptowski 1982). The interactions between the two species are further complicated because hake feed on horse mackerel (Konchina 1986). Another example from the Benguela system is that of chub mackerel *Scomber japonicus* and anchovy. The diets of both species comprise substantial proportions of macrozooplankton (Baird 1978, Armstrong *et al.* 1991), so that increased fishing on anchovy reduces competition between anchovy and chub mackerel, perhaps enabling chub mackerel to become more abundant (Shannon *et al.* 2000). Off Peru, anchoveta and hake biomass are inversely correlated (Espino and Wosnitza-Mendo 1989), probably because of predation (Muck *et al.* 1987). Heavy fishing on anchoveta affects the dominance of other species (Muck 1989).

Another direct impact of fishing is caused by the practise of discarding fish or offal at sea. Predators with flexible foraging strategies take advantage of discarded fish. This can allow certain seabirds to become more abundant, and outcompete others with less flexible modes of feeding. Off South Africa, the Cape Gannet *Morus capensis* and Kelp Gull *Larus dominicanus vetula* frequently feed on fish and offal discarded by demersal trawlers (Ryan and Moloney 1988, Berruti *et al.* 1993). Cape fur seals *Arctocephalus pusillus pusillus* scavenge fish from purse seine and trawl nets, and consume fish, in particular small hake, discarded behind trawlers (David 1987, Ryan and Moloney 1988).

2.2.4. Food environment

The energy made available when an abundant resource collapses may allow more than one species to benefit if feeding is generalised (Crawford 1987). Whether a particular species replaces the one that has collapsed will probably be influenced by the magnitude of predation and fishing during and after the collapse (Crawford 1987).

Van der Lingen and Hutchings (1995) compared the trophodynamics of the South African anchovy *E. capensis* and sardine *S. sagax* in the southern Benguela subsystem. Sardine is primarily a filter feeder (van der Lingen 1995), feeding on small particles, namely microzooplankton and phytoplankton (van der Lingen 1994). By contrast, the most energetically economical mode of feeding used by anchovy in the southern Benguela is particulate feeding on large particles, namely mesozooplankton (James 1987). When sardine are abundant they may negatively impact anchovy by feeding on eggs and naupliii of copepods, thereby reducing the number of large copepods available to anchovy (Hutchings *et al.* 1998). Off Peru, larvae of anchoveta

E. ringens and sardine *S. sagax* have different diets; anchoveta larvae feed on phytoplankton whereas sardine larvae feed on zooplankton (Muck *et al.* 1989 b). By comparison, diets are similar in older anchoveta and sardine (Muck *et al.* 1989 b). Trophic differentiation may not occur in anchovy and sardine around Japan. There is intense competition for food between the Far Eastern sardine *S. melanostictus* and the Japanese anchovy *E. japonicus*; both species feed on similar proportions of phyto- and zooplankton (Kawasaki and Omori 1988).

Physico-chemical forcing is reflected in changes in phytoplankton communities (Mitchell-Innes and Pitcher 1992) and the community structure of zooplankton (Verheye *et al.* 1998), thereby influencing food available to small pelagic fish. Kawasaki and Omori (1988) proposed that warming leads to higher sea surface temperatures and also to increases in phytoplankton populations, which allowed the Japanese sardine population to increase. However, there is no evidence that increased sardine abundance is linked to increases in primary productivity in the California system (Lluch-Belda *et al.* 1992b). Van der Lingen and Hutchings (1995) concluded that regime shifts are associated with structural changes in the ecosystem, leading to environmental conditions favouring one species over the other, including the contraction or expansion of suitable habitat.

2.2.5. Additional mechanism regulating pelagic fish populations

In addition, two other potentially important mechanisms should be mentioned briefly: natural selection and cannibalism. Cury (1988) hypothesised that strong selective pressures and the reduced influence of climatic events could be responsible for extended periods of reduced abundance of pelagic stocks, and that adaptive microevolution causes depleted stocks to recover rapidly. Therefore he proposed that in addition to the effects of climatic events and harvesting, the process of natural selection could be another mechanism regulating marine pelagic fish stocks. Secondly, cannibalism may have an important role to play. Although clupeoid stocks are not characterised by strong density-dependent regulation (Crawford *et al.* 1987), cannibalism has been shown to regulate clupeoid populations (MacCall 1980, Valdés Szeinfeld and Cochrane 1992).

2.3. REGIME SHIFTS

Daan (1980) was the first to review the concept of replacement of a depleted stock by other species. He used a very tight definition of replacement and concluded that the only true replacement of species occurred in the North Sea. Many analyses of alternating trends in abundance of fish stocks have since been undertaken, with species replacement being more loosely defined, and many hypotheses being formulated to explain these "regime shifts". An early indicator of a change in species dominance is an increase in the abundance of the sub-dominant species; a decrease in the dominant species is often only observed at a later stage (Lluch-Belda *et al.* 1992a). Catch statistics (e.g. Lluch-Belda *et al.* 1989 and 1992a, Kawasaki 1991), fish scale deposits in sediments (e.g. Baumgartner *et al.* in prep), biomass research surveys (e.g. Hampton 1992) and records of guano harvests (Crawford and Shelton 1978, Crawford and Jahncke 1999) have revealed changes in the abundance of anchovy or sardine stocks in many regions of the world. Initially, there were heated debates as to whether collapses of pelagic species were caused by overfishing, thereby allowing competing species to dominate (Francis and Hare 1994). However, fishing was soon shown to be secondary to other causes when evidence of these fluctuations was found in scale deposits for periods prior to commercial fishing off California (Soutar and Isaacs 1974, Baumgartner *et al.* 1992, Baumgartner *et al.* 1996), Peru and Chile (Baumgartner *et al.* in prep.) and off southern Africa (Shackleton 1987, M^cLachlan 1995).

Off western South Africa, guano records suggest that anchovy *E. capensis* was the dominant pelagic fish in the 1920s (Crawford and Jahncke 1999). Horse mackerel *Trachurus trachurus capensis* was abundant in the 1940s and early 1950s, sardine *S. sagax* in the late 1950s and early 1960s, chub mackerel *Scomber japonicus* in the late 1960s, *E. capensis* in the 1970s and 1980s and *S. sagax* in the mid 1990s (Crawford *et al.* 1987, Crawford 1998). The sequence of pelagic species succession differed off Namibia: *S. sagax* was dominant in the 1960s, *T. t. capensis*, pelagic goby *Sufflogobius bibarbatus* and to a lesser extent, also *E. capensis*, were abundant in the late 1970s and early 1980s, whereas *S. japonicus* was dominant in the late 1970s and early 1980s (Crawford *et al.* 1985, Crawford *et al.* 1987, Crawford and de Villiers 1984).

Despite plentiful data showing changes in abundance phases of sardine and anchovy populations in the productive regions of the world's oceans, the mechanisms responsible for initiating, sustaining and terminating sudden increases in population sizes on a decadal time-scale still remain much of a mystery (Lluch-Belda *et al.* 1989, Lluch-Belda *et al.* 1992a, Lluch-Belda *et al.* 1992b). It is likely that many of the factors accounting for variability in fish stocks play important roles in the process of regime shifts. The mechanisms involved must act on large spatial scales because there is coherence in stock fluctuations in these regions (Crawford *et al.* 1991a, Lluch-Belda *et al.* 1989, Schwartzlose *et al.* 1999). Matsuda *et al.* (1992) modelled environmental effects on pelagic species replacements, listing five possible mechanisms explaining pelagic species dominance in ecosystems: environmental change impacting different species directly, density-dependence in changes of the intrinsic reproductive rate, phase polymorphism of species, competition between species and fluctuations in a one-predator-two-prey-species situation.

There are five regions in the world where anchovy (*Engraulis* spp.) and sardine (*Sardinops sagax*) stocks co-exist and are intensively fished (Lluch-Belda *et al.* 1989). These are the Japanese system (the western boundary of the North Pacific), the California Current system (the eastern boundary of the North Pacific), the Humboldt Current system (the eastern boundary of the South Pacific), the Canary Current system (the eastern boundary of the North Atlantic) and the Benguela system (the eastern boundary of the South Atlantic). It is generally accepted that sardines in all these regions except the Canary system are the same species, namely *S. sagax* (Parrish *et al.* 1989). The Sardinellas *Sardinella aurita and S. eba* occur in the Canary Current system. Anchovies belong to different species of the genus *Engraulis*. In addition to co-occurring in these five regions, both anchovy and sardine (*S. sagax*) are also found off Australasia. However, harvesting of these species is limited in this region, therefore data are scarce and stocks in this region have been largely omitted from comparative studies in the literature. The anchovy *E. encrasicolus* and sardine *Sardina pilchardus* co-occur in the Mediterranean Sea. However, catch per unit effort data of the two species in the fishery off the Northeast coast of Spain have been less variable than those from oceanic regions where the main pelagic fisheries of the Mediterranean operate (Morales-Nin and Pertierra 1990). The authors suggest that the environment fluctuates less in this region than in productive upwelling regions, such as off California.

2.3.1. Linkages between regions

Shifts in dominance of sardine and anchovy have been discussed in depth by Lluch-Belda *et al.* (1989 and 1992a). Fluctuations in the size of the populations of these two species groups in the Japan, California and Humboldt current regions are well matched and are influenced by global scale environmental variation (Kawasaki 1983, Crawford *et al.* 1991a). In contrast, the species groups of the Benguela and Canary Current systems are out of phase with these three Pacific regions (Lluch-Belda *et al.* 1989, Schwartzlose *et al.* 1999, e.g. Fig. 2.1). Recently, Alheit and Hagen (1997) showed that alternating periods dominated by herring *Clupea harengus* and sardine *Sardina pilchardus* in the eastern Skagerrak, English Channel and Bay of Biscay are governed by the same climate variations. Trends in abundance of zooplankton and salmon in the North Pacific correspond to changes in the intensity of the Aleutian Low Pressure System (Polovina 1996). It has been suggested that water column stability, determined by strength of the Aleutian Low Pressure, influences phytoplankton production, which in turn affects species at higher trophic levels (Polovina *et al.* 1995, Gargett 1997).

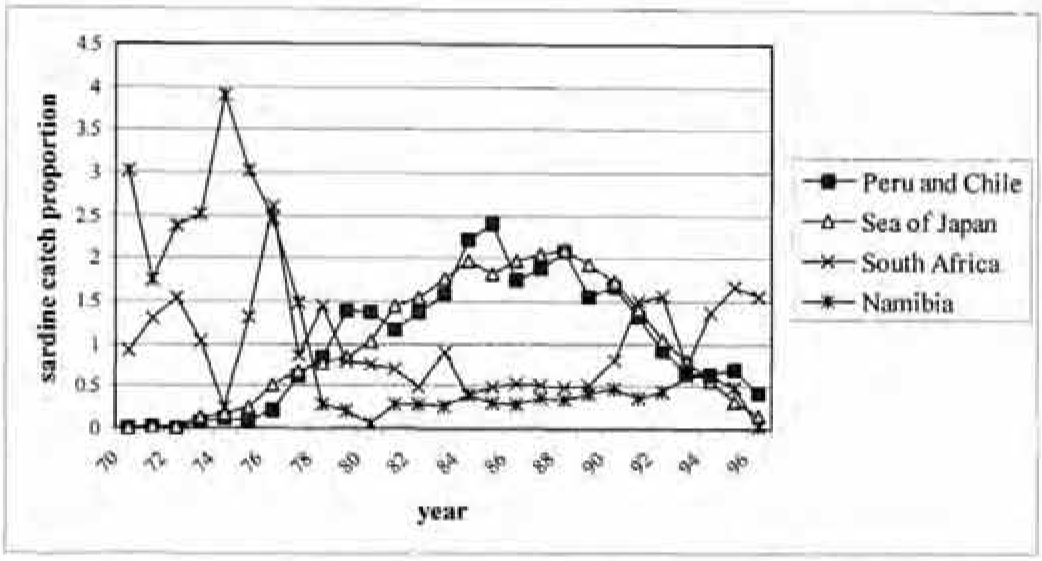


Fig. 2.1 Catches (t) of sardine in the North-Western Pacific by Japan, off Peru and Chile combined, off South Africa and off Namibia, plotted as proportions of mean annual catches in each region from 1970-1996. Data are from Schwartzlose *et al.* (1999).

In the Pacific Ocean (Japan, California and Humboldt systems), fluctuations of sardine populations in the three regions are more closely linked than fluctuations of anchovy or chub mackerel stocks (Crawford *et al.* 1991a). It is possible that the climate may influence biological aspects of sardine, which differ from those of the other two species (Crawford *et al.* 1991a). Sardine was found to be more abundant during periods of increased global air and sea temperatures, and anchovy stocks declined during such periods (Lluch-Belda *et al.* 1992a). However, manifestations of other events associated with changes in temperatures, rather than temperature changes themselves, may cause fluctuations in temperature and stocks to coincide (Lluch-Belda *et al.* 1992a). Matsuda *et al.* (1991, 1992) put forward a cyclic model of dominance of pelagic fish species off Japan, and MacCall (1996) showed a similar sequence of pelagic fish dominance off California; a peak in abundance of planktivorous *Sardinops sagax* is followed by a peak in *Engraulis* sp., then the more predatory *Scomber japonicus* dominates and the cycle repeats itself.

There is a significant negative relationship between temperature in the northern Benguela and the Canary Current systems (Crawford *et al.* 1991a). The abundance of sardine in these two regions is negatively related. The two systems seem to be linked largely through the influence of Benguela Niños, which result from the southward intrusion of tropical water into the northern Benguela system off Namibia, associated with cooling in the equatorial Atlantic (Shannon *et al.* 1986). Anchovy population sizes in the northern Benguela system are related to those in the Canary system one year later, and anchovy population sizes in the southern Benguela are related to those in the Mediterranean the same year (Crawford *et al.* 1991a).

Crawford *et al.* (1991) investigated the trans-oceanic linkages between the Atlantic and the Pacific through global climate. They postulated that three factors influence trends in abundance of fish species in the two oceans, namely solar radiation, sea surface temperature and ecosystem changes. Solar radiation influences sea surface temperature in the North Pacific in the same year, but influences sea surface temperature in the North Atlantic and air temperature in the Northern Hemisphere two years later. This is reflected in a two-year lag between sardine catches off Japan and England. Sardine in the California, Humboldt, Canary and Benguela current regions have been found to extend into cool waters during warm periods (Crawford *et al.* 1991a), and also sometimes into warm waters when cooling occurs (Lluch-Belda *et al.* 1989). Japanese sardine, although always the dominant species, tend to become more abundant as the Kuroshio Current cools (Lluch-Belda *et al.* 1992b). Hence it is possible that warming of cool areas or vice versa can allow sardine to extend its range into new areas (Crawford *et al.* 1991a). Climatic impacts on epipelagic prey species are likely to influence predators and competitors too (Crawford *et al.* 1991a).

2.3.2. Changes in spatial distribution

Associated with changes in the relative abundance of anchovy and sardine is spatial variation of the two species. Both species expand and contract the area across which they occur as stocks increase or decrease in size. MacCall's (1990) "basin hypothesis" states that spawners are expected to contract to the most favourable habitats at low levels of abundance, when effects of density dependence are low. Modelling of anchovy and sardine in the southern Benguela region showed that anchovy and sardine spawned in areas less favourable to survival when they were at low abundances (Shannon 1998). This indicated that other environmental factors may have restricted suitable areas available for spawning.

Sardine often show shifts in the alongshore direction, whereas anchovy tend to expand or contract their range about a geographic centre (Lluch-Belda *et al.* 1989). Sardine is generally more migratory than anchovy, often expanding spawning areas upstream during times of increased abundance, for example in the Humboldt system (Lluch-Belda *et al.* 1992a), off Japan (Kobayashi and Kuroda 1991) and in the southern Benguela system (Crawford 1981a). It is possible that this can have the advantage of enhancing the transport of eggs and larvae to additional nursery areas and in so doing, can be beneficial to the stock as it increases in size (Kobayishi and Kuroda 1989).

Sardine in the Joban and Boso waters of central Japan can be divided into two groups with different migratory characteristics (Hiramoto 1989). Oceanic sardines mature slowly, migrate over wide expanses and increase in abundance approximately every ten years. At the other extreme are sardine living in coastal regions and in bays. These sardine mature quickly, have limited migratory ranges, stable numbers and are maintained at low levels (Hiramoto 1991). Sardine are often less migratory when at low levels, and tend to adopt a similar strategy to anchovy during such periods. Lluch-Belda *et al.* (1989) suggest that this may be due to the limited migratory capacity of the sardine stock when it is comprised largely of younger sardine, as a result of high mortality rates. They propose that intensive fishing may cause sardine to shift from a high to a low abundance phase prematurely, by reducing the lifespan and therefore often also the migration range.

Fish catches in the South East Atlantic showed long term meridional shifts (Crawford and Shannon 1986). Catches were displaced southwards during the late 1950s and 1960s, and northwards in the mid-1970s, with matching trends in predator populations (Crawford and Shannon 1986). The distribution of fish catches in the southern Benguela region corresponds to the cumulative Southern Oscillation Index (Crawford and Shannon 1986). This is at least partly explained by changes in leakage of Agulhas Current water around the southern tip of Africa from the Indian Ocean to the Atlantic Ocean, and changes in the Antarctic Circumpolar Current, both of which depend on the macroscale wind field. The latter is supported by Tyson's (1986) work, in which he showed by means of a model that westerly winds contract polewards and become stronger in the south during the high (wet) phase of the SOI, but weaken and expand northwards during the low phase (Crawford and Shannon 1986).

During periods of negative sea surface temperature anomalies in the northern Benguela region, spawning by sardine and anchovy (*Engraulis capensis*) shifted northwards, whereas spawning occurred both to the north and farther southwards during periods of positive sea surface temperature anomalies (Le Clus 1990). Fish catches matched these trends in egg abundance (Crawford and Shannon 1986). However, anchovy in the northern Benguela region are often slower to respond to environmental change than sardine (Le Clus 1990). Le Clus (1990) stressed that changes in locality of spawning do not necessarily result from changes in age structure or biomass of the stock, nor from genetic differentiation. However, should altered environmental conditions result in changes in transport of eggs and larvae, changes in biomass can ultimately occur (Le Clus 1990).

2.3.3. Summary of important processes explored in this dissertation

Of the factors discussed in section 2.2 that influence fluctuations of fish stocks, two were examined in detail in this dissertation. These are fishing (section 2.2.3) and the food environment (section 2.2.4), both of which have been suggested as important processes when considering "regime shifts" between anchovy and sardine in Benguela ecosystems. Firstly, Chapter 12 explores the potential role that fishing had on anchovy and sardine dominance in the southern Benguela ecosystem during the 1980s and 1990s. Secondly, the trophic differentiation between anchovy and sardine feeding in the southern Benguela is explored by considering periods of warm and cool environmental conditions, which may influence the zooplankton community structure, thereby favouring either anchovy or sardine at one time. The first factor, namely fishing, has also been examined in other chapters where the direct and indirect trophic effects of fishing on all ecosystem components are considered. In Chapter 8, section 8.9, the ecosystem effects of altered fishing strategies for small pelagic fish and hakes in the southern and northern Benguela ecosystem are compared. In Chapter 9, increased fishing mortality of small pelagic fish and hakes are investigated under three different types of flow control. The main discussion of the effects of fishing appear in Chapter 10, in which a number of alternative fishing strategies are examined in terms of their potential interactions with other fisheries, and their effects on the various components of the southern Benguela ecosystem.

2.4. ECOSYSTEM MANAGEMENT USING MULTISPECIES MODELS

The concept of shifts in the dominance of pelagic fish species in many upwelling regions was introduced in the previous section, and factors operating during regime shifts described. What are the management implications of regime shifts? It is surely not enough to continue managing fisheries in isolation, when it is clear that within an ecosystem, fish stocks fluctuate synchronously. Interactions between components of ecosystems must play major roles in determining abundance levels. Francis and Hare (1994) considered salmon and zooplankton production in the Northeast Pacific in their examination of decadal scale regime shifts in large marine ecosystems. They conclude that "climate-driven regime shifts ... can cause major reorganizations of ecological relationships over vast oceanic regions". More specifically, Kawasaki (1992) points out that structural changes in pelagic fish communities are underway worldwide. It is thinking along these lines that prompted me to model the Benguela system in terms of its trophic functioning and ecosystem structure. Using these models, I compare ecological relationships during periods dominated by different pelagic fish species, and explore the possibilities for incorporating ecosystem considerations into management.

It is widely recognised that ecosystem structure and function need to be considered if we are to make any headway in managing the world's fisheries (e.g. Mercer 1982, Sherman and Alexander 1986, Shelton 1992, Gaedke 1995, Pauly 1998, Beamish and Mahnken 1999, Gislason 2000). Steele (1996) concluded that a "regime shift in fisheries management" is required if we are to successfully manage fisheries in the context of shifting regimes and ecosystem changes. Since 1950, humans have been "fishing down the food webs", that is, there has been a worldwide decline in the mean trophic level of marine and inland fish catches (Pauly *et al.* 1998a, Pauly *et al.* 2000a, Pauly *et al.* 2000b). This has been characterised by an initial increase in catches, followed by levelling or decreases in catches, indicating that current exploitation is unsustainable (Pauly *et al.* 1998a). Until recently, management of fisheries has been from a single-species perspective (Pauly *et al.* 2000a). The Convention for the Conservation of Antarctic Marine Living Resources (CCAMLR) is a working example of a programme adopting the approach of ecosystem management, as opposed to management of single species in isolation (Scully *et al.* 1986). Management of marine ecosystems has been defined by Larkin (1996) as "management of marine fisheries with awareness of ecosystem properties". Larkin (1996) considered ecosystem management to comprise holistic approaches to resource management, taking into account multispecies interactions and their dependence on underlying ecosystem dynamics. He lists three essential components of ecosystem management: 1) sustainable yield of products for consumption by humans and animals, 2) maintenance of biodiversity and 3) protection from the effects of pollution and habitat degradation. Larkin (1996) concluded that we are a long way from the stage where ecosystem models can predict variations in abundance of individual species. However, present ecosystem models describe interdependencies between trophic levels, indicating at least major changes in the system (Larkin 1996). Jennings and Kaiser (1998) propose that future fisheries management should incorporate conventional fisheries management into an ecosystem-based approach, aiming towards achieving a balance between the economic gain of fisheries and the maintenance of diversity, sustainability of top predators, ecosystem function and conservation of the ecosystem. It is particularly important that ecosystem considerations are incorporated into fisheries management of systems in which exploited fish stocks interact strongly with one another and are heavily depended upon by marine mammals and seabirds (Livingstone and Tjelmeland 2000). The Bering Sea ecosystem is an example of one for which good progress has been made towards ecosystem-based management (Witherell 1999). A successful precautionary approach to managing the Bering Sea groundfish fishery has been adopted, based on scientific research and advice, extensive monitoring, enforcement, bycatch controls, conservative quotas, conservation of habitat and the allocation of fishing seasonally and spatially to reduce potential detrimental effects on marine mammals and birds of local prey depletion.

Rose *et al.* (1996) highlighted the need for scientists to be able to discern whether a single species model is sufficient for the task at hand, or whether the multispecies modelling approach would be more appropriate. Much depends on the objectives for management of the system in question, how these are likely to be attained, and how well the model objectives address these. The use of a "toolbox" of models has been proposed, so that each decision-driven model adds to the variety of modelling approaches used to manage a particular renewable resource (Starfield *et al.* 1988, Crawford *et al.* 1989, Whipple *et al.* 2000). Starfield *et al.* (1998) and Crawford *et al.* (1989) viewed multispecies models as a means of testing the effectiveness of more specific models, as opposed to striving to understand the ecosystem or evaluate harvesting strategies. However, multispecies models of today are also useful in achieving the latter two objectives (Whipple *et al.* 2000).

Rose *et al.* (1996) emphasised the importance of interspecific interactions: what happens to one species is likely to impact other species in a system. Single-species criteria for fisheries management should be viewed in the light of effects on the ecosystem (Murawski 1991). Multispecies approaches to fisheries management should not assume the place of single-species approaches, but they should be viewed as complementary. Multispecies models can build on and improve the results of single-species models and also provide input to single species models. It has been shown that multispecies approaches yield very different long-term management advice from traditional single species models (Magnússon 1995, Stokes 1992), but that in the short term the advice is sometimes similar (Christensen 1996b). Murawski (1991) notes that conflict between management strategies for single species results from the absence of any formal process whereby the feasibility of simultaneously attaining the goals of various single-species approaches is evaluated. This is where a multispecies or ecosystem approach is applicable and useful. Hollowed *et al.* (2000) list the main advantages of multispecies approaches compared to traditional single-species approaches: estimates of natural mortality and recruitment are improved, there is greater understanding of spawner-recruit relationships and of growth rate variability, alternative views on biological reference points are provided, and multispecies models provide a framework for evaluating ecosystem properties.

Harvesting a predatory species can either cause its prey to proliferate or collapse. The latter may seem counter-intuitive yet is a real possibility as a result of complex interactions between species in a system (May *et al.* 1979); changes in harvesting strategies can cause shifts in average stock density, yield and the variance of the two. Christensen (1996b) discusses how in some lake systems, predators have been removed in an attempt to benefit prey species exploited by humans, with very different effects between ecosystems.

The first attempt at multispecies modelling was probably by Volterra (1928), who developed coupled single-species models to describe interactions between species, including predation, competition and self-regulation of populations. Yet it was not until the late 1960s and early 1970s, with the advent of digital computers, that research in the field of multispecies modelling really took off (see review by Rose *et al.* 1996). Despite major developments in computing power since, multispecies models today are still based upon the original concepts. Development of more advanced multispecies models appears to have been hampered by the vast amounts of data required (Rose *et al.* 1996). Multispecies models can be classified into three types: budget models, coupled single species models and holistic models (Rose *et al.* 1996).

Budget models describe the flows of energy or biomass between species groups. They include, among others, models of upwelling systems (Walsh 1981, Jarre *et al.* 1991, Jarre-Teichmann 1998), models of shelf ecosystems such as the North Sea (Christensen 1995) and models of coral reef systems (e.g. Polovina 1984, Opitz 1991). They facilitate assessment of ecosystem-level properties following, e.g. the theories of Odum (1969), Finn (1976) and Ulanowicz (1986), and have the advantage that different ecosystems can readily be compared (Christensen and Pauly 1993). These models have also been called aggregate system models and have been criticised for rarely including environmental forcing (Hollowed *et al.* 2000). However, as the authors note, using *Ecosim*, the dynamic simulation extension of *Ecopath*, it is now possible to model some forms of environmental forcing.

Coupled single-species models simulate the processes involved in ecosystem functioning and quantify net flows among compartments over time. Some researchers have added age and size structure to linked single-species models (e.g. Murawski 1991).

Holistic models differ from coupled single-species models in that they deal with a greater number of species, interactions between species are considered in biological detail and they are often dynamic. Mann *et al.* (1989) define the holistic approach to modelling as that in which an ecosystem is considered as functional whole, possessing distinct, "emergent" properties not found at lower levels of organisation, such as at the community or population levels. Holistic models include considerations by Beverton and Holt (1957), the famous North Sea fisheries model of Andersen and Ursin (1977) and the DYNUMES III model of the Bering Sea ecosystem (Laevastu and Larkins 1981).

Individual based models have been incorporated into multispecies models (Rutherford *et al.* 1994). Since most data are collected from individuals, modelling populations by summing the individuals seems logical. However, this type of approach is often problematic, as data required are frequently not available. Rutherford *et al.* (1994) modelled yellow perch and walleye pollock dynamics in Oneida Lake in New York. Their model tracked eggs and yolk-sac larvae by cohort, and on an individual basis for all stages after this. Computer time and memory were demanding, even when using a representative sampling method to track individuals through progressive stages (Rose *et al.* 1993). This serves as an example to highlight the limitations in extending such models to include more species on an individual basis. Therefore, although much may be learnt through individual based modelling approaches, such approaches should not replace those by which the ecosystem can be considered as a whole.

Until the late 1970s, scientific advice for fisheries management, as e.g. given by the International Council for the Exploration of the Seas (ICES), considered each commercially exploited species of the North Sea separately, assuming little effect of one species on another in the same area (Christensen 1996b). However, the work of Andersen and Ursin (1977) showed that natural mortality was influenced by predator stock sizes. Their thinking formed the basis of Multispecies Virtual Population Analysis (MSVPA; see Sparre, 1991 for an overview). Based on initial contributions by Helgason and Gislason (1979), Pope (1979) and Sparre (1980), the major development of MSVPA took place in the ICES Multispecies Working Group, established in 1981 to seek ways to include interactions between species when assessing fish stocks (Pope 1991).

MSVPA incorporates mortality due to both fishing and predation, and sometimes also the effects of these on growth and recruitment (Larkin 1996). One of the differences between *Ecopath* and MSVPA is the way in which mortality is handled. In *Ecopath*, total mortality rates (P/B) are entered as inputs and biomasses and mortality rates are constrained by these total mortalities (Christensen and Walters 2000). MSVPA is a fairly data intensive procedure (Sparre 1991), requiring age-specific catch data per quarter and extensive stomach sampling (e.g., Daan 1989)). There is much uncertainty surrounding holistic models such as MSVPA and DYNUMES because the number of parameters involved is large (Whipple *et al.* 2000). MSVPA models require the setting of suitability coefficients (Andersen and Ursin 1977), defining the relative importance of each species and age as prey for predators at each age (see reviews by Sparre (1991), Magnússon (1995), and Christensen (1996a)). Estimating diet composition and setting suitability coefficients may be problematic if, for example, predators switch between prey, or if the behaviour of a predator is influenced by feeding patterns. The ICES Multispecies Working Group has addressed most of these problems (Pope 1991, Christensen 1996a), but they continue to be a matter of debate.

Outputs of MSVPA include estimates of fishing mortality, predation mortality and stock numbers (Sparre 1991). Although still not used directly in fisheries management (e.g., ICES 1998), MSVPAs provide estimates for parameters used as input in assessment models and as such have increased insights into functioning of ecosystems (Pope 1991, Sparholt 1994, Magnússon 1995). As for all multispecies modelling techniques to date, there are many uncertainties associated with MSVPAs. Therefore it seems unlikely that MSVPA will be used directly in fisheries management in the near future (Magnússon 1995), despite the initial promise that the approach was thought to have (Sissenwine and Daan 1991). Given the limited knowledge on important parameters for single species assessments of South African fish stocks, MSVPA is not considered feasible or of high priority in South Africa (Cochrane *et al.* 1997).

Another shortcoming of the MSVPA approach is that it is not truly holistic in an ecological sense, because the species interactions have so far been limited to fish. However, Stokes (1992) believes that, in time, multispecies management approaches will become routine methods whereby fisheries management options can be investigated.

MSVPA has mainly been applied to the North and Baltic Seas, probably because of where and how it was first applied (Christensen 1996a). The need for multispecies tools that can be applied in more data-sparse regions (Larkin 1982, Pauly 1989; 1994, Christensen 1996a) led to the development of the dynamic simulation routine, *Ecosim* (Walters *et al.* 1997) based on trophic flow models of the "budget" type. Its use as a tool for multispecies and/or ecosystem management is being evaluated at present (Pauly *et al.* 2000a).

Understanding the structure and functioning of ecosystems is vital when considering the ecosystem effects of fishing. Fishing can affect the ecosystem both directly and indirectly (Goñi, 1998). Direct effects operate through mortalities caused by fisheries targeting particular species, bycatch and discarding of non-target species or individuals, as well as from the physical effects of fishing gear (Goñi 1998). Direct effects cause changes in diversity and community structure (Jennings and Kaiser 1998). Indirect effects operate through interactions, such as predation and competition, between fished species and those with which they interact (Goñi 1998). Using the mass-balanced budget approach of *Ecopath* and the dynamic simulation approach of *Ecosim*, it is possible to explore aspects of both direct and indirect effects of fishing, fulfilling the increase in use of food web theory in the management of multispecies fisheries, anticipated by Pimm *et al.* (1991).

A management-oriented approach provides the framework for this thesis. I construct budget type trophic flow models using the *Ecopath* software, and extend them to ecosystem simulation models using Walters *et al.*'s (1997) dynamic approach. Based on a model by Polovina (1984), *Ecopath* has been under development since 1987 by the International Centre for Living Aquatic Resources Management (ICLARM, Manila). Christensen and Pauly (1992, 1995) describe the model in detail. *Ecopath* *with Ecosim* (Walters *et al.* 1997) extends beyond the budget type of model, to a more dynamic approach, whereby effects of altered fishing mortality of selected groups are investigated at the ecosystem level. It is one of the techniques being used as part of a "back to the future" approach where models of past and present systems are constructed to test "what if" scenarios of altered fishing practices (Pitcher in press). This is along the same line of thinking as Steele (2000), who highlights the need for improved descriptions of pristine marine food webs to better our understanding of shifts in ecosystem structure. *Ecopath with Ecosim* , described in more detail in Chapter 3, was the modeling tool chosen for this study because the data available for the Benguela ecosystems are suitable for *Ecopath with Ecosim*, and the tool allowed a wide variety of questions to be addressed.

CHAPTER THREE
METHODS

ABSTRACT

Ecopath version 3.1 was the ecosystem modelling tool used to construct steady-state models of trophic flows in the southern Benguela upwelling system. *Ecopath with Ecosim* version 4 (alpha) was used to simulate the ecosystem dynamics of altered fishing strategies. *Ecopath* is a mass-balanced ecosystem modelling approach in which trophic flows between boxes are described so that for each living box modelled, input balances output. Estimates of biomass, production, consumption, diet composition, assimilation efficiency and exports are required as model inputs. Network analyses used in the study include estimation of total throughput, trophic levels and primary production required, and different approaches for sensitivity analyses. Many of the previous limitations to *Ecopath* have been tackled by the dynamic version, *Ecopath with Ecosim*.

3.1 INTRODUCTION

This short chapter serves as an introduction to the *Ecopath* model and the equations upon which it is based. Some of the important techniques used for analysis of ecosystem models are highlighted, and methods of sensitivity analysis are described. The chapter outlines how *Ecosim*, the new dynamic version of the *Ecopath* model, can be applied to explore the ecosystem effects of altered fishing strategies. Some limitations to the modelling approach are also mentioned.

The *Ecopath* modelling package was used to model trophic flows and effects of fishing in the Benguela ecosystem. It was chosen because it is a widely applied ecosystem modelling approach for aquatic ecosystems across the world. It is based on a model by J.J. Polovina of the US International Marine Fisheries Service, Honolulu, Hawaii (Polovina 1984) and has been under development since 1987 by the International Centre for Living Aquatic Resources Management (ICLARM). A large and diverse group of experts have contributed to the development of this complex and reliable ecosystem modelling package, providing a tool that would not be feasible to develop de novo for application to an isolated ecosystem study. The approach facilitates and encourages inter-system comparisons. For example, the European Union Framework Programme IV, Cooperation with Third Countries and International Organisations, Part C, Scientific and Technological Cooperation with the Developing Countries (INCO-DC) Concerted Action "Placing fisheries in their ecosystem context" (1996-2000) is a framework through which ecosystem models of upwelling systems in various parts of the world are being constructed and compared. *Ecopath with Ecosim* has a strong fisheries focus, making it highly suitable for modelling the Benguela upwelling system. An ecosystem is assumed to consist of a series of categories or boxes, each box containing a species or group of species of similar trophic status in the ecosystem. The required inputs to *Ecopath* models are easily obtained from available data. It is assumed that trophic interactions govern the dynamics of the ecosystem, so that physical factors are largely ignored. However, the importance of the physical environment in the Benguela ecosystem is recognized and is taken into account in this study by altering certain model parameters in Chapter 12.

3.2 THE *ECOPATH* MODELLING TOOL

Using *Ecopath*, a trophic flow budget is constructed, creating a balance for each component ("box") in the model, and a balance for the flows between boxes. The box balance is based on Winberg's (1956) balanced energy equation:

Consumption (Q) = Production (P) + Respiration (R) +unassimilated food (U).

…… Equation 3.1

Thus for each living group of organisms in a system in steady state over a given period of time, input balances output. Faeces and dead organic matter not consumed by detritivores are accumulated in the non-living detritus box. A set of simultaneous linear equations describes the interactions between living boxes within the ecosystem:

Production of box (i) is balanced by the sum of predation on the box by other boxes, export from the system (fishing or emigration) and other mortality:

Production by (i) = All predation on (i) + nonpredatory biomass losses of (i) + fishery catches of (i) + other exports of (i) .

…… Equation 3.2

By re-expressing these terms as follows, a balance is established for each interaction of (i) with predator (j):

Production by (i) = $B_i \cdot P/B_i$

Predatory losses of (i) = $\Sigma_j (B_j \cdot Q/B_j \cdot DC_{j,i})$

Other losses of (i) = $(1 - EE_i) \cdot B_i \cdot P/B_i$

where

i	indicates a box (stock, species, species group) in the model
j	any of the predators of i,
B_i	the biomass of i,
P/B_i	the production of i per unit of its biomass (= total mortality under steady-state conditions),
Q/B_i	the consumption of a box per unit of its biomass,
$DC_{j,i}$	the average fraction of i in the diet of j (in terms of mass),
EE_i	the ecotrophic efficiency of i (the fraction of the total production that is consumed by predators or exported from the system). "Other mortality" is (1- EE_i) and accounts for deaths as a result of disease and starvation, for example. In the case of primary producers such as phytoplankton, EE is often near to 0.5 because a large proportions of phytoplankton blooms tend to simply die off.

Therefore for each box i within the ecosystem,

$$B_i \cdot P/B_i \cdot EE_i - \Sigma_j (B_j \cdot Q/B_j \cdot DC_{j,i}) - Ex_i = 0$$

…… Equation 3.3

where

Ex_i the export of i from the system (e.g., by emigration or harvesting).

For each component of the ecosystem, the *Ecopath* model requires the following input data: biomass (B), production per unit biomass (P/B), total consumption per unit biomass (Q/B), assimilation efficiency, diet composition, exports (mortality and other exports) and ecotrophic efficiency (EE). One of B, P/B, Q/B or EE may be unknown and will then be estimated through solving the linear equations. In *Ecopath*, respiration is calculated as the difference between the assimilated part of consumption and that part of production that is not attributable to primary production, and is only used for balancing flows between boxes. Non-assimilated food and dead matter (from "other mortalities") feed in to the detritus pool.

More often than not, the initial modelling attempt produces an unbalanced model. Imbalances are the result of bringing together into one model various average parameters estimated from a variety of different data series averaged over different time and spatial scales. Further, estimates of parameters are often only available for some of the species in a box, and may not fully represent the average values for the whole box. In addition, there is some error around these estimates, for example, it may be known that a stock size is underestimated during surveys but not by how much. Imbalances usually appear as ecotrophic efficiencies greater than unity, indicating that production of a box is insufficient to support its growth and mortality (predation, natural mortality and catches). In addition, the modeller may find that gross food conversion efficiencies (ratio of production to consumption) are unrealistic (usually they lie in the range 0.1-0.3), or that respiration cannot be estimated. It is then necessary to re-evaluate input parameters, modifying those about which uncertainty is large, according to knowledge of the rest of the system. Once acceptable results for the unknown parameters and respiration values have been obtained, the model is mass-balanced and can be analyzed further.

Execution of Ecopath

Ecopath is run on PC computers, with versions 3 and 4 operating in a windows environment. *Ecopath* 3.1 was used for all analyses in this study, with the exception of time-dependent simulations (Chapters 9-12) run using *Ecopath with Ecosim* version 4. Only the alpha version of *Ecopath with Ecosim 4* was available at the time of the study, so results may not be error free. Part of the work for this study involved extensive testing of the alpha version.

3.3 NETWORK ANALYSES OF *ECOPATH*

3.3.1 Total system throughput

Total system throughput is an important index of flow. It is calculated by *Ecopath* as the sum of all flows in a system, i.e. the sum of consumption, export (including catches), respiration and flows to detritus. This term represents the "size of the entire system in terms of flow" (Ulanowicz 1986) and is useful when comparing systems or the same system during different periods.

3.3.2 Trophic levels

The components of ecosystems can be aggregated into discrete trophic levels (Lindeman 1942), giving an indication of the average number of steps in food webs and their efficiencies. Transfer efficiency is the fraction of total throughput at a discrete trophic level, either exported or transferred to another trophic level (through consumption). Analysis of fifty models of estuarine and marine ecosystems showed that in general, the mean transfer efficiency between trophic levels is approximately 10%, although variance is large (Christensen and Pauly 1995). Transfer efficiencies can be used to construct three-dimensional trophic pyramids, scaled so that the volume of each level (representing a discrete trophic level) is proportional to the throughput at that level. For each system, the top angle of the pyramid is inversely proportional to the geometric mean of the transfer efficiencies between trophic levels. Thus narrow pyramids have large transfer efficiencies and broad pyramids have small transfer efficiencies.

Ecopath also computes non-integer trophic levels (Pauly *et al.* 2000a). By definition, producers are assigned to trophic level 1. Consumers are assigned to a trophic level of 1 plus the average trophic level of their prey, weighted by the proportion in the predator's diet. A routine in *Ecopath* facilitates the graphic representation of all flows and biomasses as a flow diagram, where each ecosystem component is plotted as a box along the y-axis at its trophic level (Christensen and Pauly 1995).

3.3.3 Primary production required

Ecopath offers a routine for the quantification of primary production required by a group to support consumption by its predators, and that required to sustain harvests. This is accomplished by converting the flow in each path to primary production equivalents, and summing for each ecosystem component. Primary production equivalents are used to compare effects of fishing at different trophic levels (Pauly and Christensen 1995). For example, harvesting of fish at low trophic levels is ecologically less expensive than fishing at a higher trophic level, given the inefficient transfer of energy up the food web. Primary production required depends on the intensity of fishing as well as the species targeted. For 1988-1991, 8% of global aquatic primary production was required to support the sum of the mean reported world fish catches (94.3 million tons) and discards (27 million tons). Pauly and Christensen (1995) calculated that the mean primary production required to sustain fisheries (catches and discards) in upwelling systems amounted to 25.1%, with the 95% confidence interval from 17.8% to 47.9%.

3.4 SENSITIVITY ANALYSIS

There are a number of approaches by which sensitivity of the model to estimated parameters can be examined. These include mixed trophic impact assessment, the *Ecoranger* utility, sensitivity analysis built in to *Ecopath* and sensitivity analysis using user-defined alternative estimates.

3.4.1 Mixed trophic impact assessment

Mixed trophic impact assessment is a technique measuring the relative impact of a change in the biomass of one component on other components of the ecosystem (Ulanowicz and Puccia 1990). It is based on an input-output method for assessing direct and indirect economic interactions in the United States of America (Leontief 1951). In this way, positive effects that a prey has on its prey, negative effects that a predator has on its prey, and positive and negative effects that a group may have on another group through interactions with other groups (i.e. indirect effects) are all quantified. Therefore, matrices of relative, net impacts of each box on all other boxes are constructed. Net impacts are scaled between –1 and 1. Mixed trophic impact assessment assumes that trophic structure is constant, i.e. the technique cannot be used for predictive purposes, but should rather be considered as a simple form of sensitivity analysis. It is an indicator of which groups have negligible effects on others within the system, and for which there is likely to be little gained from an effort to collect additional data to refine estimates. Conversely, it identifies groups having large trophic impacts on others, and for which it would be useful to refine estimates.

3.4.2 Ecoranger

Ecoranger is a Monte Carlo approach within *Ecopath* (Christensen and Pauly 1995, Christensen and Pauly 1996, Pauly *et al.* 2000a), enabling one to incorporate variability about values for the basic input parameters: B, Q/B, P/B, EE and diet composition of all groups. It allows one to enter the mean or mode and range of these parameters and to define a frequency distribution (uniform, normal, log-normal or triangular) from which random samples are drawn to generate distributions for output variables. To put *Ecoranger* into a semi-Bayesian context, a "sampling/importance resampling" procedure based upon that of McAllister *et al.* (1994) is used (Christensen and Pauly 1996). Each possible model output is evaluated and of all the runs, the best-fit model is selected using a least square method. The best-fit model is that giving the smallest residuals (based on mean/mode of each selected parameter and the squared deviations of each), or the smallest deviation from three other user-defined criteria, namely maximum system biomass, maximum throughput or maximum ascendancy. More details on the use of *Ecoranger* are given in Chapter 6 where it is applied to incorporate variability about parameters in models of the southern Benguela ecosystem.

3.4.3 Step-wise sensitivity analysis

Included in *Ecopath* is a routine that quantifies the effects of increasing and decreasing each input parameter in steps of 10%, by up to 50% of its original value. Model output is in the form of a table of the difference between the new estimated output and its original value, as a proportion of the original value.

3.4.4 Alternative estimates

The modeller may wish to compare the model to one in which defined alternative estimates of certain input parameters are used. This was the approach taken in Chapter 7, in which, for example, an alternative estimate of gelatinous zooplankton biomass was available for the northern Benguela sub-system during the 1980s.

3.5 *ECOSIM*

A dynamic simulation routine has been incorporated into the steady-state *Ecopath* modelling package, leading to the release of *Ecopath with Ecosim* (Walters *et al.* 1997). The primary aim of developing *Ecopath with Ecosim* is to provide a tool for addressing fisheries policy questions that single-species approaches are not equipped to answer (Christensen and Walters 2000). When *Ecosim* is used for single-species assessments, similar results are obtained to traditional single-species approaches (Christensen and Walters 2000). However, *Ecosim* has the additional capacity of providing insight useful in interpreting the effects of regime changes (Christensen and Walters 2000).

In order to run the *Ecosim* utility, it is necessary to have constructed a mass-balanced *Ecopath* model, and to have analysed it, as described above. In the *Ecopath with Ecosim* model, the sets of linear equations used in the old *Ecopath* 3.1 model are re-expressed as differential equations.

At equilibrium, equation 3.3 can be re-expressed as:

$$B_i \cdot (P/B)_i - F_i \cdot B_i - M_0 B_i - \Sigma_j Q_{ij} = 0$$

...... Equation 3.4

where Q_{ij} is the quantity of box i consumed by box j, M_0 is the mortality rate not accounted for by consumption within the system and F_i is the fishing mortality rate for box i (Walters *et al.* 1997). A dynamic model is constructed from equation 3.4 by modelling the rate of biomass change (dB_i/dt) and converting static consumption into a function $c_{ij}(B_i, B_j)$ predicting how consumption will change in relation to changes in biomasses of boxes i and j. The dynamic equation, whether or not the system is in equilibrium, is then:

$$dB_i/dt = f(B) - M_0 B_i - F_i B_i - \Sigma_j c_{ij}(B_i, B_j)$$

...... Equation 3.5

If i is a primary producer, $f(B)$ is a function of B_i whereas if i is a consumer,

$$f(B) = g_i \Sigma_j \, c_{ji}(B_i\, , B_j)$$

...... Equation 3.6

where g_i is growth efficiency of box i.

Integrating equation 3.5 for the system when F_i varies temporally facilitates dynamic biomass predictions for each box i affected directly by fishing, predation and changes in available food and indirectly by fishing and predation on other boxes with which box i interacts (Walters *et al.* 1997). In this way, dynamic trophic interactions that vary with biomasses and fishing strategies are described. A spatially explicit simulation technique called *Ecospace* has also been incorporated into *Ecosim* (Walters *et al.* 2000a), and is likely to assist in management of marine protected areas. It has not been applied here.

One of the main improvements of *Ecosim* over *Ecopath* is the incorporation of vulnerability of prey into calculations of consumption. This opens the way for testing hypotheses about top-down and bottom-up control in an ecosystem (Walters *et al.* 1997, and see Mackinson *et al.* 1997). Low vulnerability of a prey box indicates bottom-up or donor-control, whereas a high vulnerability indicates top-down control of the prey by its predators. In *Ecosim*, each prey pool B_i is viewed as having an available or "vulnerable" part V_{ij} to each consumer j over time. This is incorporated in the following equation describing the exchange between vulnerable biomass V_{ij} with the unavailable biomass pool (B_i-V_{ij}):

$$\mathrm{d}V_{ij}/\mathrm{d}t = v_{ij}(B_i - V_{ij}) - v_{ij}V_{ij} - a_{ij}V_{ij}B_j$$

...... Equation 3.7

where v_{ij} is the rate of exchange of biomass from the currently unavailable pool to the available biomass pool. The consumer j removes biomass from the vulnerable biomass pool V_{ij} at rate $a_{ij}V_{ij}B_j$ where a_{ij} is the instantaneous mortality rate on prey box i per unit biomass of predator box j, corresponding the search rate of the predator (Walters *et al.* 1997).

Assuming a fast equilibrium in exchange between B_i and V_i implies that

$$V_{ij} = v_{ij}B_i/(2v_{ij} + a_{ij}B_j).$$

...... Equation 3.8

Therefore, flow from prey i to predator j in the form of consumption varies according to:

$$c_{ij}(B_i, B_j) = a_{ij}v_{ij}B_iB_j/(2v_{ij} + a_{ij}B_j).$$

...... Equation 3.9.

Another advantage is that *Ecosim* can incorporate trophic ontogeny to an extent using a two-pool delay differential equation, keeping account of biomasses and numbers simultaneously (Walters *et al.* 1997). The modeller can specify constraints such as growth parameters, proportion of consumption used for reproduction, average age and weight at recruitment, foraging time, etc., and juveniles then graduate to the adult pool according to the user-defined constraints (Walters *et al.* 1997, Walters *et al.* 2000b). This is a vast improvement over the simple *Ecopath* solution to differences between adults and juveniles (including cannibalism), requiring that juvenile and adults of a species were regarded as two independent entities. However, *Ecosim* may not necessarily account completely for the effects of intra-guild or intra-specific predation. For example, in the southern Benguela ecosystem, anchovy eggs and larvae are consumed by sardine, a guild species (Valdés Szeinfeld and Cochrane 1992). In models of the southern Benguela ecosystem, anchovy eggs and larvae are included in zooplankton boxes (Chapter 4) and therefore the impacts of this form of intra-guild predation are not modelled implicitly.

Larkin (1996) notes that in order to achieve successful ecosystem management, it is necessary i) to distinguish between environmental and fishing effects, ii) to understand the dynamics underlying interactions between species and iii) to consider the ways in which fisheries will respond to changes in stocks. Using *Ecopath with Ecosim*, it is possible to partly address the latter two actions. *Ecopath with Ecosim* builds on the mass-balance approach and makes it possible to explore the effects of altered fishing mortality of selected groups on the whole ecosystem. In this way, resistance and resilience of the ecosystem towards different fisheries management options can be explored. In discussing the strengths of *Ecosim*, Whipple *et al.* (2000) mention its usefulness in focussing monitoring effort on variables that are likely to be sensitive to changes over time. Jennings and Kaiser (1998) state that, if refined, *Ecopath with Ecosim* should prove to be a valuable tool with which to assess ecosystem effects of fishing, assisting development of ecosystem management advice, as shown through this dissertation.

3.6 LIMITATIONS OF THE *ECOPATH WITH ECOSIM* APPROACH

The *Ecopath* approach came under criticism from Larkin (1996), who was concerned that it did not incorporate temporal and spatial dynamics. Development of *Ecosim* and *Ecospace* has tackled these problems. Larkin (1996) further criticised *Ecopath* models for possibly being based upon general ecosystem principles rather than being based upon parameters measured independently. This is a consequence of the lack of specific information (Larkin 1996); the criticism is applicable to all ecosystem models, and should not deter efforts to build models of ecosystems, which can be revised and updated as more data become available. Pimm *et al.* (1991) also pointed out the limitation caused by lack of data to support the food web theory. However, they viewed the lack of standards in food web methodology to be a bigger problem. *Ecopath* and *Ecosim* provide a standardised modelling approach to analyse food webs, facilitating meaningful comparisons to be made between ecosystems. *Ecopath* and *Ecosim* consider the ecosystem holistically, and operate at a level of complexity sufficiently low to facilitate parameter estimation and simulation in many instances (Magnusson 1999). However, Magnusson (1999) noted that *Ecosim* is not statistically based and that the empirical basis for estimation of some of the parameters was weak.

Many of the same risks pertaining to single-species models are associated with *Ecosim*, such as inaccurate estimates of biomass, misinterpretation of trends in data and not accounting for the effects of environmental changes interacting with effects of fishing (Christensen and Walters 2000). Data of poor quality may limit the period over which simulations can be regarded as reliable (Walters *et al.* 1997). On the other hand, there is a risk of missing long-term effects if only short time periods are considered (Mackinson *et al.* 1997, Walters *et al.* 1997). Here, ecosystem effects of fishing are simulated over time periods not exceeding 50 years, well within the 65-70 year period over which decadal changes in small pelagic fish have been reported for both the Benguela and Californian systems (Baumgartner 1992, 1995, M^{c}Laghlan 1995).

Ecopath with Ecosim can produce inaccurate results if input data are erroneous. These usually result from errors in a few key input parameters rather than from general uncertainties in the whole model (Christensen and Walters 2000). Christensen and Walters (2000) list five main pitfalls of the *Ecopath with Ecosim* model:

i) prey that is rarely found in the diet of a predator may be omitted from diet composition estimates, leading to inaccuracies in the modelled effects of the predator on these prey, and visa-versa.

ii) trophic mediation effects may be overlooked (these are the indirect effects that the behaviour or presence of a third group may have on a predator-prey interaction)

iii) predation vulnerabilities are often underestimated, lessening the modelled impacts of predation

iv) predators share foraging arenas; if abundance of one predator decreases, another may fill its place so that prey species do not benefit.

v) temporal variation in factors affecting species-specific habitats is not incorporated.

A major advantage of *Ecosim* above MSVPA type models is that trophic interactions for all trophic levels are well represented, including those at lower trophic levels, often lumped into a category such as "other food" in MSVPA models (Walters *et al.* 1997). Further, MSVPA-type models are data-intensive, requiring extensive and time-consuming parameterization, causing high uncertainties in model simulations (Whipple *et al.* 2000). By comparison, *Ecopath with Ecosim* can be applied to a wider range of ecosystems because data requirements are fewer and sufficient data are usually readily available (Whipple *et al.* 2000).

Walters *et al.* (1997) list three major disadvantages of *Ecosim* compared to other modelling approaches. These are i) switching and satiation in predators are not represented, ii) complex but smooth changes in predation rates associated with rapid changes in size structure are not well represented by average interaction rates defined for individual groups in *Ecosim*, and iii) *Ecosim* is dependent on the mass-balance (equilibrium) assumption of *Ecopath.* The latter assumption means that care should be taken to avoid errors in the interpretation of *Ecosim* results, which may occur when results are extrapolated far beyond the equilibrium for which *Ecopath* data are available (Mackinson *et al.* 1997, Walters *et al.* 1997). In other words, *Ecosim* assumes that changes in the fisheries occur within a given regime and that there are no additional regime changes during the simulation period. To accommodate this assumption, separate models of the Southern Benguela ecosystem have been constructed for two periods dominated by different pelagic species.

CHAPTER FOUR

TROPHIC FLOWS THROUGH THE SOUTHERN BENGUELA ECOSYSTEM: MODEL CONSTRUCTION

ABSTRACT

Biomass, production, consumption, catches and diet composition are estimated for 31 living groups in the southern Benguela ecosystem. Mass-balanced models are constructed of the trophic flows in the ecosystem during two periods: 1980-1989 and 1990-1997. In the balanced models, there is a 10% increase in zooplankton biomass between the 1980s and the 1990s, in agreement with observed trends of increased zooplankton abundance off South Africa over the last few decades. Hake biomass required in balanced models is 34% larger than survey estimates for the 1980s and 22% larger in the 1990s. This is not unexpected given the likely undersampling of hake. Anchovy were the dominant pelagic fish in the 1980s whereas sardine abundance increased in the 1990s. Model biomass and mean annual production of five important small pelagic fish groups were larger in the 1990s, and total catches were smaller than in the 1980s. Simulations suggest that the southern Benguela ecosystem was less tightly constrained by predators and availability of zooplankton in the 1990s than in the 1980s. Mesopelagic fish and redeye are not commercially important groups but have high ecotrophic efficiencies in the models, reflecting their important trophic roles in the ecosystem.

4.1. INTRODUCTION

To date, a few attempts have been made to summarize the flow of carbon through the southern Benguela ecosystem, focusing attention on various aspects, namely the pelagic component (Shannon and Field 1985, Bergh *et al.* 1985, Moloney and Field 1985), the planktonic foodweb (Moloney 1992) and comparison of ecosystem properties (Baird *et al.* 1991). In 1989, at a workshop of experts on the different species groups in the Benguela upwelling region, both published and unpublished data were brought together to construct simple input-output carbon budgets of the southern and northern Benguela ecosystems. These data, together with those that have since become available, were used to construct the first *Ecopath* model of the southern Benguela (Jarre-Teichmann *et al.* 1998) and northern Benguela (Shannon and Jarre-Teichmann 1999a and b) ecosystems during the 1980s. Subsequently, the first model of the southern Benguela ecosystem was modified by separating some components for clarity and incorporating new hake data. Based on this revised 1980s model, a second model was constructed of trophic flows through the southern Benguela ecosystem during the 1990s. For this study, these models were refined further by dividing groups such as horse mackerel, hakes, demersal fish and chondrichthyans into size or feeding classes. This helped to reduce problems arising from intra-group cannibalism and major within-group differences in feeding modes. Models were run with updated data. Models of the southern Benguela ecosystem cover the shelf region to approximately the 500m depth contour, extending from 29°S (in the vicinity of the Orange River mouth, the boundary between Namibia and South Africa) southwards along the west coast and eastwards to 28°E (East London). The area covers 220 000 km^2 and incorporates the upwelling area along the west coast, the Agulhas Bank and the south coast of South Africa.

In this chapter, I tackle the first key question 1 a "what are the biomass, production, consumption and catches of the components of the southern Benguela ecosystem during periods of a) anchovy dominance (1980s) and b) sardine dominance (1990s)?" The focus of the work is the trophic functioning of the pelagic ecosystem, using an annual time scale. Temporal changes in biomass of groups such as phytoplankton and zooplankton, operating on shorter time scales (days or weeks), cannot be represented adequately in this model. Therefore no attempt has been made to subdivide plankton groups according to size or species assemblages beyond the few groups used (phytoplankton, micro-, meso- and macro-zooplankton, and gelatinous zooplankton). To model the trophic interactions of these groups in more detail would require that *Ecopath* models be customized for smaller time and space scales. Similarly, the demersal fish assemblages of the Benguela ecosystem were not a primary focus of this study. The generally poorly-known demersal fish component was divided into nine boxes: small shallow water hake *(Merluccius capensis),* large shallow water hake, small deep water hake *(M paradoxus)*, large deep water hake, other benthic-feeding demersal fish, other pelagic-feeding demersal fish, pelagic-feeding chondrichthyans, benthic-feeding chondrichthyans and apex predatory chondrichthyans.

4.2. INPUT DATA

Input data are tabulated and sources given in Appendix A, Tables A.1- A.9. Where parameter values used in the models differ from original estimates, revised values used are indicated and comments provided.

4.2.1 Plankton

Input data for the plankton groups are presented in Table A.1.

Estimating zooplankton biomass in the 1990s

Over the past few decades, there have been changes in abundances of zooplankton in the St Helena Bay area (Verheye and Richardson 1998, Verheye *et al.* 1998). Between 1951 and 1996, zooplankton abundance increased by at least an order of magnitude in all size classes. The biomass of copepods (including some large calanoid copepods that are macrozooplankton) increased by about 60% between the late 1980s and 1995/6 (Verheye *et al.* 1998). There was uncertainty about how to convert abundance (numbers) to biomass (tonnage) for the various zooplankton components of the whole southern Benguela sub-system. Therefore, the model was used to estimate biomass for micro-, meso- and macro-zooplankton from the production required to sustain other groups in the system during the 1990s.

It is likely that the biomass of gelatinous zooplankton also increased between the 1980s and 1990s; tunicates were more abundant in the 1990s than earlier in the century (Verheye *et al.* 1998). Since little gelatinous zooplankton seems to be required to support other groups within the system (ecotrophic efficiency was 4% in preliminary models of the 1980s), the model was not used to estimate biomass of this group. Instead, gelatinous zooplankton biomass was increased by 10% from the 1980s to the 1990s, the estimated increase required for other zooplankton groups in the model.

4.2.2 Small pelagic fish

The small pelagic fish component consists mainly of clupeoids. Clupeoids belong to the order Clupeiformes, comprising two groups: clupeids (sardines, herrings, round herrings and sardinellas) and engraulids (anchovies). Off southern Africa, commercially important purse seine fisheries for clupeoids have been in operation since the 1940s. Large catches of sardine *Sardinops sagax* (locally known as "pilchard") were made in the 1950s and 1960s, but Namibian and South African sardine fisheries subsequently collapsed. Anchovy *Engraulis capensis* became the mainstay of the purse-seine fishery off South Africa in the mid-1980s, whereas anchovy remained at low levels off Namibia. By the 1990s, abundance of anchovy in the southern Benguela ecosystem was fluctuating and declining, whereas sardine biomass was increasing (Fig. 4.1). This study focuses in particular on the role of clupeoids in the southern and northern Benguela sub-systems.

Four groups of small pelagic fish were modelled: in the southern Benguela models, these were anchovy, sardine, redeye *Etrumeus whiteheadi* and other small pelagic fish, the latter including saury (Scomberesocidae), flying fish (Exocoetidae) and other less common species. In the northern Benguela ecosystem, redeye is scarce and is included in the other small pelagic fish box. The fourth small pelagic fish box in the northern Benguela model is the pelagic goby *Sufflogobius bibarbatus.*

Table A.2 contains input data for small pelagic fish in models of the southern Benguela ecosystem. Considering the zooplanktivorous diets of small pelagic fish, assimilation efficiency was assumed to be 65% (Jarre-Teichmann *et al.* 1998).

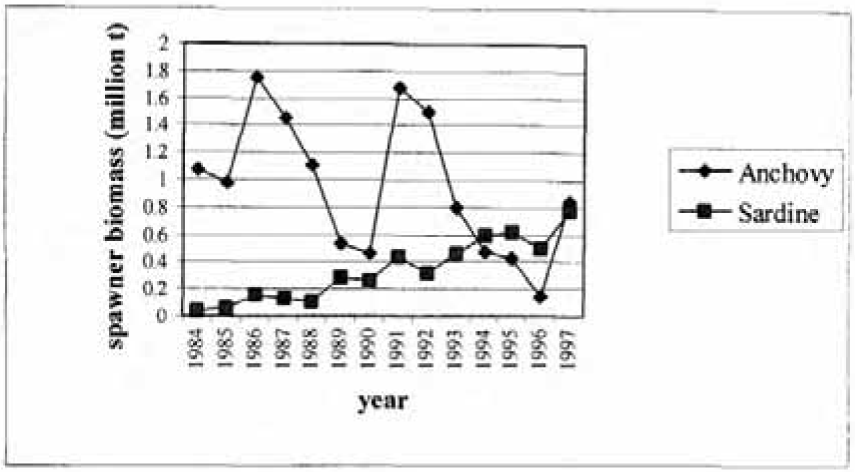


Fig. 4.1 Estimates of spawner biomass of anchovy and sardine off South Africa (Hampton 1992, 1996 and Barange *et al.* 1999, updated by Schwartzlose *et al.* 1999).

4.2.3 Other pelagic fish

Seven additional groups of other pelagic fish were modelled (Tables A.3, A.4 and A.5): small and large horse mackerel *(Trachurus trachurus capensis),* chub mackerel *(Scomber japonicus),* two groups of large pelagic fish, cephalopods and mesopelagic fish. Commercially important large pelagic fish of the region include snoek *Thyrsites atun,* kob *Argyrosomus inodorus,* geelbek *Atractoscion aequidens,* yellowtail *Seriola lalandi* and tuna *Thunnus* spp. The most abundant large pelagic fish is snoek, estimated to comprise 65% of the biomass of the group (Penney *et al.* 1991a). This group was modelled separately, and remaining large pelagic fish species were grouped.

Horse mackerel

Because juvenile horse mackerel (<20 cm) are pelagic and zooplanktivorous, whereas adult horse mackerel (>20 cm, older than 2 years) are midwater feeders and partially piscivorous, the horse mackerel group was split in two. This was sensible also because catches by purse seiners are almost entirely of horse mackerel smaller than 20 cm, whereas adult horse mackerel are caught in trawls (unpublished data, MCM). Applying a revised length-weight relationship (equation 4.1, from M. Kerstan, unpublished data) to data collected during research surveys (unpublished demersal trawl data from research cruises, MCM), the proportion (by mass) of small (<20 cm) and large (>20 cm) horse mackerel in research trawls was estimated for the 1980s and 1990s separately.

$$W = 0.0093685 \text{ x } L^{29'0'} \qquad \text{...equation 4.1}$$

where W is weight in cm and L is total length in cm.

In the 1980s, 1% and 3% of horse mackerel biomass in demersal surveys consisted of small horse mackerel on the south and west coasts respectively. During the 1990s, 9% and 11% of such biomass was of small horse mackerel on the south and west coasts. To what extent the Namibian and South African horse mackerel stocks are distinct is uncertain (Crawford *et al.* 1987), and the increased contribution of juveniles to biomass on the west coast in the 1990s may be explained by southward migration of Namibian horse mackerel (E. Klingelhoeffer, National Marine Information and Research Centre, Namibia, pers. comm., cited by Barange *et al.* 1998). Because demersal trawls are likely to miss the pelagic portion of the stock, juveniles are likely to be under-represented. Small horse mackerel were considered to contribute at least 10% of total horse mackerel biomass in the 1980s, and double this during the 1990s (Table A.3). These fractions are similar to that calculated from Kinloch *et al's* (1986) VPA estimates; fish less than 2 years comprised 17% of total horse mackerel biomass.

4.2.4 Hakes

The Cape hakes *Merluccius capensis* (shallow water) and *M paradoxus* (deep water) are of great commercial importance in the Benguela region. Because cannibalism is common in the two species, and because small *M paradoxus* are eaten by large *M capensis,* hake were modelled as four separate groups according to size and species. Small hake were those aged 0-2 years, and large hake were aged 3 years and older. Biomass of small (0-2 year olds) and large (3 years and older) hake (both species combined) for 1980-1989 and 1990-1996 was estimated from production models (Leslie 1996). Combined biomass was separated for the west and south coast populations. More detailed data were available for the west coast than for the south coast, so that different methods of separation were used for the two coasts.

For the west coast, species-specific numbers per age-class and year were derived from numbers-at-length and age-at-length keys available for 1985-1988 and 1990-1994. The mean weight-at-age of hake was used to calculate the proportion by mass of each species per age class. Proportions were multiplied by the biomass on the west coast to give biomass by age group, species and decade for the west coast.

For the south coast, based on estimates of biomass by species for both the 0-200 m and 0-500 m depth strata from surveys between 1988-1995, the ratio of biomass of *M capensis* to *M paradoxus* was estimated to be 19:1. Using survey data for 1988-1997 for the 0-200 m-isobath region of the south coast, Leslie (1998b) calculated mass-at-age for both species combined. This shows that 9% of south coast hake biomass is in the age class 0-2 years, and 91% in the age class 3 years and older. Using the relative proportions by species and by age class, the overall proportions were calculated and used to assign south coast hake biomass into that per age group, species and decade. Summing west and south coast values, biomass estimates by species and size groups were calculated for hake off South Africa (Table A.6).

4.2.5 Other demersal fish and chondrichthyans

Other demersal fish

Biomass of other demersal fish was estimated to be 230 000 t on the Agulhas Bank for 1986-1992 (Japp *et al.* 1994), comparable to 175 000 t when biomass indices from 1986-1990 are summed over applicable species (Badenhorst and Smale 1991; Smale and Badenhorst 1991). Many of these indices are thought to be underestimates of biomass because during surveys gear was not specifically rigged for species such as sole, and gear avoidance is a fundamental problem. Further, many of the species occur over untrawlable grounds and would have been missed during surveys (Badenhorst and Smale 1991). Species such as Agulhas sole *Austroglossus pectoralis* are patchily distributed, making indices unreliable as estimates of biomass (Badenhorst and Smale 1991). At a workshop in 1989, held under the auspices of the Benguela Ecology Programme and at which available data series were summarised into ecosystem spreadsheet models (see also Chapter 7, section 7.1), biomass of other demersal fish in the southern Benguela ecosystem was estimated to be 232 061 t. This is likely to have been a gross underestimate considering indices are nearly this for the south coast alone.

Initially, demersal fish (excluding hake) were grouped into one box. However, intra-box consumption (seen as cannibalism) was high and it was advisable to split the group into two, following the trophic groupings of Meyer and Smale (1991a and b). Pelagic-feeding demersal fish include the following non-commercial species: buttersnoek (ribbonfish) *Lepidopus caudatus,* Cape John Dory *Zeus capensis,* southern rover *Emmelichthys nitidus nitidus,* pencil cardinal *Epigonus denticulatus,* windtoy *Spicara axillaris,* cutlass fish *Trichiurus lepturus* and jutjaw *Parascorpis typus* (Meyer and Smale 1991a). The major commercially valuable pelagic feeder is the angelfish *Brama brama.*

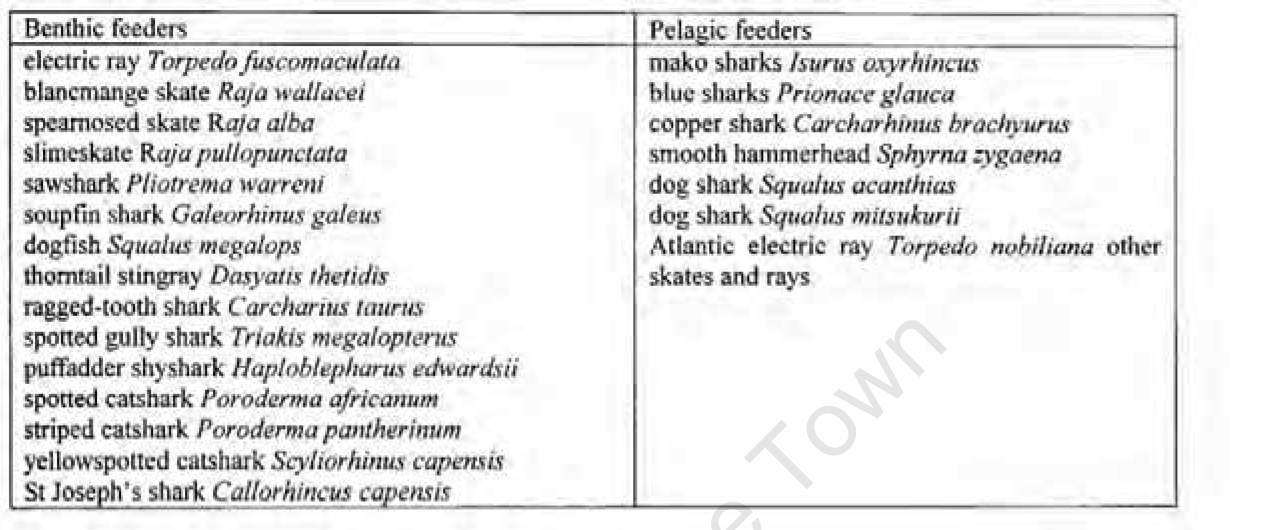
Meyer and Smale's (1991b) benthic-feeding demersal fish group includes piscivorous species and those feeding on benthic invertebrates: Cape gurnard *Chelidonichthys capensis,* African gurnard *Trigloporus 1. africanus,* bank steenbras *Chirodactylus grandis,* hairy conger *Bassanago albescens,* lesser gurnard *Chelidonichthys queketti,* redspotted tonguefish *Cynoglossus zanzibarensis,* beaked sandfish *Gonorhynchus gonorhyncus,* spinenose horsefish *Congipodus spinifer,* smooth horsefish *Congiopodus torvus,* large-scaled rattail *Coelorinchus fasciatus,* smooth-scaled rattail *Malacocephalus laevis* and jacopever *Helicolenus dactylopterus.* In addition, commercially important species such as Agulhas *sole,* west coast sole *A. microlepis,* kingklip *Genypterus capensis,* monkfish *Lophius sp.* and panga *Pterogymnus laniarius* are benthic-feeders.

Table A.7 contains input data for pelagic-feeding and benthic-feeding demersal fish.

Chondrichthyans

Initially (Jarre-Teichmann *et al.* 1998, Shannon and Jarre-Teichmann 1999b, Shannon *et al.* 2000), a single chondrichthyan group was used. However, intra-group cannibalism and the divergent diets of species belonging to different feeding guilds, led to the group being divided into three in accordance with Penney *et al.* (1991a and b): benthic and pelagic feeders (Table 4.1) and apex predators (Table A.7). Great white shark *(Carcharodon carcharias),* six-gilled shark *(Hexanchus griseus)* and seven-gilled shark *(Notorhinchus cepedianus)* are apex predators.

Table 4.1 Chondrichthyans belonging to benthic and pelagic feeding guilds in the southern Benguela ecosystem.



Benthic feeders	Pelagic feeders
electric ray *Torpedo fuscomaculata*	mako sharks *Isurus oxyrhincus*
blancmange skate *Raja wallacei*	blue sharks *Prionace glauca*
spearnosed skate *Raja alba*	copper shark *Carcharhinus brachyurus*
slimeskate *Raja pullopunctata*	smooth hammerhead *Sphyrna zygaena*
sawshark *Pliotrema warreni*	dog shark *Squalus acanthias*
soupfin shark *Galeorhinus galeus*	dog shark *Squalus mitsukurii*
dogfish *Squalus megalops*	Atlantic electric ray *Torpedo nobiliana* other skates and rays
thorntail stingray *Dasyatis thetidis*	
ragged-tooth shark *Carcharius taurus*	
spotted gully shark *Triakis megalopterus*	
puffadder shyshark *Haploblepharus edwardsii*	
spotted catshark *Poroderma africanum*	
striped catshark *Poroderma pantherinum*	
yellowspotted catshark *Scyliorhinus capensis*	
St Joseph's shark *Callorhincus capensis*	

4.2.6 Marine mammals and birds

Marine mammals were divided into two groups: seals and cetaceans (Table A.8). Only those cetaceans feeding in South African waters were included in the trophic models. Amongst these are Heavyside's dolphin *Cephalorhynchus heavisidii,* common dolphin *Delphinus delphis,* dusky dolphin *Lagenorhynchus obscurus,* bottlenose dolphin *Tursiops truncatus,* Bryde's whale *Balaenoptera edeni* and sperm whale (Physeteridae). Neither humpback whale *Megaptera novaeangliae* nor southern right whale *Eubalaena australis* are considered to feed regularly off the South African coast (Smale *et al.* 1994). However, right whales have been reported to eat large quantities of mesozooplankton in the southern Benguela sub-system (Verheye *et al.* 1992), and there are reports of fish and stomatopods being consumed by humpback whales off the west coast of South Africa (Findlay and Best 1995).

There are 15 species of seabirds breeding in southern Africa: African penguin *Spheniscus demersus,* Cape gannet *Morus capensis,* four cormorants *Phalacrocorax* spp., white pelican *Pelecanus onocrotalus,* three gulls *Larus* spp., four terns *Sterna* spp. (Cooper *et al.* 1984) and on petrel (Whittington *et al.* 1999). In addition, migrant seabirds also feed in the ecosystem (Crawford *et al.* 1991 b). Estimates of abundance and diet are available for all species breeding off South Africa and for the more numerous migrant species feeding in the sub-system (Crawford *et al.* 1991b). In quantitative trophic terms (their consumption and their contribution as food to other animals), seabirds are relatively unimportant in the southern Benguela (Bergh *et al.* 1985). However, like marine mammals, seabirds may play an important role in the stabilisation of trophic flows by preying on a variety of small fish, and switching prey according to availability (Bergh *et al.* 1985).

4.2. 7 Benthos

Biomass information on benthic communities deeper than 20 m in the southern Benguela sub-system is limited. Biomass of the benthos is likely to be limited by the hypoxic conditions along the west coast of South Africa. Christie (1975) and Field (1971) studied the composition and community structure of benthos in the region of Lambert's Bay on the west coast of South Africa (10-200m), and False Bay (10-120m), but did not estimate biomass. Therefore, biomass required by the southern Benguela system was estimated using *Ecopath,* based on P/B and P/Q ratios from other systems (Jarre-Teichmann *et al.* 1998, Table A.9).

4.2.8 Detritus

The non-living detritus group receives inputs (faecal deposits, dead organisms, decaying remains as "other mortalities" and un-assimilated food) from all other model groups. *Ecopath* does not require other information. The group was not split further (e.g. into carcasses, POC, DOC) due to lack of data from the region.

4.3 CATCHES

Catches in the southern Benguela ecosystem during the 1980s and 1990s are tabulated by group (Table 4.2). Because a less detailed breakdown of catches according to gear was available in the 1980s, and so that scenarios of altered harvesting between the two decades were comparable, catches were separated into those using the following six gear types: purse seine nets, demersal trawls, midwater trawls, long lines, lines, other (includes recreational, beach seine, set nets, squid jigs etc.).

4.3.1 Catches of hake

Total catches of hake of both species averaged close to 140 000 t in the southern Benguela ecosystem during the 1980s (Punt 1994) and 144 100 t between 1990 and 1996 (Leslie 1998a and b). Hake catches were allocated to the two size classes, according to Leslie 1998a and Leslie 1998b for the west and south coasts respectively. Of the large hake caught on the south coast, 33% of total catches on the south coast were adult *M paradoxus* (R.W. Leslie, MCM, pers. comm.). Research cruise data (unpublished data of MCM) collected between the 0 and 200 m isobaths on the south coast (the main area of fishing on the south coast) in autumn 1988-1997, show that the ratio of *M capensis* biomass to *M paradoxus* biomass is 0.95:0.05. This ratio was used to allocate catches of hake by species to the small size class on the south coast. It was assumed that all small hake caught on the west coast are *M paradoxus*. For the west coast, research survey data from summer cruises showed that the relative proportions of the two hake species on the west coast were 25% *M capensis* and 75% *M paradoxus* for both decades. This ratio was assumed for total hake caught by commercial vessels on the west coast, i.e. 75% of total catches are *M paradoxus* (includes small and large), 25% are *M capensis* (large fish only). Combining estimates for the west and south coasts, total annual catches of hake by species and decade were calculated. Catches by gear were available for both species combined, and for the two coasts separately. Based on combined hake catches by gears on the west and south coasts (Leslie 1998a and b), catches were apportioned according to gear type (Table 4.2). For simplicity, longline and handline catches (together comprising less than 2% of total catches) were considered to be of hake in the large size classes. Reported catches of hake caught in inshore trawls on the south coast were increased to account for the estimated discard of 24% of the hake catch in this fishery (Anonymous 1997, Table 4.2).

Table 4.2 Mean annual catches in the southern Benguela ecosystem during the 1980s and 1990s (t.y^{-1}). *The way in which annual hake catches were split according to group and gear is explained in section 4.3.1. "1989 Workshop" refers to the mass-balanced Benguela ecosystem modelling workshop held in 1989 (see section 4.1).

Group	1980s			1990s		
	Catch	Gear	Source	Catch	Gear	Source
CAPE ANCHOVY (*ENGRAULIS CAPENSIS*)	345 820	Purse seine	Unpublished data, MCM	178 680	Purse seine	Unpublished data, MCM
SARDINE (*SARDINOPS SAGAX*)	39 680	Purse seine	Unpublished data, MCM	74 780	Purse seine	Unpublished data, MCM
RED EYE (*ETRUMEUS WHITEHEADI*)	39 560	Purse seine	Unpublished data, MCM	51 427	Purse seine	Unpublished data, MCM
OTHER SMALL PELAGIC FISH	200	Purse seine	1989 Workshop (79 t) and estimates of additional spp.	200	Purse seine	Assumed same as 1980s
SMALL (<20 cm) HORSE MACKEREL (*TRACHURUS TRACHURUS CAPENSIS*)	4 830	Purse seine	Badenhorst 1995	7 219	Purse seine	Stuttaford 1997
				2	Beach seine and gill nets	Lamberth *et al.* 1998
LARGE (>20 cm) HORSE MACKEREL (*TRACHURUS TRACHURUS CAPENSIS*)	31 620	Demersal trawl	Badenhorst 1995	19 432	Demersal trawl	Stuttaford 1997
				4 005	Midwater trawl	
CHUB MACKEREL (*SCOMBER JAPONICUS*)	976	Purse seine	Japp *et al.* 1994; Stuttaford 1997	2 344	Purse seine	Stuttaford 1997
	6 054	Demersal trawl	Japp *et al.* 1994	4 820	Demersal trawl	
	38	Line fishery		115	Midwater trawl	
SNOEK (*THYRSITES ATUN*)	3 303	Line fishery	Unpublished data, MCM ICSEAF reports (1983-1987)	7 362	Line fishery	Unpublished data, MCM
	7 489	Demersal trawl		10 910	Demersal trawl	Stuttaford 1997
	220	Midwater trawl		4	Midwater trawl	
	130	Recreational		294	Recreational	Using Sauer & Erasmus' (1996) recreational: commercial catch ratio
				0.05	Beach seines and gill nets	Lamberth *et al.* 1998, Sauer and Erasmus 1996
LARGE PELAGIC FISH	5 384	Line fishery	ICSEAF reports (1983-1987); Penney *et al.* (1991a); unpublished data, MCM	5 233	Line fishery	Unpublished data, MCM
	308	Sport and recreational		330	Sport and recreational	Penney *et al.* 1991a; unpublished data, MCM
	270	Demersal trawl		146	Demersal trawl	Stuttaford 1997
	11	Long line		0.3	Midwater trawl	
				80	Beach seine and gill net	Lamberth *et al.* 1998

CEPHALOPODS (MAINLY CHOKKA SQUID *LOLIGO* SPP.)	2 400	Demersal trawl	Roel 1998	616	Demersal trawl	Stuttaford 1997
	3 600	Jig fishery		9	Midwater trawl	
				5 456	Jig fishery	FAO 1997a
MESOPELAGIC FISH (MAINLY *LAMPANYCTODES HECTORIS*)	6 820	Purse seine	Unpublished data, MCM	670	Purse seine	Stuttaford 1997
SMALL CAPE HAKE (*MERLUCCIUS CAPENSIS*)	5222	Demersal trawl	*	2 913	Demersal trawl	*
	1 492	Discards		1 592	Discards	
LARGE CAPE HAKE (*M. CAPENSIS*)	49 935	Demersal trawl	*	54 763	Demersal trawl	*
	681	Long line		941	Long line	
	30	Handline		549	Handline	
SMALL DEEP-WATER HAKE (*M. PARADOXUS*)	25 601	Demersal trawl	*	7 441	Demersal trawl	*
	627	Discards		726	Discards	
LARGE DEEP-WATER HAKE (*M. PARADOXUS*)	57 160	Demersal trawl	*	76 320	Demersal trawl	*
	1 193	Long line		913	Long line	
	15	Handline		276	Handline	
PELAGIC-FEEDING DEMERSAL FISH	4 816	Demersal trawl	ICSEAF reports (1983-1987); 1989 Workshop	12 615	Demersal trawl	Stuttaford 1997
	25	Midwater trawl		85	Midwater trawl	
				16	Long line	
BENTHIC-FEEDING DEMERSAL FISH	17 499	Demersal trawl	ICSEAF reports (1983-1987); 1989 Workshop	11 431	Demersal trawl	Stuttaford 1997
	50	Midwater trawl		34	Midwater trawl	
	2 799	Long line		266	Long line	
	25	Other		0.15	Beach seine and gill net	
PELAGIC-FEEDING CHONDRICHTHYANS	30	Demersal trawl	Smale 1996; FAO 1997a; M. Kroese, pers. comm.	30	Demersal trawl	Smale 1996; FAO 1997a; M. Kroese, pers. comm.
	390	Line fishery		390	Line fishery	
BENTHIC-FEEDING CHONDRICHTHYANS	2 070	Demersal trawl	Smale 1996; FAO 1997a; M.Kroese, MCM, pers. comm.	2 070	Demersal trawl	Smale 1996; FAO 1997a; M. Kroese, MCM, pers. comm.
	300	Seine and gill nets		300	Seine and gill nets	
	210	Longline		210	Longline	
SEALS (*ARCTOCEPHALUS PUSILLUS PUSILLUS*)	470	Harvests	Wickens *et al.* 1991	0	No harvests	Wickens *et al.* 1991
	710	Fishery-related deaths	Wickens *et al.* 1992a	710	Fishery-related deaths	Assumed same as in 1980s

4.4 DIET DATA

Diet compositions based on available data (Table 4.3) are tabulated (Table 4.4). Because many of the species present in high abundance in the southern Benguela are opportunistic feeders, there is a large amount of overlap in diet composition (Crawford *et al.* 1989).

4.4.1 Sardine and anchovy diets

Louw *et al.* (1998) found that in mixed shoals off the west coast of South Africa, anchovy and sardine eat similar prey (crustacean eggs and nauplii and copepods), but that sardine consumed significantly smaller prey than anchovy. The modal size class of prey consumed by anchovy was 600-900 pm, compared to 300 p.m for sardine. Dietary differences are probably due to a combination of factors: differences in gill raker morphology, individual position within mixed shoals and feeding behaviour. Sardine is primarily a filter feeder (van der Lingen 1994, 1995) whereas anchovy is primarily a particulate feeder (James and Findlay 1989). Louw *et al.* (1998) concluded that competition between anchovy and sardine for food might be limited.

4.5 BALANCING THE MODELS

Modelling using the raw input data gave ecotrophic efficiencies greater than unity for many of the model ecosystem components. This indicated that model production of these groups was insufficient to support the model consumption by other groups, and in some cases the catches. Since much uncertainty surrounded many of the estimates of diet composition, especially those for the 1990s, the models were mostly balanced by adjusting the diets of some groups.

4.5.1. Zooplankton

There was uncertainty concerning the most appropriate factor to convert zooplankton carbon to wet mass. A carbon:wet mass ratio of 14.25 was used for all ecosystem components by Jarre-Teichmann *et al.* (1998), whereas a conversion factor of 25 was used for zooplankton by Verheye *et al.* (1992). Conversion factors depend on the contribution of various taxa to each zooplankton group (H. Verheye, MCM, pers. comm.). When the smaller conversion ratio of 14.25 was applied to the microzooplankton biomass estimate of $8.5X10^4$ t C (Jarre-Teichmann *et al.* 1998), wet biomass was insufficient to balance the model. Apart from uncertainty in converting from carbon to wet mass, the larger biomass of microzooplankton required may be explained by the fact that microzooplankton are frequently underestimated through sampling procedures (Nielsen and Sabatini 1996). For both decades, *Ecopath* was used to estimate the biomass of micro-, meso- and macrozooplankton required by other components of the ecosystem.

In the 1980s model, required biomass of microzooplankton was 7.5 $t.km^{-2}$. This estimate lies between the biomasses estimated using carbon: wet mass ratios of 14.25 and 25. Required biomass of mesozooplankton (8.0 $t.km^{-2}$) was less than estimates based on carbon tonnage in Hutchings *et al.* (1991) and the conversion factor of 25 suggested by Verheye (MCM, pers. comm.). This would be expected given the mismatch in timing of production of various zooplankton species in the Benguela region (L. Hutchings, MCM, pers. comm.). By comparison, required biomass of macrozooplankton (13.3 $t.km^{-2}$) was much higher than that calculated from Hutchings *et al.* (1991) using Verheye's (MCM, pers. comm.) conversion factor of 12.5, but lay within the range of 1.8 and 21.9 $t.km^{-2}$ estimated for 1983-1987 by H. Verheye (MCM, pers. comm.). It was also closer to the estimate of 11 $t.km^{-2}$, calculated by converting Pillar *et al.'s* (1992) dry mass estimate of euphausiid biomass in the southern Benguela ecosystem. Further, biomass of this group would be expected to be higher than Hutchings *et al.'s* (1991) estimate because this was of crustacean zooplankton, whereas by definition macrozooplankton in the models include fish eggs and larvae, likely a large part of the group in terms of biomass.

In the 1990s, the model estimated that biomass of all zooplankton groups was required to be 10% larger than that in the 1980s (discussed further in section 4.6.2).

4.5.2 Hakes

Hake biomass indices from surveys (Badenhorst and Smale 1991) are greater than biomass estimated by the production model (Leslie 1996). Further, it is likely that hake biomass exceeds the survey indices because untrawlable ground is not covered and small, pelagic hake may be missed. Therefore, it is expected that biomass, in particular that of small hake, is larger than the production model estimates. The models showed that production of small hake was insufficient to support the consumption by large hake and other predators. Therefore the required biomass of small hake was estimated, assuming an ecotrophic efficiency (proportion of production consumed or exported from the system) of 99.9%.

Models showed that required biomass of hake was 34% (1980s) and 22% (1990s) more than the production model index. The additional biomass was in the small hake classes, indicating that juvenile mortality is likely to be underestimated in current models, as might be expected (R.W. Leslie, MCM, pers. comm.).

4.5.3 Diets

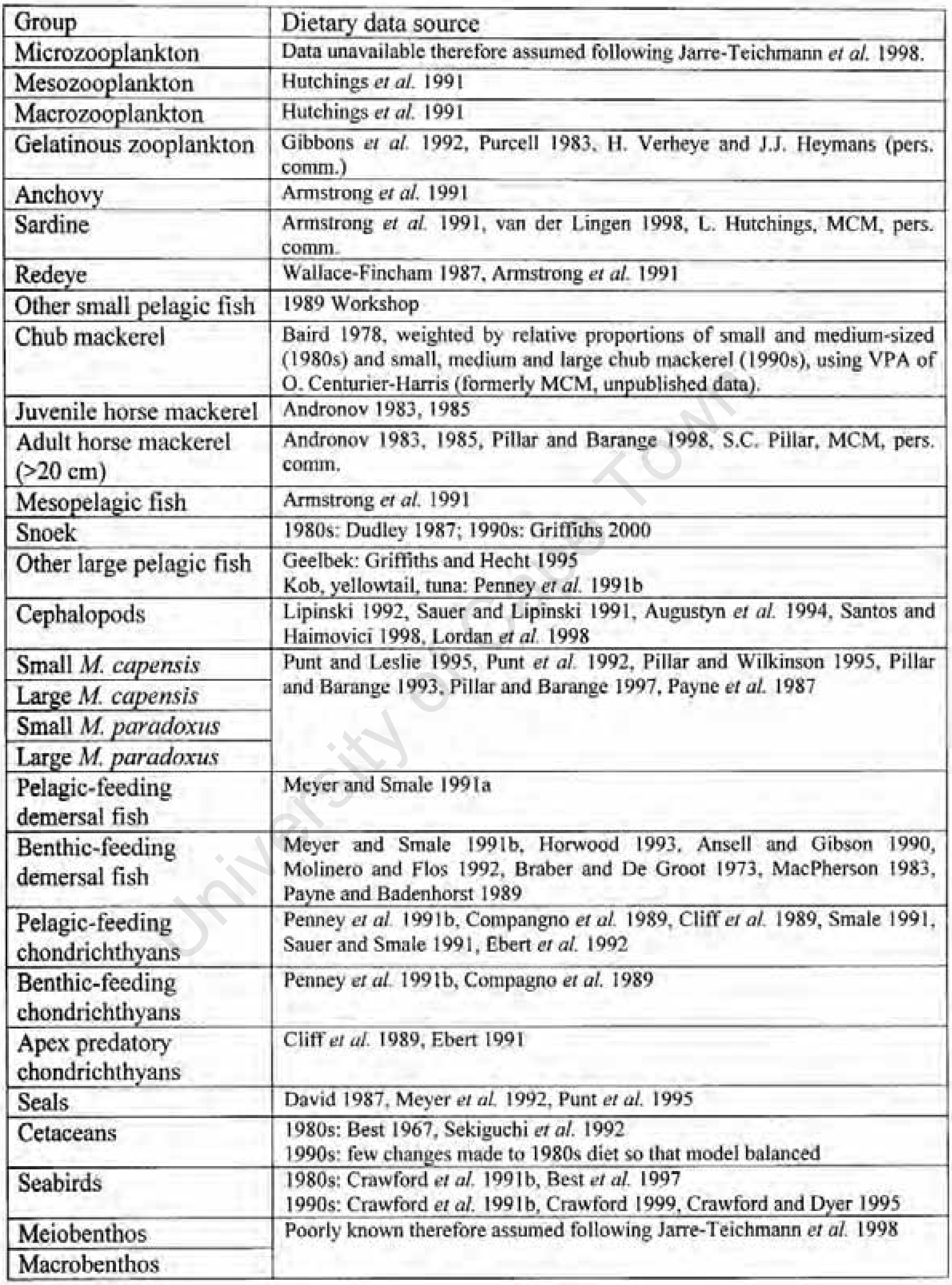
There are some fundamental problems with the estimation of dietary compositions in many cases. Often, dietary data are only available for part of the periods or area modeled, biasing the mean dietary estimates. Taxonomic resolution is low in some stomach analyses. These are amongst the reasons for predation on some components exceeding their production. Therefore, it was necessary to alter the contributions of some prey in the diets of certain predators (Table 4.4). Cells are shaded where changes have been made to balance the model (Table 4.5).

In particular, the relative dietary contributions of small pelagic fish during the two decades required altering to balance the models. Anchovy in the diet of chub mackerel in the 1990s was reduced from 3% to 2%, and 1% sardine was considered to have been consumed. Consumption of sardine by large pelagic fish during the 1980s was reduced to 10% and the remainder added to redeye. Redeye contribution to diet of large pelagics was assumed the same in the 1990s, and anchovy was reduced from 25% to 20% so that sardine contributed 15%. The proportion of anchovy in the diet of seals was reduced from 25% to 20%, and the remainder added to the redeye contribution. Insufficient snoek production required that snoek contributed not more than 0.5% of seal diet, and 0.5% was added to other large pelagics and to other demersal fish.

In the 1990s, the initial estimate of consumption of anchovy and sardine by seabirds caused consumption of these fish to exceed their production. This was probably because the estimated diet was based on data from only four species (African penguin, Cape gannet, Cape cormorant and swift tern). Further, there is both temporal and spatial variability in the diets of seabirds in the Benguela system, reflecting prey availability (Crawford *et al.* 1991b). It is unlikely that the proportion of anchovy in the diet of seabirds was larger in the 1990s when biomass was reduced. Therefore, the anchovy contribution was reduced to 30%, and sardine to 22% (the latter is still almost four times the contribution in the previous decade when sardine biomass was small). It was estimated that redeye contributed 7% to the diet of birds in the 1990s. When migrant seabirds feeding in the region are considered, it is unlikely that the contribution of macrozooplankton to seabird diet would have been lower in the 1990s than in the 1980s. Therefore, the macrozooplankton proportion was assumed constant in both decades.

Consumption of cephalopods by benthic-feeding chondrichthyans caused an imbalance and was reduced from 7 to 3%, with 4% added to the macrobenthos contribution.

Table 4.3 Sources of dietary data used to compile the original diet matrices for southern Benguela *Ecopath* models during the 1980s and 1990s.



Group	Dietary data source
Microzooplankton	Data unavailable therefore assumed following Jarre-Teichmann *et al.* 1998.
Mesozooplankton	Hutchings *et al.* 1991
Macrozooplankton	Hutchings *et al.* 1991
Gelatinous zooplankton	Gibbons *et al.* 1992, Purcell 1983, H. Verheye and J.J. Heymans (pers. comm.)
Anchovy	Armstrong *et al.* 1991
Sardine	Armstrong *et al.* 1991, van der Lingen 1998, L. Hutchings, MCM, pers. comm.
Redeye	Wallace-Fincham 1987, Armstrong *et al.* 1991
Other small pelagic fish	1989 Workshop
Chub mackerel	Baird 1978, weighted by relative proportions of small and medium-sized (1980s) and small, medium and large chub mackerel (1990s), using VPA of O. Centurier-Harris (formerly MCM, unpublished data).
Juvenile horse mackerel	Andronov 1983, 1985
Adult horse mackerel (>20 cm)	Andronov 1983, 1985, Pillar and Barange 1998, S.C. Pillar, MCM, pers. comm.
Mesopelagic fish	Armstrong *et al.* 1991
Snoek	1980s: Dudley 1987; 1990s: Griffiths 2000
Other large pelagic fish	Geelbek: Griffiths and Hecht 1995 Kob, yellowtail, tuna: Penney *et al.* 1991b
Cephalopods	Lipinski 1992, Sauer and Lipinski 1991, Augustyn *et al.* 1994, Santos and Haimovici 1998, Lordan *et al.* 1998
Small *M. capensis*	Punt and Leslie 1995, Punt *et al.* 1992, Pillar and Wilkinson 1995, Pillar and Barange 1993, Pillar and Barange 1997, Payne *et al.* 1987
Large *M. capensis*	
Small *M. paradoxus*	
Large *M. paradoxus*	
Pelagic-feeding demersal fish	Meyer and Smale 1991a
Benthic-feeding demersal fish	Meyer and Smale 1991b, Horwood 1993, Ansell and Gibson 1990, Molinero and Flos 1992, Braber and De Groot 1973, MacPherson 1983, Payne and Badenhorst 1989
Pelagic-feeding chondrichthyans	Penney *et al.* 1991b, Compangno *et al.* 1989, Cliff *et al.* 1989, Smale 1991, Sauer and Smale 1991, Ebert *et al.* 1992
Benthic-feeding chondrichthyans	Penney *et al.* 1991b, Compagno *et al.* 1989
Apex predatory chondrichthyans	Cliff *et al.* 1989, Ebert 1991
Seals	David 1987, Meyer *et al.* 1992, Punt *et al.* 1995
Cetaceans	1980s: Best 1967, Sekiguchi *et al.* 1992 1990s: few changes made to 1980s diet so that model balanced
Seabirds	1980s: Crawford *et al.* 1991b, Best *et al.* 1997 1990s: Crawford *et al.* 1991b, Crawford 1999, Crawford and Dyer 1995
Meiobenthos	Poorly known therefore assumed following Jarre-Teichmann *et al.* 1998
Macrobenthos	

Table 4.4 Original diet composition of groups in the southern Benguela ecosystem during the 1980s and 1990s. Where there are differences between decades, the cell is shaded and the contribution to diet during the 1990s is tabulated below the 1980s contribution. Prey groups are listed in rows, predators in columns. < indicates a dietary proportion of less than 0.5%.

Prey/ predator	Microzoo.	Mesozoo.	Macrozoo.	Gelatinous	Anchovy	Sardine	Redeye	Small pelagics	Chub Mack.	Juv. Horse M.	Ad. Horse M.	Mesopelagics	Snoek	Large pelagics	Cephalopods	Small *M. cap.*	Large *M. cap.*	Small *M. para.*	Large *M. para.*	Pelagic dems.	Benthic dems.	Pelagic chond.	Benthic chond.	Apex chond.	Seals	Cetaceans	Seabirds	Meiobenthos	Macrobenthos
Phytoplankton	40	50	60		5	32																							
Benthic prod.																												5	5
Microzoo.	20	50			4	32																							
Mesozoo.			40	64	57	29	60	81	1 5	75	39	40								1	1					3	1		
Macrozoo.				12	34	7	40	16	80 66	25	52	60	17 10	8	27	72 73	10	78 77	21	65	5					4	10 <		
Gelatinous				4				3																					
Anchovy									2 3		2		48 12	25	5 3	2	13 8	2	1 <	1 0	1	2			25	30 20	37 39		
Sardine											1		3 22	15	0 2	0 1	0 5	0 1	0 <	<		1			3	7 10	8 34		
Red eye									1		6		6 5	3	5	5 3	9	5	0 3	10 11	3	5			<	3 14	2		
Small pelagics													0 3	3			1	<	2			2			<	2 4	6 <		
Chub Mack.													0 1	3			2					1			1		<		

Prey/ predator	Microzoo.	Mesozoo.	Macrozoo.	Gelatinous	Anchovy	Sardine	Red eye	Small pelagics	Chub Mack.	Juv. Horse M.	Ad. Horse M.	Mesopelagics	Snoek	Large pelagics	Cephalopods	Small *M. cap.*	Large *M. cap.*	Small *M. para.*	Large *M. para.*	Pelagic dems.	Benthic dems.	Pelagic chond.	Benthic chond.	Apex chond.	Seals	Cetaceans	Seabirds	Meiobenthos	Macrobenthos
Juv. Horse M.													1 6	5			3								1		1 3		
Ad. Horse M.													0 5				16					9	1	3	2	27			
Mesopelagics									16 25				5 14	2	10	8	10	8	36	15	5	25	1		1	4	10		
Snoek													0 <				<		<			1		7	2		<		
Large pelagics														<								1		1					
Cephalopods													1	14	5	5	5	1	10	2	2	20	7		23	16 10	7		
Small *M. cap.*													2 3	1	2		15			<	<				10	1 <	4 0		
Large *M. cap.*																					<	4	1		2	1			
Small *M. para.*													6 13	3	8	2	15		15	2	<				10	2	13 <		
Large *M. para.*																			2		<	5			2	1			
Pelagic dems.													11 4	9		5	1	5	3	3	2	5	5	1	3		1		
Benthic dems.																1	1	1	9	1	2	10	20	1	8				
Pelagic chond.																						10		10					
Benthic chond.																					1		5	43					
Apex chond.																													

Prey/ predator	Microzoo.	Mesozoo.	Maccrozoo.	Gelatinous	Anchovy	Sardine	Red eye	Small pelagics	Chub Mack.	Juv. Horse M.	Ad. Horse M.	Mesopelagics	Snoek	Large pelagics	Cephalopods	Small *M. cap.*	Large *M. cap.*	Small *M. para.*	Large *M. para.*	Pelagic dems.	Benthic dems.	Pelagic chond.	Benthic chond.	Apex chond.	Seals	Cetaceans	Seabirds	Meiobenthos	Macrobenthos
Seals																								20			<		
Cetaceans																								15					
Seabirds																											<		
Meiobenthos																													8
Macrobenthos														3	38						78		60		7				7
Detritus	40			20																								95	80
Import														5															

Table 4.5 Balanced diet composition of groups in the southern Benguela ecosystem during the 1980s and 1990s. Shaded cells indicate dietary contributions altered in the balancing of the model. Where diet differs between decades, the contribution to diet during the 1990s is tabulated below the 1980s contribution. Prey groups are listed in rows, predators in columns. < indicates a dietary proportion of less than 0.5%.

Prey/ predator	Microzoo.	Mesozoo.	Macrozoo.	Gelatinous	Anchovy	Sardine	Red eye	Small pelagics	Chub Mack.	Juv. Horse M.	Ad. Horse M.	Mesopelagics	Snoek	Large pelagics	Cephalopods	Small *M. cap*	Large *M. cap.*	Small *M. para.*	Large *M. para.*	Pelagic dems.	Benthic dems.	Pelagic chond.	Benthic chond.	Apex chond.	Seals	Cetaceans	Seabirds	Meiobenthos	Macrobenthos
Phytoplankton	40	50	60		5	32																							
Benthic prod.																												5	5
Microzoo.	20	50			4	32																							
Mesozoo.			40	64	57	29	60	81	1 5	75	39	40								1	1					3	1		
Macrozoo.				12	34	7	40	16	80 66	25	52	60	17 10	8	27	72 73	10	78 77	21	65	5					4	10 10		
Gelatinous				4				3																					
Anchovy									2 2		2		48 12	25 20	5 3	2	13 8	2	1 <	1 0	1	2			20 15	30 20	37 30		
Sardine									0 1		1		3 22	10 15	0 2	0 1	0 5	0 1	0 <	<		1			3	7 10	8 22		
Red eye									1		6		6 5	8 8	5	5 3	9	5	0 3	10 11	3	5			5 11	3 14	2 7		
Small pelagics													0 3	3			1	<	2			2			<	2 4	6 6		
Chub Mack.													0 1	3			2					1			1		<		

Prey/ predator	Microzoo.	Mesozoo.	Maccrozoo.	Gelatinous	Anchovy	Sardine	Red eye	Small pelagics	Chub Mack.	Juv. Horse M.	Ad. Horse M.	Mesopelagics	Snoek	Large pelagics	Cephalopods	Small *M. cap.*	Large *M. cap.*	Small *M. para.*	Large *M. para.*	Pelagic dems.	Benthic dems.	Pelagic chond.	Benthic chond.	Apex chond.	Seals	Cetaceans	Seabirds	Meiobenthos	Macrobenthos
Juv. Horse M.													1 6	5			3								1		1 3		
Ad. Horse M.													0 5				16					9	1	3	2	27			
Mesopelagics									16 25				5 14	2	10	8	10	8	36	15	5	25	1		1	4	10		
Snoek													0 <				<		<			1		7	1		<		
Large pelagics														<								1		1	1				
Cephalopods													1	14	5	5	5	1	10	2	2	20	3		23	16 10	7		
Small *M. cap.*													2 3	1	2		11			<	<				10	1 <	4 0		
Large *M. cap.*																	4				<	4	1		2	1			
Small *M. para.*													6 13	3	8	2	15		15	2	<				10	2	13 3		
Large *M. para.*																			2		<	5			2	1			
Pelagic dems.													11 4	9		5	1	5	3	3	2	5	5	1	4		1		
Benthic dems.																1	1	1	9	1	2	10	20	1	8				
Pelagic chond.																						10		10					
Benthic chond.																					1		5	43					
Apex chond.																													

Prey/ predator	Microzoo.	Mesozoo.	Maccrozoo.	Gelatinous	Anchovy	Sardine	Red eye	Small pelagics	Chub Mack.	Juv. Horse M.	Ad. Horse M.	Mesopelagics	Snoek	Large pelagics	Cephalopods	Small *M. cap.*	Large *M. cap.*	Small *M. para.*	Large *M. para.*	Pelagic dems.	Benthic dems.	Pelagic chond.	Benthic chond.	Apex chond.	Seals	Cetaceans	Seabirds	Meiobenthos	Macrobenthos
Seals																								20			<		
Cetaceans																								15					
Seabirds																											<		
Meiobenthos																													8
Macrobenthos														3	38						78		64		7				7
Detritus	40			20																								95	80
Import														5															

4.6 SUMMARY OF SOUTHERN BENGUELA MODELS

4.6.1 Biomass and production offish

The small fish group is taken to include five model groups: anchovy, sardine, redeye, juvenile horse mackerel and other small pelagic fish. During the 1980s, anchovy was the dominant small pelagic fish in the southern Benguela ecosystem (Fig. 4.2). By the 1990s, the size of the anchovy population had decreased and populations of sardine, redeye, horse mackerel and both species of hake had increased in size (Fig. 4.2 and Table 4.6). Summed biomasses of small pelagic fish (anchovy, sardine, redeye, juvenile horse mackerel and other small pelagic fish) increased from 2.62 million tons in the 1980s to 2.80 million tons in the 1990s (Fig. 4.3. Mean annual production by these five small pelagic groups was 3.1 million tons in the 1980s and 3.3 million tons in the 1990s, half accounted for by anchovy and sardine. Shannon and Field (1985) estimated that a maximum biomass and annual production of 2 million tons of small pelagic fish could be supported in the southern Benguela ecosystem. Accounting for the smaller area (Orange River to Cape Agulhas) considered by Shannon and Field (1985), and their use of a lower conversion ratio from carbon to wet mass, models in this study support their estimates.

Moloney and Field (1985) estimated that only 25% of pelagic fish production off southern Africa is exploitable by humans. This is equivalent to 775 000 ty $^{-1}$ in the 1980s and 825 000 ty^{-1} in the 1990s. However, Moloney and Field (1985) did not recommend full exploitation of pelagic fish production because areas such as the Agulhas Bank are important for spawning pelagic fish and are likely to be important buffers against the large catches made off the west coast of South Africa. Total annual catches of the five small pelagic fish groups were larger in the 1980s (430 100 tons) than in the 1990s (312 400 tons) (Fig. 4.3). The opposite was the case for predatory snoek; annual catches rose from 11 000 tons to 18 000 tons over the last decade (Table 4.6).

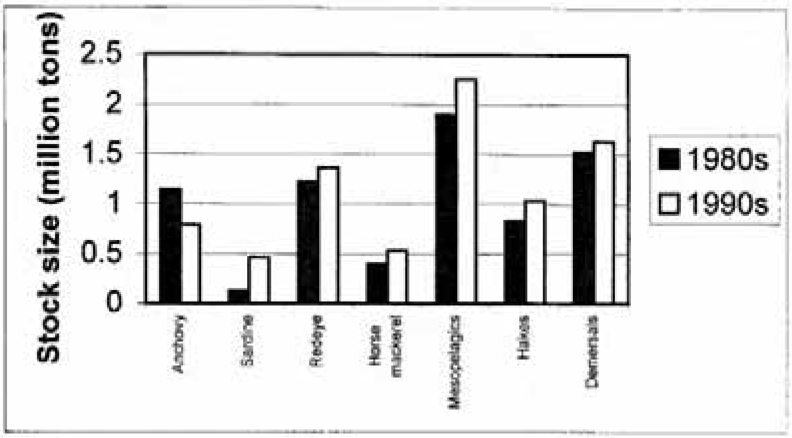
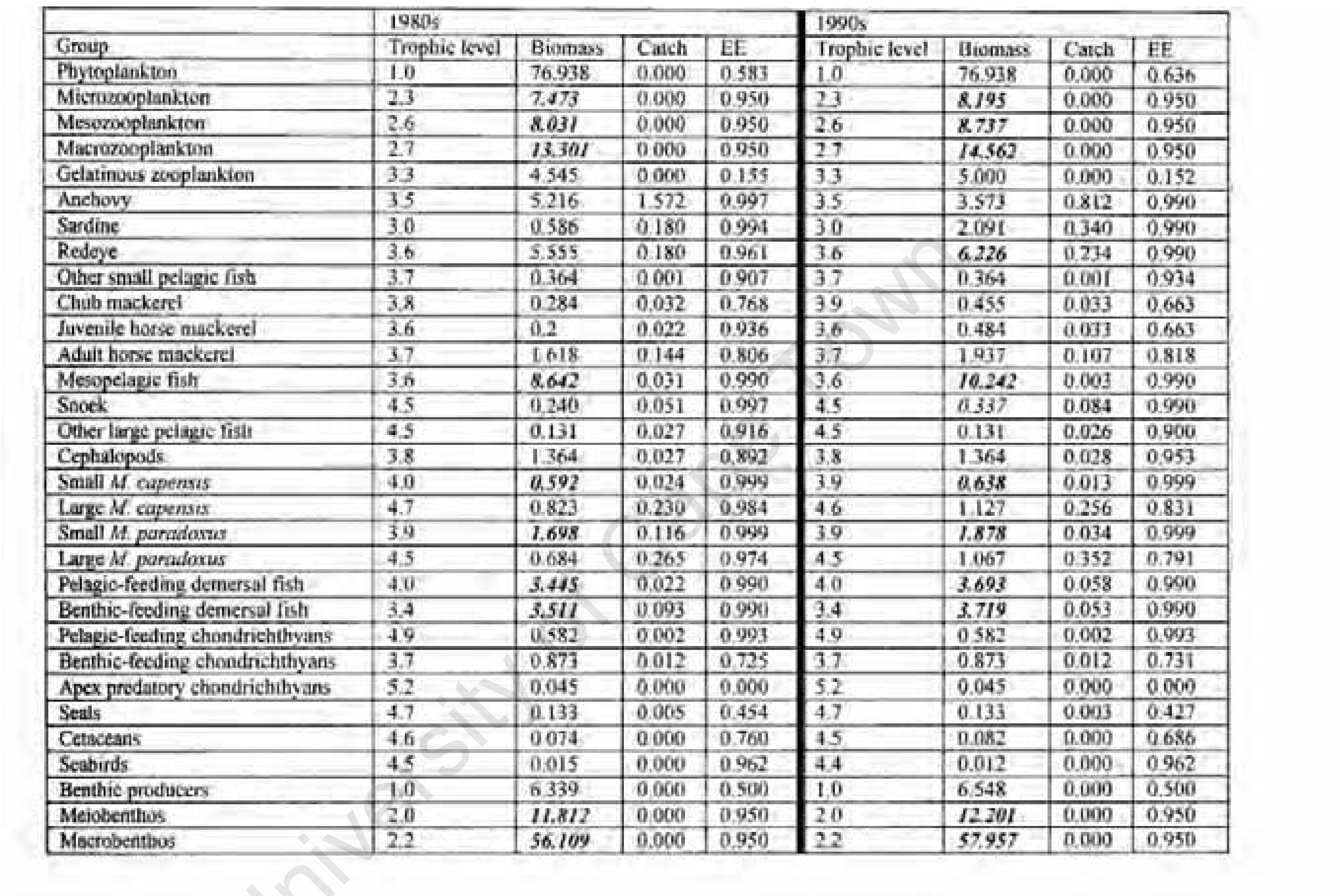


Fig. 4.2 Average annual stock sizes (millions of tons) of important fish in the southern Benguela ecosystem during the 1980s and 1990s. Stock sizes of anchovy, sardine and horse mackerel in both decades, and of redeye in the 1980s, were estimated from data and were input to the *Ecopath* models. Stock sizes of mesopelagic fish, hakes and other demersal fish in both decades, and of redeye during the 1990s, were estimated as the sizes required to support consumption by all groups within the system, given estimates of EE which were input to the models (Table 4.6).

Although groups such as mesopelagic fish and redeye are not caught in large quantities in the southern Benguela ecosystem, they play a potentially large role in the trophic functioning of the southern Benguela ecosystem by providing food for other species. For example, the model estimates that hake consumed 1.1 million tons of mesopelagic fish during the 1990s. This far exceeds earlier estimates by Payne *et al.* (1987) and Bergh *et al.* (1985), and is in agreement with Armstrong and Prosch's (1991) conclusion that annual consumption of lightfish in the southern Benguela ecosystem is considerably larger than initially thought.

Table 4.6 Trophic levels, biomass (t.km^{-2}), catches (t.km^{-2}.y^{-1}) and ecotrophic efficiencies (EEs, expressed as proportions of production either passed up the food web or exported, see Chapter 3, section 3.2) of all boxes in balanced southern Benguela ecosystem models during two decades. Italicized and bold parameters indicate the biomass required to sustain other components of the system, and were estimated using assumed EEs.



	1980s				1990s			
Group	Trophic level	Biomass	Catch	EE	Trophic level	Biomass	Catch	EE
Phytoplankton	1.0	76.938	0.000	0.583	1.0	76.938	0.000	0.636
Microzooplankton	2.3	***7.473***	0.000	0.950	2.3	***8.195***	0.000	0.950
Mesozooplankton	2.6	***8.031***	0.000	0.950	2.6	***8.737***	0.000	0.950
Macrozooplankton	2.7	***13.301***	0.000	0.950	2.7	***14.562***	0.000	0.950
Gelatinous zooplankton	3.3	4.545	0.000	0.155	3.3	5.000	0.000	0.152
Anchovy	3.5	5.216	1.572	0.997	3.5	3.573	0.812	0.990
Sardine	3.0	0.586	0.180	0.994	3.0	2.091	0.340	0.990
Redeye	3.6	5.555	0.180	0.961	3.6	***6.226***	0.234	0.990
Other small pelagic fish	3.7	0.364	0.001	0.907	3.7	0.364	0.001	0.934
Chub mackerel	3.8	0.284	0.032	0.768	3.9	0.455	0.033	0.663
Juvenile horse mackerel	3.6	0.2	0.022	0.936	3.6	0.484	0.033	0.663
Adult horse mackerel	3.7	1.618	0.144	0.806	3.7	1.937	0.107	0.818
Mesopelagic fish	3.6	***8.642***	0.031	0.990	3.6	***10.242***	0.003	0.990
Snoek	4.5	0.240	0.051	0.997	4.5	***0.337***	0.084	0.990
Other large pelagic fish	4.5	0.131	0.027	0.916	4.5	0.131	0.026	0.900
Cephalopods	3.8	1.364	0.027	0.892	3.8	1.364	0.028	0.953
Small *M. capensis*	4.0	***0.592***	0.024	0.999	3.9	***0.638***	0.013	0.999
Large *M. capensis*	4.7	0.823	0.230	0.984	4.6	1.127	0.256	0.831
Small *M. paradoxus*	3.9	***1.698***	0.116	0.999	3.9	***1.878***	0.034	0.999
Large *M. paradoxus*	4.5	0.684	0.265	0.974	4.5	1.067	0.352	0.791
Pelagic-feeding demersal fish	4.0	***3.445***	0.022	0.990	4.0	***3.693***	0.058	0.990
Benthic-feeding demersal fish	3.4	***3.511***	0.093	0.990	3.4	***3.719***	0.053	0.990
Pelagic-feeding chondrichthyans	4.9	0.582	0.002	0.993	4.9	0.582	0.002	0.993
Benthic-feeding chondrichthyans	3.7	0.873	0.012	0.725	3.7	0.873	0.012	0.731
Apex predatory chondrichthyans	5.2	0.045	0.000	0.000	5.2	0.045	0.000	0.000
Seals	4.7	0.133	0.005	0.454	4.7	0.133	0.003	0.427
Cetaceans	4.6	0.074	0.000	0.760	4.5	0.082	0.000	0.686
Seabirds	4.5	0.015	0.000	0.962	4.4	0.012	0.000	0.962
Benthic producers	1.0	6.339	0.000	0.500	1.0	6.548	0.000	0.500
Meiobenthos	2.0	***11.812***	0.000	0.950	2.0	***12.201***	0.000	0.950
Macrobenthos	2.2	***56.109***	0.000	0.950	2.2	***57.957***	0.000	0.950

4.6.2 Zooplankton biomass required

Zooplankton biomass was estimated by the model as the amount required to support predators. In the 1990s it was 10% larger than that required in the 1980s (Fig. 4.3). This result is in agreement with the observed increases in abundance of zooplankton in the region of St Helena Bay, on the west coast of South Africa (Verheye *et al.* 1998). Verheye *et al.* (1998) concluded that there has been a long-term change in the food environment of small pelagic fish in the southern Benguela since the 1950s. Because the model biomass of zooplankton and the stocks of small pelagic fish were larger in the 1990s than in the 1980s, there was more food available to their predators during this decade. This, and the larger catches of small pelagic fish in the 1980s, meant that the southern Benguela ecosystem was more tightly constrained by predators (including the fishery) and availability of food in the 1980s than in the 1990s. This conclusion is explored further in Chapter 10. Tight constraints are also reflected in the higher individual ecotrophic efficiencies of most fish groups in the 1980s compared to those in the 1990s (Table 4.6).

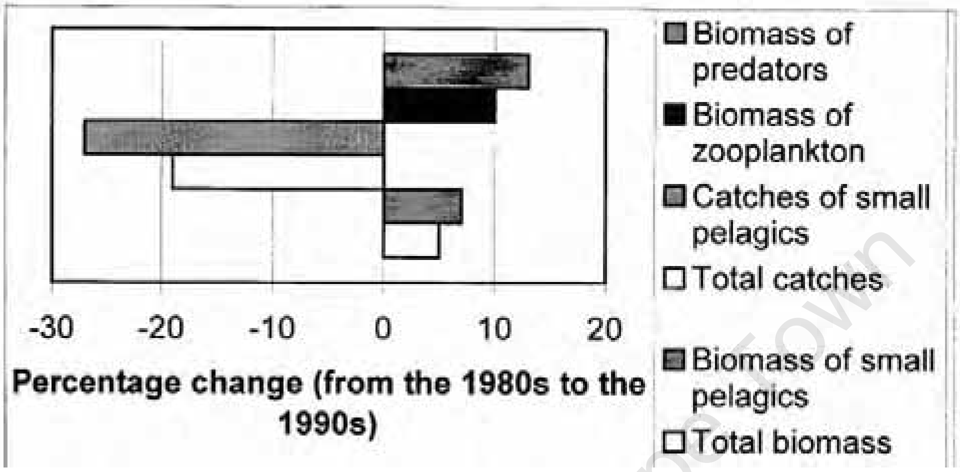


Fig. 4.3 Relative changes in key statistics between the 1980s and 1990s, from *Ecopath* models of the southern Benguela ecosystem.

4.6.3 Trophic levels

In Table 4.6, non-integer trophic levels of boxes in models of the southern Benguela ecosystem during the 1980s and 1990s are tabulated (see Chapter 3, section 3.3.2). Trophic levels of modelled boxes are similar in the two decades, and are represented graphically for the 1980s in Fig. 4.4. Phytoplankton, benthic producers and detritus are located at trophic level 1, whereas the trophic levels of consumers are 1 plus the average trophic level of their prey, weighted by the proportion in the predator's diet. Small pelagic fish occupy trophic levels between 3 and 4, whereas top predators such as seals, seabirds, pelagic-feeding chondrichthyans and apex chondrichthyans are at trophic levels

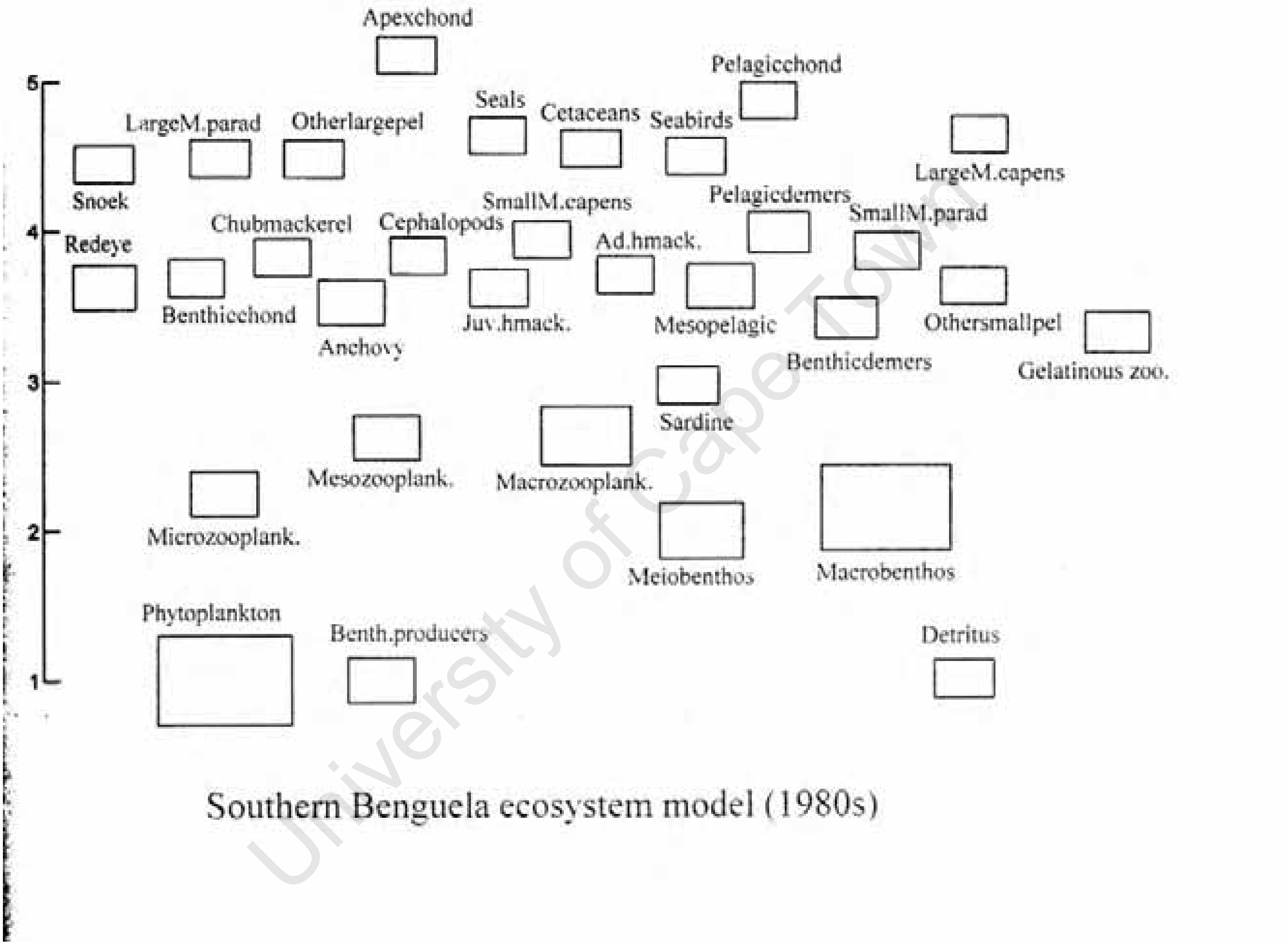


Fig 4.4 Diagram of the boxes in models of the southern Benguela ecosystem during the 1980s, arranged along vertical axis by trophic level. Biomass values are given in Table 4.6.

larger than 4 (Table 4.6). Trophic levels of seals and cetaceans are in the upper part of the range reported by Pauly *et al.* (1998b) for these groups, indicating that they are feeding fairly high in the southern Benguela food web.

Differences in availability of prey meant that top pelagic predators were forced to consume larger quantities of prey lower in the food web during the 1990s than the 1980s, leading to marginally reduced trophic levels of some predators of small pelagic fish. The trophic levels of cetaceans and seabirds were reduced by small amounts in the 1990s (Table 4.6). This is explained by sardine (trophic level of 3.0) becoming more abundant and anchovy (trophic level of 3.5) decreasing from the 1980s to the 1990s. These differences are surprisingly small, being buffered by the increase in the contribution of redeye to the diets of cetaceans and seabirds in the 1990s. Redeye occupies a higher trophic level than anchovy and sardine, at 3.6. Heavy fishing on large chub mackerel during the late 1970s and 1980s left a population in the 1980s dominated by young fish that are largely zooplanktivorous. By the 1990s, the population structure had recovered, with large chub mackerel eating mostly fish, this being indicated by their slightly higher trophic level (Table 4.6).

4.7 FURTHER COMPARISONS

This section explains the construction of mass-balanced models of trophic flows in the southern Benguela ecosystem, gives the sources of data and discusses the motivation behind estimation of parameters used as input to the models. The way has been prepared to compare abundance and trophic interactions between species in the southern Benguela ecosystem in the two decades using more detailed methods of analysis. These comparisons are made in Chapter 5.

CHAPTER FIVE

COMPARING SOUTHERN BENGUELA TROPHIC MODELS DURING TWO DIFFERENT DECADES

ABSTRACT

Similarities in biomass per trophic level, transfer efficiencies, mixed trophic impacts and many other ecosystem attributes suggest that trophic functioning of the southern Benguela ecosystem was similar in the 1980s and 1990s. There are fewer differences between the trophic models of the 1980s and 1990s than might be expected from the large changes in biomass and catches per species or group from the 1980s to the 1990s. However, considering ecosystem-level attributes of an extension of E.P. Odum's ecosystem development theory suggests that the ecosystem was more mature in the 1990s than in the 1980s, when the ecosystem was more tightly constrained by predators of small pelagic fish (including the fishery) and zooplankton food availability. In both decades, fishing took place at relatively low trophic levels. Despite smaller total catches in the 1990s, fishing was more ecologically expensive during the 1990s than in the 1980s because snoek and hake catches were large. There was greater shared niche overlap of small pelagic fish predators in the 1990s than in the 1980s. Mean transfer efficiency was 12%. Transfer of biomass at trophic levels III-V appears to be more efficient in the southern Benguela than in other upwelling ecosystems. Primary production required to sustain catches in the southern Benguela ecosystem is more similar to estimates for open ocean and coastal regions than for other upwelling systems.

5.1 INTRODUCTION

There have been changes in the trophic structure of the southern Benguela ecosystem during the 1980s and 1990s (Chapter 4). In particular, these are related to the abundance of small pelagic fish, which differed between the two decades. As in Chapter 4, here the small pelagic fish group is taken to include five model groups: anchovy, sardine, redeye, juvenile horse mackerel and other small pelagic fish. Small pelagic fish are important prey for larger fish, birds and mammals, and are the source of large mortalities of zooplankton upon which they feed. Many of their fish predators are themselves commercially important species. In addition, the group is of economic importance because anchovy and sardine are the mainstay of the purse seine fishery off the west coast of South Africa. In this chapter, models of the southern Benguela ecosystem during the 1980s and 1990s are compared to assess how observed differences in abundance, catches and dietary composition affected the overall trophic functioning of the southern Benguela ecosystem. The chapter tackles key questions lb and Id by answering i) how mass-balanced models of these two regimes compare and ii) how the trophodynamics of the southern Benguela ecosystem change as there is a shift in dominance of pelagic species. Where applicable, attributes of the southern Benguela ecosystem are compared to those in other systems to put the work into context.

5.2 METHODS

Data described in Chapter 4 were used to construct mass-balanced models of the trophic flows through the southern Benguela ecosystem, one model each for the 1980s and 1990s. *Ecopath* 3.1 (final version, February 1998) was used because debugging of *Ecopath with Ecosim* (version 4) was not complete at the time of running these models (October 1999). However, software errors in the *Ecopath* 3.1 models caused overflow errors in the routines to calculate primary production required. Therefore the alpha version of *Ecopath with Ecosim* 4 was used to obtain results for this routine. Results and discussion are presented together in the sections of this chapter so that the reader is immediately able to view them in the context of findings of previous studies and models of other upwelling systems.

Outputs of the models include estimation of missing parameters (such as biomasses of groups for which there were few reliable data, Chapter 4, Section 4.6) and total flows through the system. Estimated total flows include total consumption, total catches, total production and total system throughput (the sum of total export, total respiration and total flows to detritus; Chapter 3, section 3.3.1), the latter representing the overall size of a system in terms of flow. Aggregation of flows and biomasses into discrete trophic levels are estimated and the transfer efficiencies of biomass between trophic levels are computed (Chapter 3, section 3.3.2). Catches are compared by converting flows in each path (towards the catch of a particular wider range of ecosystems because data requirements are fewer and sufficient data are usually readily available (Whipple *et al.* 2000).

Walters *et al.* (1997) list three major disadvantages of *Ecosim* compared to other modelling approaches. These are i) switching and satiation in predators are not represented, ii) complex but smooth changes in predation rates associated with rapid changes in size structure are not well represented by average interaction rates defined for individual groups in *Ecosim*, and iii) *Ecosim* is dependent on the mass-balance (equilibrium) assumption of *Ecopath.* The latter assumption means that care should be taken to avoid errors in the interpretation of *Ecosim* results, which may occur when results are extrapolated far beyond the equilibrium for which *Ecopath* data are available (Mackinson *et al.* 1997, Walters *et al.* 1997). In other words, *Ecosim* assumes that changes in the fisheries occur within a given regime and that there are no additional regime changes during the simulation period. To accommodate this assumption, separate models of the Southern Benguela ecosystem have been constructed for two periods dominated by different pelagic species.

CHAPTER FOUR

TROPHIC FLOWS THROUGH THE SOUTHERN BENGUELA ECOSYSTEM: MODEL CONSTRUCTION

ABSTRACT

Biomass, production, consumption, catches and diet composition are estimated for 31 living groups in the southern Benguela ecosystem. Mass-balanced models are constructed of the trophic flows in the ecosystem during two periods: 1980-1989 and 1990-1997. In the balanced models, there is a 10% increase in zooplankton biomass between the 1980s and the 1990s, in agreement with observed trends of increased zooplankton abundance off South Africa over the last few decades. Hake biomass required in balanced models is 34% larger than survey estimates for the 1980s and 22% larger in the 1990s. This is not unexpected given the likely undersampling of hake. Anchovy were the dominant pelagic fish in the 1980s whereas sardine abundance increased in the 1990s. Model biomass and mean annual production of five important small pelagic fish groups were larger in the 1990s, and total catches were smaller than in the 1980s. Simulations suggest that the southern Benguela ecosystem was less tightly constrained by predators and availability of zooplankton in the 1990s than in the 1980s. Mesopelagic fish and redeye are not commercially important groups but have high ecotrophic efficiencies in the models, reflecting their important trophic roles in the ecosystem.

4.1. INTRODUCTION

To date, a few attempts have been made to summarize the flow of carbon through the southern Benguela ecosystem, focusing attention on various aspects, namely the pelagic component (Shannon and Field 1985, Bergh *et al.* 1985, Moloney and Field 1985), the planktonic foodweb (Moloney 1992) and comparison of ecosystem properties (Baird *et al.* 1991). In 1989, at a workshop of experts on the different species groups in the Benguela upwelling region, both published and unpublished data were brought together to construct simple input-output carbon budgets of the southern and northern Benguela ecosystems. These data, together with those that have since become available, were used to construct the first *Ecopath* model of the southern Benguela (Jarre-Teichmann *et al.* 1998) and northern Benguela (Shannon and Jarre-Teichmann 1999a and b) ecosystems during the 1980s. Subsequently, the first model of the southern Benguela ecosystem was modified by separating some components for clarity and incorporating new hake data. Based on this revised 1980s model, a second model was constructed of trophic flows through the southern Benguela ecosystem during the 1990s. For this study, these models were refined further by dividing groups such as horse mackerel, hakes, demersal fish and chondrichthyans into size or feeding classes. This helped to reduce problems arising from intra-group cannibalism and major within-group differences in feeding modes. Models were run with updated data. Models of the southern Benguela ecosystem cover the shelf region to approximately the 500m depth contour, extending from 29°S (in the vicinity of the Orange River mouth, the boundary between Namibia and South Africa) southwards along the west coast and eastwards to 28°E (East London). The area covers 220 000 km^2 and incorporates the upwelling area along the west coast, the Agulhas Bank and the south coast of South Africa.

In this chapter, I tackle the first key question 1 a "what are the biomass, production, consumption and catches of the components of the southern Benguela ecosystem during periods of a) anchovy dominance (1980s) and b) sardine dominance (1990s)?" The focus of the work is the trophic functioning of the pelagic ecosystem, using an annual time scale. Temporal changes in biomass of groups such as phytoplankton and zooplankton, operating on shorter time scales (days or weeks), cannot be represented adequately in this model. Therefore no attempt has been made to subdivide plankton groups according to size or species assemblages beyond the few groups used (phytoplankton, micro-, meso- and macro-zooplankton, and gelatinous zooplankton). To model the trophic interactions of these groups in more detail would require that *Ecopath* models be customized for smaller time and space scales. Similarly, the demersal fish assemblages of the Benguela ecosystem were not a primary focus of this study. The generally poorly-known demersal fish component was divided into nine boxes: small shallow water hake *(Merluccius capensis),* large shallow water hake, small deep water hake *(M paradoxus)*, large deep water hake, other benthic-feeding demersal fish, other pelagic-feeding demersal fish, pelagic-feeding chondrichthyans, benthic-feeding chondrichthyans and apex predatory chondrichthyans.

4.2. INPUT DATA

Input data are tabulated and sources given in Appendix A, Tables A.1- A.9. Where parameter values used in the models differ from original estimates, revised values used are indicated and comments provided.

4.2.1 Plankton

Input data for the plankton groups are presented in Table A.1.

Estimating zooplankton biomass in the 1990s
Over the past few decades, there have been changes in abundances of zooplankton in the St Helena Bay area (Verheye and Richardson 1998, Verheye *et al.* 1998). Between 1951 and 1996, zooplankton abundance increased by at least an order of magnitude in all size classes. The biomass of copepods (including some large calanoid copepods that are macrozooplankton) increased by about 60% between the late 1980s and 1995/6 (Verheye *et al.* 1998). There was uncertainty about how to convert abundance (numbers) to biomass (tonnage) for the various zooplankton components of the whole southern Benguela sub-system. Therefore, the model was used to estimate biomass for micro-, meso- and macro-zooplankton from the production required to sustain other groups in the system during the 1990s.

It is likely that the biomass of gelatinous zooplankton also increased between the 1980s and 1990s; tunicates were more abundant in the 1990s than earlier in the century (Verheye *et al.* 1998). Since little gelatinous zooplankton seems to be required to support other groups within the system (ecotrophic efficiency was 4% in preliminary models of the 1980s), the model was not used to estimate biomass of this group. Instead, gelatinous zooplankton biomass was increased by 10% from the 1980s to the 1990s, the estimated increase required for other zooplankton groups in the model.

4.2.2 Small pelagic fish

The small pelagic fish component consists mainly of clupeoids. Clupeoids belong to the order Clupeiformes, comprising two groups: clupeids (sardines, herrings, round herrings and sardinellas) and engraulids (anchovies). Off southern Africa, commercially important purse seine fisheries for clupeoids have been in operation since the 1940s. Large catches of sardine *Sardinops sagax* (locally known as "pilchard") were made in the 1950s and 1960s, but Namibian and South African sardine fisheries subsequently collapsed. Anchovy *Engraulis capensis* became the mainstay of the purse-seine fishery off South Africa in the mid-1980s, whereas anchovy remained at low levels off Namibia. By the 1990s, abundance of anchovy in the southern Benguela ecosystem was fluctuating and declining, whereas sardine biomass was increasing (Fig. 4.1). This study focuses in particular on the role of clupeoids in the southern and northern Benguela sub-systems.

Four groups of small pelagic fish were modelled: in the southern Benguela models, these were anchovy, sardine, redeye *Etrumeus whiteheadi* and other small pelagic fish, the latter including saury (Scomberesocidae), flying fish (Exocoetidae) and other less common species. In the northern Benguela ecosystem, redeye is scarce and is included in the other small pelagic fish box. The fourth small pelagic fish box in the northern Benguela model is the pelagic goby *Sufflogobius bibarbatus.*

Table A.2 contains input data for small pelagic fish in models of the southern Benguela ecosystem. Considering the zooplanktivorous diets of small pelagic fish, assimilation efficiency was assumed to be 65% (Jarre-Teichmann *et al.* 1998).

and large (>20 cm) horse mackerel in research trawls was estimated for the 1980s and 1990s separately.

$$W = 0.0093685 \text{ x } L^{29'0'}$$

...equation 4.1

where W is weight in cm and L is total length in cm.

In the 1980s, 1% and 3% of horse mackerel biomass in demersal surveys consisted of small horse mackerel on the south and west coasts respectively. During the 1990s, 9% and 11% of such biomass was of small horse mackerel on the south and west coasts. To what extent the Namibian and South African horse mackerel stocks are distinct is uncertain (Crawford *et al.* 1987), and the increased contribution of juveniles to biomass on the west coast in the 1990s may be explained by southward migration of Namibian horse mackerel (E. Klingelhoeffer, National Marine Information and Research Centre, Namibia, pers. comm., cited by Barange *et al.* 1998). Because demersal trawls are likely to miss the pelagic portion of the stock, juveniles are likely to be under-represented. Small horse mackerel were considered to contribute at least 10% of total horse mackerel biomass in the 1980s, and double this during the 1990s (Table A.3). These fractions are similar to that calculated from Kinloch *et al's* (1986) VPA estimates; fish less than 2 years comprised 17% of total horse mackerel biomass.

4.2.4 Hakes

The Cape hakes *Merluccius capensis* (shallow water) and *M paradoxus* (deep water) are of great commercial importance in the Benguela region. Because cannibalism is common in the two species, and because small *M paradoxus* are eaten by large *M capensis,* hake were modelled as four separate groups according to size and species. Small hake were those aged 0-2 years, and large hake were aged 3 years and older. Biomass of small (0-2 year olds) and large (3 years and older) hake (both species combined) for 1980-1989 and 1990-1996 was estimated from production models (Leslie 1996). Combined biomass was separated for the west and south coast populations. More detailed data were available for the west coast than for the south coast, so that different methods of separation were used for the two coasts.

For the west coast, species-specific numbers per age-class and year were derived from numbers-at-length and age-at-length keys available for 1985-1988 and 1990-1994. The mean weight-at-age of hake was used to calculate the proportion by mass of each species per age class. Proportions were multiplied by the biomass on the west coast to give biomass by age group, species and decade for the west coast.

For the south coast, based on estimates of biomass by species for both the 0-200 m and 0-500 m depth strata from surveys between 1988-1995, the ratio of biomass of *M capensis* to *M paradoxus* was estimated to be 19:1. Using survey data for 1988-1997 for the 0-200 m-isobath region of the south coast, Leslie (1998b) calculated mass-at-age for both species combined. This shows that 9% of south coast hake biomass is in the age class 0-2 years, and 91% in the age class 3 years and older. Using the relative proportions by species and by age class, the overall proportions were calculated and used to assign south coast hake biomass into that per age group, species and decade. Summing west and south coast values, biomass estimates by species and size groups were calculated for hake off South Africa (Table A.6).

4.2.5 Other demersal fish and chondrichthyans

Other demersal fish

Biomass of other demersal fish was estimated to be 230 000 t on the Agulhas Bank for 1986-1992 (Japp *et al.* 1994), comparable to 175 000 t when biomass indices from 1986-1990 are summed over applicable species (Badenhorst and Smale 1991; Smale and Badenhorst 1991). Many of these indices are thought to be underestimates of biomass because during surveys gear was not specifically rigged for species such as sole, and gear avoidance is a fundamental problem. Further, many of the species occur over untrawlable grounds and would have been missed during surveys (Badenhorst and Smale 1991). Species such as Agulhas sole *Austroglossus pectoralis* are patchily distributed, making indices unreliable as estimates of biomass (Badenhorst and Smale 1991). At a workshop in 1989, held under the auspices of the Benguela Ecology Programme and at which available data series were summarised into ecosystem spreadsheet models (see also Chapter 7, section 7.1), biomass of other demersal fish in the southern Benguela ecosystem was estimated to be 232 061 t. This is likely to have been a gross underestimate considering indices are nearly this for the south coast alone.

Initially, demersal fish (excluding hake) were grouped into one box. However, intra-box consumption (seen as cannibalism) was high and it was advisable to split the group into two, following the trophic groupings of Meyer and Smale (1991a and b). Pelagic-feeding demersal fish include the following non-commercial species: buttersnoek (ribbonfish) *Lepidopus caudatus,* Cape John Dory *Zeus capensis,* southern rover *Emmelichthys nitidus nitidus,* pencil cardinal *Epigonus denticulatus,* windtoy *Spicara axillaris,* cutlass fish *Trichiurus lepturus* and jutjaw *Parascorpis typus* (Meyer and Smale 1991a). The major commercially valuable pelagic feeder is the angelfish *Brama brama.*

Meyer and Smale's (1991b) benthic-feeding demersal fish group includes piscivorous species and those feeding on benthic invertebrates: Cape gurnard *Chelidonichthys capensis,* African gurnard *Trigloporus 1. africanus,* bank steenbras *Chirodactylus grandis,* hairy conger *Bassanago albescens,* lesser gurnard *Chelidonichthys queketti,* redspotted tonguefish *Cynoglossus zanzibarensis,* beaked sandfish *Gonorhynchus gonorhyncus,* spinenose horsefish *Congipodus spinifer,* smooth horsefish *Congiopodus torvus,* large-scaled rattail *Coelorinchus fasciatus,* smooth-scaled rattail *Malacocephalus laevis* and jacopever *Helicolenus dactylopterus.* In addition, commercially important species such as Agulhas *sole,* west coast sole *A. microlepis,* kingklip *Genypterus capensis,* monkfish *Lophius sp.* and panga *Pterogymnus laniarius* are benthic-feeders.

Table A.7 contains input data for pelagic-feeding and benthic-feeding demersal fish.

Chondrichthyans

Initially (Jarre-Teichmann *et al.* 1998, Shannon and Jarre-Teichmann 1999b, Shannon *et al.* 2000), a single chondrichthyan group was used. However, intra-group cannibalism and the divergent diets of species belonging to different feeding guilds, led to the group being divided into three in accordance with Penney *et al.* (1991a and b): benthic and pelagic feeders (Table 4.1) and apex predators (Table A.7). Great and diet are available for all species breeding off South Africa and for the more numerous migrant species feeding in the sub-system (Crawford *et al.* 1991b). In quantitative trophic terms (their consumption and their contribution as food to other animals), seabirds are relatively unimportant in the southern Benguela (Bergh *et al.* 1985). However, like marine mammals, seabirds may play an important role in the stabilisation of trophic flows by preying on a variety of small fish, and switching prey according to availability (Bergh *et al.* 1985).

4.2.7 Benthos

Biomass information on benthic communities deeper than 20 m in the southern Benguela sub-system is limited. Biomass of the benthos is likely to be limited by the hypoxic conditions along the west coast of South Africa. Christie (1975) and Field (1971) studied the composition and community structure of benthos in the region of Lambert's Bay on the west coast of South Africa (10-200m), and False Bay (10-120m), but did not estimate biomass. Therefore, biomass required by the southern Benguela system was estimated using *Ecopath,* based on P/B and P/Q ratios from other systems (Jarre-Teichmann *et al.* 1998, Table A.9).

4.2.8 Detritus

The non-living detritus group receives inputs (faecal deposits, dead organisms, decaying remains as "other mortalities" and un-assimilated food) from all other model groups. *Ecopath* does not require other information. The group was not split further (e.g. into carcasses, POC, DOC) due to lack of data from the region.

4.3 CATCHES

Catches in the southern Benguela ecosystem during the 1980s and 1990s are tabulated by group (Table 4.2). Because a less detailed breakdown of catches according to gear was available in the 1980s, and so that scenarios of altered harvesting between the two decades were comparable, catches were separated into those using the following six gear types: purse seine nets, demersal trawls, midwater trawls, long lines, lines, other (includes recreational, beach seine, set nets, squid jigs etc.).

4.3.1 Catches of hake

Total catches of hake of both species averaged close to 140 000 t in the southern Benguela ecosystem during the 1980s (Punt 1994) and 144 100 t between 1990 and 1996 (Leslie 1998a and b). Hake catches were allocated to the two size classes, according to Leslie 1998a and Leslie 1998b for the west and south coasts respectively. Of the large hake caught on the south coast, 33% of total catches on the south coast were adult *M paradoxus* (R.W. Leslie, MCM, pers. comm.). Research cruise data (unpublished data of MCM) collected between the 0 and 200 m isobaths on the south coast (the main area of fishing on the south coast) in autumn 1988-1997, show that the ratio of *M capensis* biomass to *M paradoxus* biomass is 0.95:0.05. This ratio was used to allocate catches of hake by species to the small size class on the south coast. It was assumed that all small hake caught on the west coast are *M paradoxus*. For the west coast, research survey data from summer cruises showed that the relative proportions of the two hake species on the west coast were 25% *M capensis* and 75% *M paradoxus* for both decades. This ratio was assumed for total hake caught by commercial vessels on the west coast, i.e. 75% of total catches are *M paradoxus* (includes small and large), 25% are *M capensis* (large fish only). Combining estimates for the west and south coasts, total annual catches of hake by species and decade were calculated. Catches by gear were available for both species combined, and for the two coasts separately. Based on combined hake catches by gears on the west and south coasts (Leslie 1998a and b), catches were apportioned according to gear type (Table 4.2). For simplicity, longline and handline catches (together comprising less than 2% of total catches) were considered to be of hake in the large size classes. Reported catches of hake caught in inshore trawls on the south coast were increased to account for the estimated discard of 24% of the hake catch in this fishery (Anonymous 1997, Table 4.2).

4.4 DIET DATA

Diet compositions based on available data (Table 4.3) are tabulated (Table 4.4). Because many of the species present in high abundance in the southern Benguela are opportunistic feeders, there is a large amount of overlap in diet composition (Crawford *et al.* 1989).

4.4.1 Sardine and anchovy diets

Louw *et al.* (1998) found that in mixed shoals off the west coast of South Africa, anchovy and sardine eat similar prey (crustacean eggs and nauplii and copepods), but that sardine consumed significantly smaller prey than anchovy. The modal size class of prey consumed by anchovy was 600-900 pm, compared to 300 p.m for sardine. Dietary differences are probably due to a combination of factors: differences in gill raker morphology, individual position within mixed shoals and feeding behaviour. Sardine is primarily a filter feeder (van der Lingen 1994, 1995) whereas anchovy is primarily a particulate feeder (James and Findlay 1989). Louw *et al.* (1998) concluded that competition between anchovy and sardine for food might be limited.

4.5 BALANCING THE MODELS

Modelling using the raw input data gave ecotrophic efficiencies greater than unity for many of the model ecosystem components. This indicated that model production of these groups was insufficient to support the model consumption by other groups, and in some cases the catches. Since much uncertainty surrounded many of the estimates of diet composition, especially those for the 1990s, the models were mostly balanced by adjusting the diets of some groups.

4.6 SUMMARY OF SOUTHERN BENGUELA MODELS

4.6.1 Biomass and production offish

The small fish group is taken to include five model groups: anchovy, sardine, redeye, juvenile horse mackerel and other small pelagic fish. During the 1980s, anchovy was the dominant small pelagic fish in the southern Benguela ecosystem (Fig. 4.2). By the 1990s, the size of the anchovy population had decreased and populations of sardine, redeye, horse mackerel and both species of hake had increased in size (Fig. 4.2 and Table 4.6). Summed biomasses of small pelagic fish (anchovy, sardine, redeye, juvenile horse mackerel and other small pelagic fish) increased from 2.62 million tons in the 1980s to 2.80 million tons in the 1990s (Fig. 4.3. Mean annual production by these five small pelagic groups was 3.1 million tons in the 1980s and 3.3 million tons in the 1990s, half accounted for by anchovy and sardine. Shannon and Field (1985) estimated that a maximum biomass and annual production of 2 million tons of small pelagic fish could be supported in the southern Benguela ecosystem. Accounting for the smaller area (Orange River to Cape Agulhas) considered by Shannon and Field (1985), and their use of a lower conversion ratio from carbon to wet mass, models in this study support their estimates.

Moloney and Field (1985) estimated that only 25% of pelagic fish production off southern Africa is exploitable by humans. This is equivalent to 775 000 ty $^{-1}$ in the 1980s and 825 000 ty^{-1} in the 1990s. However, Moloney and Field (1985) did not recommend full exploitation of pelagic fish production because areas such as the Agulhas Bank are important for spawning pelagic fish and are likely to be important buffers against the large catches made off the west coast of South Africa. Total annual catches of the five small pelagic fish groups were larger in the 1980s (430 100 tons) than in the 1990s (312 400 tons) (Fig. 4.3). The opposite was the case for predatory snoek; annual catches rose from 11 000 tons to 18 000 tons over the last decade (Table 4.6).

larger than 4 (Table 4.6). Trophic levels of seals and cetaceans are in the upper part of the range reported by Pauly *et al.* (1998b) for these groups, indicating that they are feeding fairly high in the southern Benguela food web.

Differences in availability of prey meant that top pelagic predators were forced to consume larger quantities of prey lower in the food web during the 1990s than the 1980s, leading to marginally reduced trophic levels of some predators of small pelagic fish. The trophic levels of cetaceans and seabirds were reduced by small amounts in the 1990s (Table 4.6). This is explained by sardine (trophic level of 3.0) becoming more abundant and anchovy (trophic level of 3.5) decreasing from the 1980s to the 1990s. These differences are surprisingly small, being buffered by the increase in the contribution of redeye to the diets of cetaceans and seabirds in the 1990s. Redeye occupies a higher trophic level than anchovy and sardine, at 3.6. Heavy fishing on large chub mackerel during the late 1970s and 1980s left a population in the 1980s dominated by young fish that are largely zooplanktivorous. By the 1990s, the population structure had recovered, with large chub mackerel eating mostly fish, this being indicated by their slightly higher trophic level (Table 4.6).

4.7 FURTHER COMPARISONS

This section explains the construction of mass-balanced models of trophic flows in the southern Benguela ecosystem, gives the sources of data and discusses the motivation behind estimation of parameters used as input to the models. The way has been prepared to compare abundance and trophic interactions between species in the southern Benguela ecosystem in the two decades using more detailed methods of analysis. These comparisons are made in Chapter 5.

CHAPTER FIVE

COMPARING SOUTHERN BENGUELA TROPHIC MODELS DURING TWO DIFFERENT DECADES

ABSTRACT

Similarities in biomass per trophic level, transfer efficiencies, mixed trophic impacts and many other ecosystem attributes suggest that trophic functioning of the southern Benguela ecosystem was similar in the 1980s and 1990s. There are fewer differences between the trophic models of the 1980s and 1990s than might be expected from the large changes in biomass and catches per species or group from the 1980s to the 1990s. However, considering ecosystem-level attributes of an extension of E.P. Odum's ecosystem development theory suggests that the ecosystem was more mature in the 1990s than in the 1980s, when the ecosystem was more tightly constrained by predators of small pelagic fish (including the fishery) and zooplankton food availability. In both decades, fishing took place at relatively low trophic levels. Despite smaller total catches in the 1990s, fishing was more ecologically expensive during the 1990s than in the 1980s because snoek and hake catches were large. There was greater shared niche overlap of small pelagic fish predators in the 1990s than in the 1980s. Mean transfer efficiency was 12%. Transfer of biomass at trophic levels III-V appears to be more efficient in the southern Benguela than in other upwelling ecosystems. Primary production required to sustain catches in the southern Benguela ecosystem is more similar to estimates for open ocean and coastal regions than for other upwelling systems.

5.1 INTRODUCTION

There have been changes in the trophic structure of the southern Benguela ecosystem during the 1980s and 1990s (Chapter 4). In particular, these are related to the abundance of small pelagic fish, which differed between the two decades. As in Chapter 4, here the small pelagic fish group is taken to include five model groups: anchovy, sardine, redeye, juvenile horse mackerel and other small pelagic fish. Small pelagic fish are important prey for larger fish, birds and mammals, and are the source of large mortalities of zooplankton upon which they feed. Many of their fish predators are themselves commercially important species. In addition, the group is of economic importance because anchovy and sardine are the mainstay of the purse seine fishery off the west coast of South Africa. In this chapter, models of the southern Benguela ecosystem during the 1980s and 1990s are compared to assess how observed differences in abundance, catches and dietary composition affected the overall trophic functioning of the southern Benguela ecosystem. The chapter tackles key questions lb and Id by answering i) how mass-balanced models of these two regimes compare and ii) how the trophodynamics of the southern Benguela ecosystem change as there is a shift in dominance of pelagic species. Where applicable, attributes of the southern Benguela ecosystem are compared to those in other systems to put the work into context.

5.2 METHODS

Data described in Chapter 4 were used to construct mass-balanced models of the trophic flows through the southern Benguela ecosystem, one model each for the 1980s and 1990s. *Ecopath* 3.1 (final version, February 1998) was used because debugging of *Ecopath with Ecosim* (version 4) was not complete at the time of running these models (October 1999). However, software errors in the *Ecopath* 3.1 models caused overflow errors in the routines to calculate primary production required. Therefore the alpha version of *Ecopath with Ecosim* 4 was used to obtain results for this routine. Results and discussion are presented together in the sections of this chapter so that the reader is immediately able to view them in the context of findings of previous studies and models of other upwelling systems.

Outputs of the models include estimation of missing parameters (such as biomasses of groups for which there were few reliable data, Chapter 4, Section 4.6) and total flows through the system. Estimated total flows include total consumption, total catches, total production and total system throughput (the sum of total export, total respiration and total flows to detritus; Chapter 3, section 3.3.1), the latter representing the overall size of a system in terms of flow. Aggregation of flows and biomasses into discrete trophic levels are estimated and the transfer efficiencies of biomass between trophic levels are computed (Chapter 3, section 3.3.2). Catches are compared by converting flows in each path (towards the catch of a particular group) to primary production equivalents using the product of catch, production/consumption and the proportion of each group in the path in the diets of the other groups (Chapter 3, section 3.3.3). This allows the ecological cost of fishing to be compared across groups at different trophic levels. Fishing and predation mortalities are compared between species and decades. Relative impacts of each group on all other groups in the system are quantified using mixed trophic impact analysis (Chapter 3, section 3.4.1), and serve to highlight those groups playing important roles in the system, and those having only small effects on other system components. Finally, the degree of overlap is considered between predators consuming common prey resources, and between prey groups having common predators. Comparing these varied outputs of the models of the 1980s and 1990s allows assessment of the trophic functioning of the southern Benguela ecosystem during two decades dominated by different pelagic fish species.

5.3 CONSUMPTION

Relative consumption by the various groups highlights differences between periods (Fig. 5.1 a and b). In the 1980s, anchovy, redeye and mesopelagic fish consumed the greatest proportions of production. Relative consumption by anchovy decreased in the 1990s, and that by redeye, horse mackerel, mesopelagic fish and sardine increased. Consumption by marine mammals and birds was small in both decades.

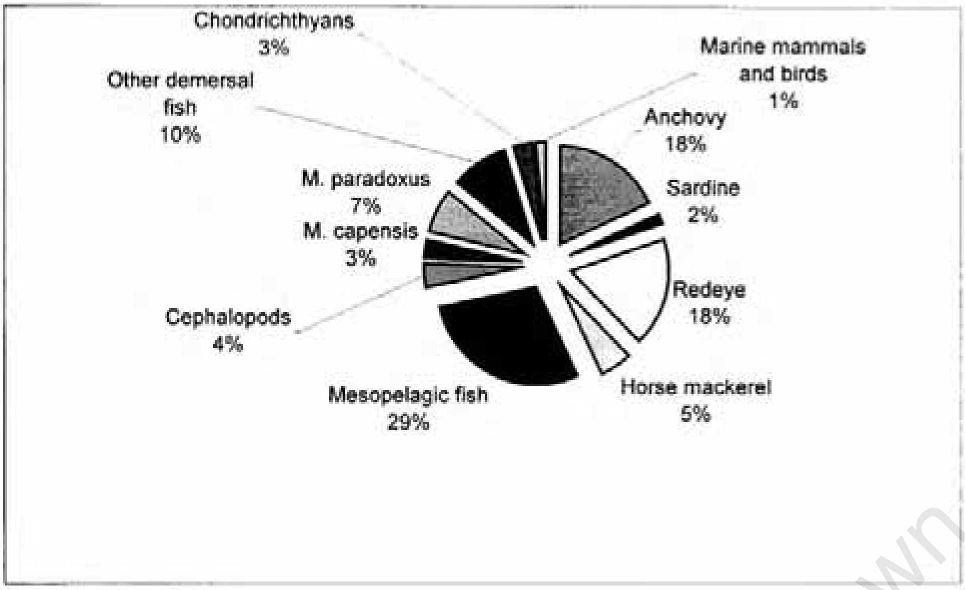


Fig. 5.1a Relative consumption by fish and top predators estimated by the mass-balanced **model** of the southern Benguela ecosystem in the 1980s.

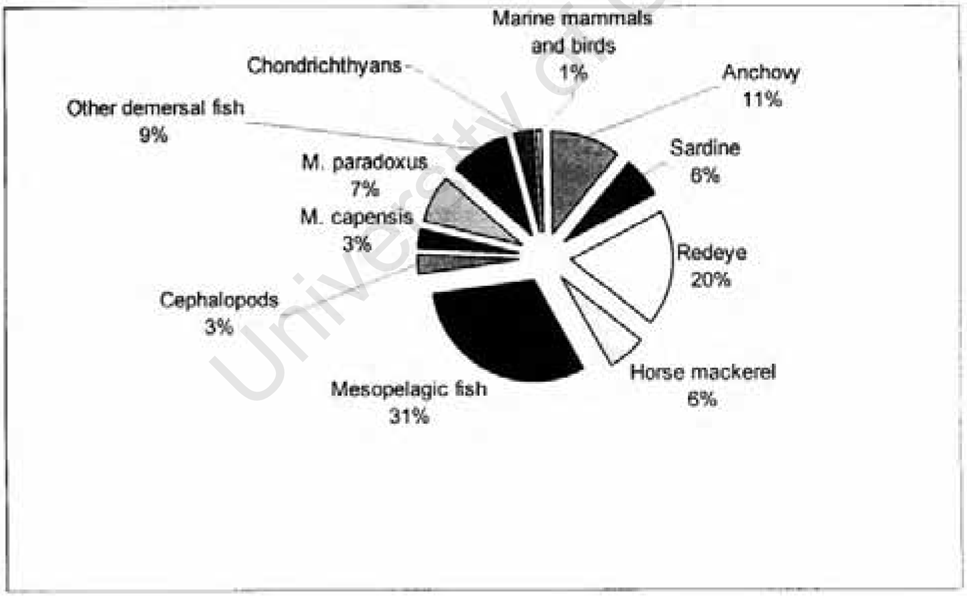


Fig. 5.1b Relative consumption by fish and top predators estimated by the mass-balanced **model of** the southern Benguela ecosystem in the 1990s.

In models of the 1980s and 1990s respectively, predators consumed 11.9 $t.km^{-2}.y^{-1}$ and 13.4 $t.km^{-2}.y^{-1}$ of small pelagic fish, corresponding to 84% and 88% of their production. Hake were the dominant consumers of small pelagic fish production, followed by other demersal fish (Fig. 5.2 a and b). Model estimates indicate that consumption of anchovy by hake amounted to 70% of the anchovy caught during the 1980s. This differs from Field *et al.*'s (unpublished) estimate that hake consumed twice the quantity of anchovy taken by the fishery during the 1980s. Estimates of diet and stock sizes of many of the model groups have been revised since Field *et al.*'s (unpublished) preliminary model, accounting for the differences between their results and those presented here. This points out sensitivity of results to best estimates that may not be accurate.

Adult horse mackerel, large pelagic fish (including snoek), cephalopods, marine mammals and seabirds all consumed similar proportions of small pelagic fish production (between 8% and 13%). The small proportion of small pelagic fish production consumed by seabirds (8%) in the southern Benguela ecosystem is at the top of the 5-8% range estimated for seabirds in the North Sea (Bailey 1986), and much less than the 20-30% estimate of Furness (1982) and MacCall (1982) for seabirds in other upwelling systems. Of the 9% of small pelagic fish production that is consumed by marine mammals, consumption by seals accounted for two thirds of this, reconfirming Bergh *et al.*'s (1985) suggestion that whales and dolphins play a small trophic role in the southern Benguela ecosystem.

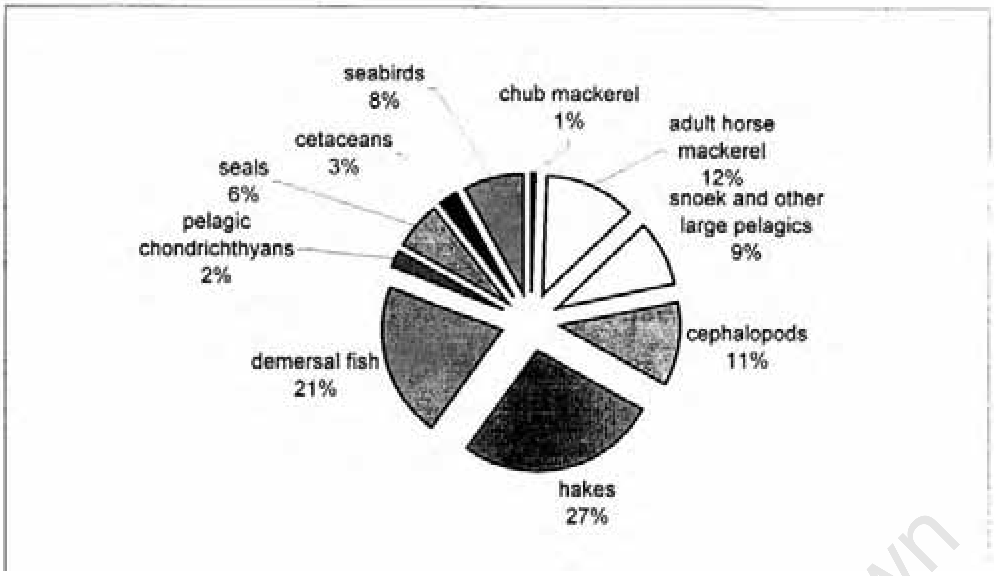


Fig. 5.2a Relative consumption of small pelagic fish production by predators, estimated by the mass-balanced model of the southern Benguela ecosystem in the 1980s.

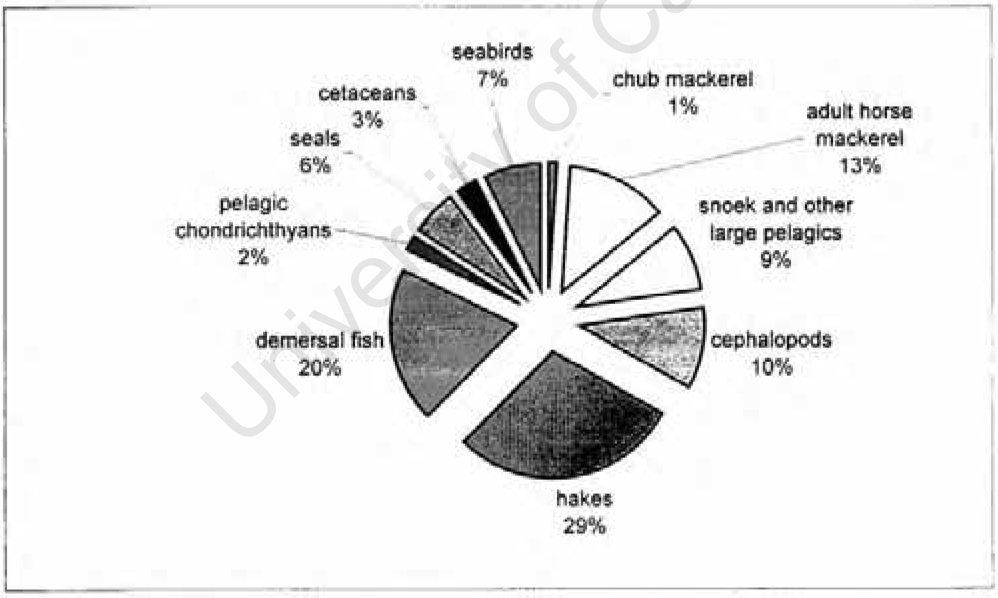


Fig. 5.2b Relative consumption of small pelagic fish production by predators, estimated by the mass-balanced model of the southern Benguela ecosystem in the 1990s.

5.4 TROPHIC AGGREGATION

It is possible to aggregate components of a system into discrete abstract trophic levels, so that producers are on the first trophic level (TL), primary consumers on TL 2, secondary consumers on TL 3 and so on (Ulanowicz 1995, based on Lindeman 1942). Small proportions of the throughput at TL II, V, VI, VII and VIII were consumed by predators, whereas at intermediate trophic levels III and IV, larger proportions went to predation (Fig. 5.3). Microzooplankton, having a high respiration rate, accounted for the large proportion of throughput going to respiration at TL II. Predation and flows to detritus were negligible at TL IX, where top predators (apex chondrichthyans, seals, cetaceans and seabirds) are placed.

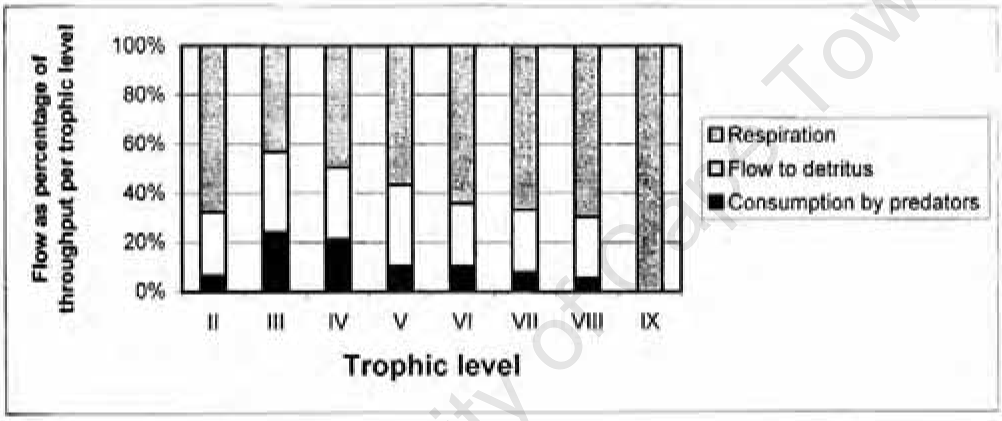
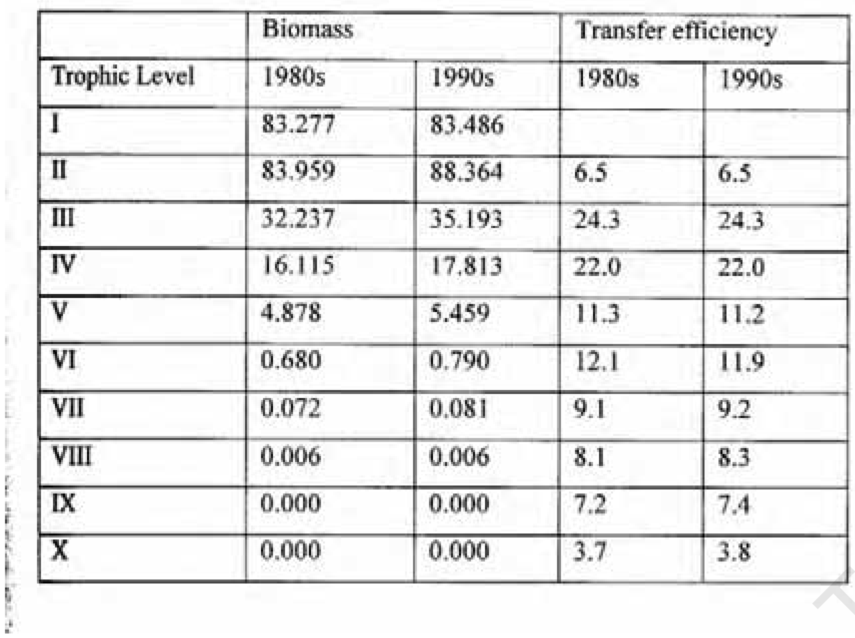


Fig. 5.3 The fate of throughput at each discrete trophic level in the model of the southern Benguela ecosystem in the 1980s, expressed as the percentage of throughput used for respiration, flow to detritus and consumption by predators.

Transfer efficiency (TE; Chapter 3, section 3.3.2) is the fraction of total throughput at a discrete trophic level (TL) that is either exported or transferred to another trophic level (through consumption). TEs between trophic levels and biomass at each trophic level are almost identical in both decades (Table 5.1).

Table 5.1 Biomass (t.km $^{-2}$) and transfer efficiency (%) at each discrete trophic level in models of the southern Benguela ecosystem in the 1980s and 1990s.



	Biomass		Transfer efficiency	
Trophic Level	1980s	1990s	1980s	1990s
I	83.277	83.486		
II	83.959	88.364	6.5	6.5
III	32.237	35.193	24.3	24.3
IV	16.115	17.813	22.0	22.0
V	4.878	5.459	11.3	11.2
VI	0.680	0.790	12.1	11.9
VII	0.072	0.081	9.1	9.2
VIII	0.006	0.006	8.1	8.3
IX	0.000	0.000	7.2	7.4
X	0.000	0.000	3.7	3.8

In upwelling ecosystems, TEs are generally low (Jarre-Teichmann 1992, Christensen and Pauly 1993, Jarre-Teichmann and Pauly 1993, Jarre-Teichmann and Christensen 1998a), less than the mean of 10% calculated from 48 models of aquatic ecosystems (Christensen and Pauly 1995). This is true for flows through TL II (consumption of phytoplankton by microzooplankton) in the southern Benguela ecosystem. Only 55% and 60% of net primary production is consumed by herbivores in the southern Benguela ecosystem during the 1980s and 1990s respectively. Although larger than the 39% estimated previously (Baird *et al.* 1991), these efficiencies are still much smaller than those in the Peruvian upwelling system and may be explained by the mismatch in space and time between phytoplankton blooms and zooplankton production (Baird *et al.* 1991). Results agree with the work of Shannon and Field (1985), who estimated that 44%-73% of phytoplankton production was not consumed by zooplankton or fish. Because of the nature of the pulsed upwelling events in the southern Benguela ecosystem, the migration of pelagic fish through the system, and because some phytoplankton are of unsuitable quality or size, pelagic fish are probably only able to utilise about 12.5% of primary production in the system (Shannon and Field 1985).

Walker and Peterson (1991) estimated that copepods consume between 12% and 42% of primary production along the productive west coast of South Africa. By comparison, this study of the southern Benguela sub-system, covering a larger region and including the productive upwelling regions along the west coast as well as the less productive Agulhas Bank and south coast areas, shows that mesozooplankton consume only 4-5% of primary production and that microzooplankton consumed 49% and 53% of total modelled primary production in the 1980s and 1990s respectively. In their preliminary carbon budget for the southern Benguela ecosystem, Walker and Peterson (1991) estimated that 75% of phytoplankton production was lost from the euphotic zone as detritus. By comparison, models suggest that only 45% and 39% of phytoplankton production is lost in the form of detritus and sedimentation from the southern Benguela ecosystem during the 1980s and 1990s respectively. This may suggest more efficient use of phytoplankton than previously thought. On the other hand, it is likely that a portion of the phytoplankton production that is not consumed by groups within the system is advected out of the system and its fate is not described further.

Transfer of biomass at TL III-V appears to be more efficient in the southern Benguela ecosystem than in other upwelling ecosystems (Jarre-Teichmann *et al.* 1998). The geometric mean TE of biomass for TL II-IV in the southern Benguela system was 15.1% in both decades. TEs at each TL are all greater than means estimated by Christensen and Pauly (1995) for upwelling ecosystems. These large values indicate a "bottleneck" of flows at the levels of zooplankton (TL II and III) and small pelagic fish (TL III and IV), pointing to the groups as being important in the overall trophic structure of the ecosystem. The high TEs also indicate that the southern Benguela ecosystem may be food-limited.

This is in agreement with the suggestion by Shannon and Field (1985) that at large stock sizes, anchovy and sardine may be food-limited in the southern Benguela ecosystem (see section 4.6.1). During both the 1980s and 1990s, the geometric mean transfer efficiency for TL II-VIII (containing biomass > 0.000 t.km^{-2}) was 12.0%, close to Baird *et al.'s* (1991) estimate of 12.1%. Biomass was concentrated in trophic levels I and II, i.e. the producer (phytoplankton) and detritus level (TL 1) and the primary consumer (microzooplankton) level gable 5.1). This is true of many ecosystems such as coral reefs (e.g. Alino *et al.* 1993, Opitz 993), coastal regions (e.g. De Paula E Silva *et al.* 1993, Vega-Cendejas *et al.* 1993), shelf Fosystems (e.g. Arrenguin-Sanchez *et al.* 1993) and other upwelling systems (e.g. Jane-eichmann and Christensen 1998a).

5.5 SUMMARY STATISTICS AND FLOWS

5.5.1 Putting the southern Benguela ecosystem into the global picture

Five upwelling systems, including the southern Benguela during the 1980s, were ranked according to primary production, biomass, system throughput and catches, all measures of ecosystem size (Jarre-Teichmann and Christensen 1998a, Jarre-Teichmann *et al.* 1998). In terms of biomass and throughput, the southern Benguela system was most similar to the Peruvian system during the 1970s, after the collapse of the Peruvian anchovy *Engraulis ringens* fishery. The southern Benguela ecosystem ranked between the Peruvian and northern Benguela systems in terms of primary production (Jarre-Teichmann *et al.* 1998). However, the southern Benguela ecosystem is larger in biomass and catches, has a higher total system throughput and is more productive than the Californian system (Jarre-Teichmann *et al.* 1998). Ware (1992) estimated that the catch efficiency (catch divided by primary production) on the South African west coast was larger than that for the Californian ecosystem. This suggests that although primary production is not efficiently utilised in the southern Benguela ecosystem, the Californian ecosystem is even less efficient, probably because of its sizeable alongshore extent and the consequent large losses of primary production through offshore transport (Ware 1992).

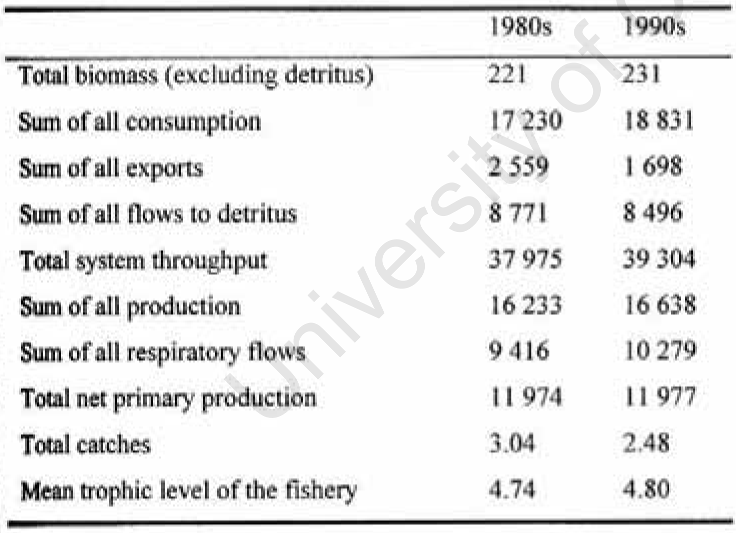
5.5.2 Path length

Mean path length (Finn 1976), corresponding to the mean number of trophic links in each trophic pathway, was 3.17 for the 1980s and 3.28 for the 1990s, longer than the path length of 2.54 in the Benguela model of Baird *et al.* (1991), showing that at least some summary statistics are to a certain degree dependent on model structure. In the models of the southern Benguela ecosystem, the maximum number of steps from primary producer to top predator (chain length) is ten. By comparison, a maximum chain length of eight was reported for upwelling and oceanic systems, whereas paths in models of some shelf and coastal systems were longer (Christensen and Pauly 1993). Maximum chain length of the southern Benguela models is large because not only do the models include the upwelling zones along the west coast, they also extend over the Agulhas Bank region. Even longer maximum chain lengths would be expected if planktonic groups were considered in more detail in models of the southern Benguela ecosystem.

5.5.3 Flows

Total biomass and many total flows through the southern Benguela upwelling ecosystem were larger in the 1990s model than the 1980s model (Table 5.2). Catches of small pelagic fish and the total annual catches of all species were larger in the 1980s than in the 1990s, although even these 1980s catches were lower than those in the Peruvian, northwest African and northern Benguela ecosystems (Jarre-Teichmann *et al.* 1998).

Table 5.2. Comparison of summary statistics from models of the southern Benguela ecosystem for the 1980s and 1990s. Flows are in t.km^{-2}.y^{-1}. biomass in t.km-2.



	1980s	1990s
Total biomass (excluding detritus)	221	231
Sum of all consumption	17 230	18 831
Sum of all exports	2 559	1 698
Sum of all flows to detritus	8 771	8 496
Total system throughput	37 975	39 304
Sum of all production	16 233	16 638
Sum of all respiratory flows	9 416	10 279
Total net primary production	11 974	11 977
Total catches	3.04	2.48
Mean trophic level of the fishery	4.74	4.80

5.5.4 Ecosystem indicators and system maturity

Ascendancy measures a system's average mutual information and is scaled by system throughput (Ulanowicz and Norden 1990). It is the product of total system throughput and the diversity of flows in a system, and is a measure representing size of flows as well as the organization of flows in a system (Field *et al.* 1989). Ascendancy A is calculated as:

$$A = T\sum_{i=1}^{n}\sum_{j=1}^{n}(f_{ij}/T)\log(f_{ij}T/T_iT_j)$$

…… Equation 5.1

where T is throughput, f is flow and i and j are compartments or boxes in the ecosystem (Kay *et al.* 1989).

Development capacity C is a measure of the potential of an ecosystem to develop, and is defined by Kay *et al.* (1989) as:

$$C = -T\sum_{i=1}^{n}(T_i/T)\log(T_i/T)$$

…… Equation 5.2

Relative ascendancy, defined as A/C, is a suitable measure for comparing different ecosystems and was previously estimated to be 51% in the Benguela ecosystem (Baird *et al.* 1991). In this study, relative ascendancy is less than half this during both decades (Table 5.3). This result is more in line with the findings of Jarre-Teichmann (1992) for the Peruvian upwelling system, where relative ascendancy varied around 30%, and relative overhead around 70%. The Peruvian system shows characteristics of a typical upwelling system (Jarre-Teichmann *et al.* 1998) in that it is even less stable ("mature") than the southern Benguela system, with a lower relative overhead (70% for the Peruvian system vs. 80% for the southern Benguela system). Relative overhead values for the models of upwelling systems compared in Jarre-Teichmann (1998) ranged from 63% to 70% (A. Jarre, pers. comm.) and support this interpretation, although it should be viewed with some caution given the differences in model structure. In a model with a very different structure, focussed on trophic interactions in the benthic community of the Antarctic eastern Weddell Sea shelf, Jane-Teichmann *et al.* (1997) found a relative overhead of 77%, and suggested that this was a characteristic indicating stability of the system to external perturbations — in this particular case, scraping of the bottom by icebergs in combinations with low turnover rates (caused by low temperature).

Considering the work of Odum (1969) on the development of ecosystems, Christensen (1995a) looked at a suite of attributes to characterise ecosystem development or maturity using steady-state ecosystem models. He found that system overhead (defined in Table 5.3) is positively correlated with maturity and is a possible measure of stability. Based on the work of Odum (1969) and Christensen (1995a), values of many "maturity" attributes (Table 5.3) indicate that the southern Benguela ecosystem had developed towards a slightly more mature, less heavily exploited ecosystem in the 1990s than the 1980s. However, for several attributes there are no detectable differences between decades, suggesting that development of the ecosystem between the 1980s and 1990s was only small, as can be expected for a system that is subject to change in a rapidly fluctuating environment. Lower net system production (production minus respiration) in the 1990s than in the 1980s (Table 5.3) is due in part to the 10% increase in biomass of microzooplankton, having high respiration rates. The larger system throughput and biomass of the 1990s suggests a more mature system during this decade than the 1980s. Some of the attributes are dependent on aggregation of components in a modelled ecosystem, e.g. mean path length and information content. The way in which detritus is handled in an ecosystem model may influence values of some of the attributes.

Ecosystem maturity is expected to decrease when a previously unexploited ecosystem is disturbed by fishing (Christensen 1995a). Christensen and Pauly (1998) compared maturity attributes of present-day models of the eastern central Pacific and Gulf of Mexico and models nstructing these ecosystems for previous periods during which top predators were more abundant and there were no catches. Their results were consistent with E.P. Odum's theory of system development; exploitation by fisheries has degraded the ecosystems so that they not using primary production efficiently. Christensen (1995) showed that relative ndancy is negatively correlated with maturity, in contrast to the suggestion by Ulanowicz 1986) that relative ascendancy is an indication of the ability of a system to sustain bations. The trend towards greater maturity in the southern Benguela ecosystem in the

1990s than the 1980s (Table 5.3) corresponds to the reduced exploitation from the 1980s to the 1990s and a less constrained system in the 1990s than in the 1980s, in terms of predation (including the fisheries) and availability of zooplankton as food for pelagic fish (Chapter 4, section 4.6.2). If ecosystem maturity is potentially a measure of ecosystem health (Christensen and Walters 2000), it might be suggested that the ecosystem health of the southern Benguela improved a little between the 1980s and 1990s.

Table 5.3 Some attributes of steady-state models of the southern Benguela ecosystem that potentially measure ecosystem maturity (Christensen (1995a), based on Odum's (1969) 24 attributes of ecosystem maturity).

	1980s	1990s	Comment
Total primary production/total respiration	1.272	1.165	1990s more mature
Net system production	2 558.6 t.km^{-2}.y^{-1}	1 698.4 t.km^{-2}.y^{-1}	1990s more mature
Total primary production/total biomass	54.1 y^{-1}	51.8 y^{-1}	1990s more mature
Total biomass/total throughput	0.006 y	0.006 y	No detectable difference between decades
System omnivory index	0.234	0.236	Defined as average omnivory index of all consumers, weighted by logarithm of food intakes
Proportion of total flows originating from detritus	0.45	0.45	Larger flows to and from detritus in 1990s with exception of more detritus exported from system in 1980s. Overall indication that 1990s more mature because larger energy flows through detritus-based food web in this decade.
Total flows to detritus	1 761 t.km^{-2}.y^{-1}	1 924 t.km^{-2}.y^{-1}	
Total consumption of detritus	7 025 t.km^{-2}.y^{-1}	7 648 t.km^{-2}.y^{-1}	
Total detritus exported from the system	2 183 t.km^{-2}.y^{-1}	1 322 t.km^{-2}.y^{-1}	
Total throughput of detritus	15 795 t.km^{-2}.y^{-1}	16 142 t.km^{-2}.y^{-1}	
Christensen and Pauly's (1992) connectance index	0.230	0.239	Defined as ratio of no. of actual links to no. of possible links (Gardner and Ashby 1970); unclear relationship between index and system development; more actual links in 1990s
System overhead	104 304	108 820	Units = flowbits (= bits.t.km^{-2}.y^{-1}); reflects the potential of a system to increase its ascendancy to meet unexpected perturbations (Ulanowicz 1986); 1990s more mature
Relative ascendancy	21.0 %	19.9 %	Defined as ascendancy/capacity; ascendancy measures system size and organisation and its ability to cope with a perturbation (Ulanowicz 1986, Field *et al.* 1989); 1990s more mature

Nutrient conservation	**3.991 t.km^{-2}.y^{-1}**	**4.695 t.km^{-2}.y^{-1}**	**Defined as difference between total throughput and throughput cycled through non-detrital chains; 1990s more mature**
Finn's (1980) mean path length	3.17	3.28	Defined as throughput/ (exports+respiration); 1990s more mature
Finn's (1980) cycling index	18.2 %	20.1 %	Defined as proportion of total system throughput that is recycled; divergent views on relation to maturity
Christensen and Pauly's (1992) predatory cycling index	14.3 %	14.4 %	No detectable difference between decades
Residence time	54.1 y	51.8 y	Defined as total system biomass (here excluding detritus) / (exports+respiration); 1980s more mature
Total system biomass/ total system production	0.014	0.014	Turnover rate, an index of average size of organisms in system; no detectable difference between decades
Total respiration/total biomass (excluding detritus) (Schrödinger ratio, Odum 1971)	42.6 y^{-1}	44.5 y^{-1}	1990s more mature
Information content	0.747 bits	0.705 bits	Ave. mutual information is the reduction in uncertainty about where a unit of energy will flow to next if the location if known; 1990s less mature

5.6 FISHING IN THE SOUTHERN BENGUELA ECOSYSTEM

5.6.1 Primary production required to sustain catches

As suggested by Pauly and Christensen (1995), primary production equivalents may be used to compare the effects of fishing at different trophic levels (Chapter 3, section 3.3.3). The units are expressed as percentages of the total primary production available in the system during the period modelled (decade). The greatest amounts of total primary production required (PPR) to support catches in models of the southern Benguela ecosystem during both decades are those of anchovy, large hakes and snoek (Fig. 5.4). PPR for all fisheries is 4.39% of the total primary production in the 1980s and 4.47% in the 1990s. These are small proportions in comparison to the Peruvian system (13-15%), and less than the 9.5% mean for the seven upwelling systems examined by Jarre-Teichmann and Christensen (1998a). PPR for catches in the southern Benguela ecosystem are more in line with percentages required to sustain catches in open ocean (small primary production and catch densities) or coastal regions (large primary production and catches) than in other upwelling systems (Pauly and Christensen 1995). Jarre-Teichmann and Christensen (1998a) explained the discrepancy between their mean PPR for upwelling systems with the mean of 25% estimated by Christensen and Pauly (1995); the latter authors considered the 1990s, when there were large catches (off Peru in particular), whereas Jarre-Teichmann and Christensen (1998a) focussed on the 1970s and early 1980s in their study, when catches were smaller. Further, Christensen and Pauly (1995) included discards in their estimates whereas Jarre-Teichmann and Christensen (1998a) used nominal catches. Here, discards were not included in southern Benguela models of this study (but see Chapter Six, section 6.3.5). Catches in the southern Benguela ecosystem are small in comparison to other upwelling systems, and primary production is larger than that of the northern Benguela, northwest African and Californian upwelling systems (Jarre-Teichmann *et al.* 1998). In addition, fishing in the southern Benguela ecosystem takes place at low trophic levels, with the overall result that the percentage PPR to sustain catches is small (Fig. 5.4).

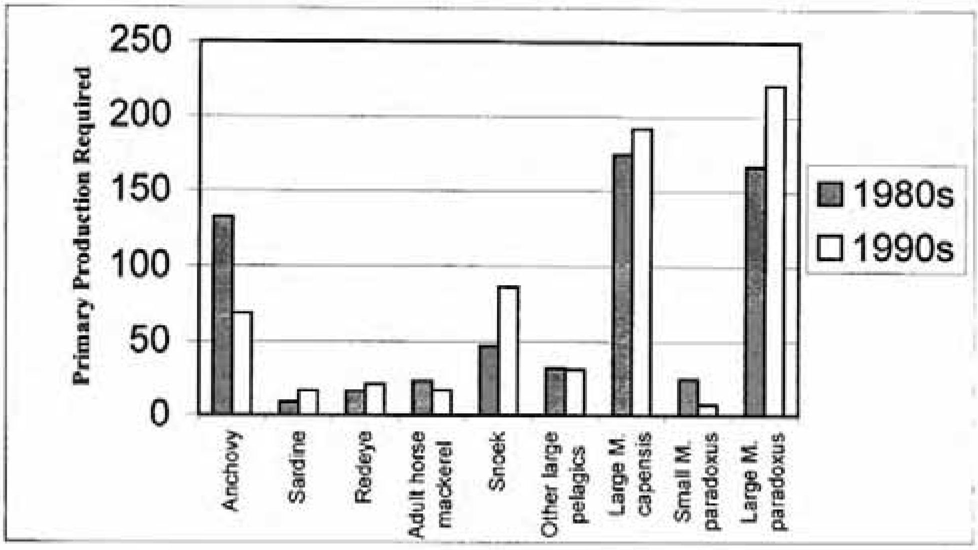


Fig. 5.4 Modelled primary production required (t.km $^{-2}$.y^{-1}) to sustain catches of commercially important species in the southern Benguela ecosystem during the 1980s and 1990s. Species requiring less than 15 t.lcm^{-2}.y^{-1} during both decades are omitted.

The ratio of PPR by the fisheries to total annual harvest is 290 in the 1990s compared to 228 in the 1980s. This is despite 19% smaller total annual catches during the 1990s. Therefore, the fishery in the 1990s was more ecologically expensive than that of the 1980s. A larger proportion of the catch in the 1990s was of snoek and hakes, which occur at higher trophic levels than small planktivorous fish. In the 1990s, the proportion of the catch in discrete trophic levels IV, V and VI is larger than in the 1980s (Fig. 5.5). The mean trophic level of the fishery is 4.74 in the 1980s and 4.80 in the 1990s, i.e. the catch of herbivores increased from the 1980s to the 1990s because sardine is more herbivorous than anchovy. Therefore, in the southern Benguela ecosystem, we do not appear to be "fishing down the food web" as has been shown for many regions (Pauly *et al.* 1998a, Pauly *et al.* 2000a, Pauly *et al.* 2000b). The mean trophic level of the fishery in upwelling systems in 1988-1991 is 3.8 (Pauly and Christensen 1995). This is lower than that in the southern Benguela ecosystem (4.7-4.8) where not only small pelagic fish but also hake and snoek are targeted. By comparison, the mean trophic level of the fishery off Peru was 3.5 in the 1960s when anchovy was targeted, and 3.7 in the 1970s when more sardine and hake were caught (Jarre-Teichmann 1998).

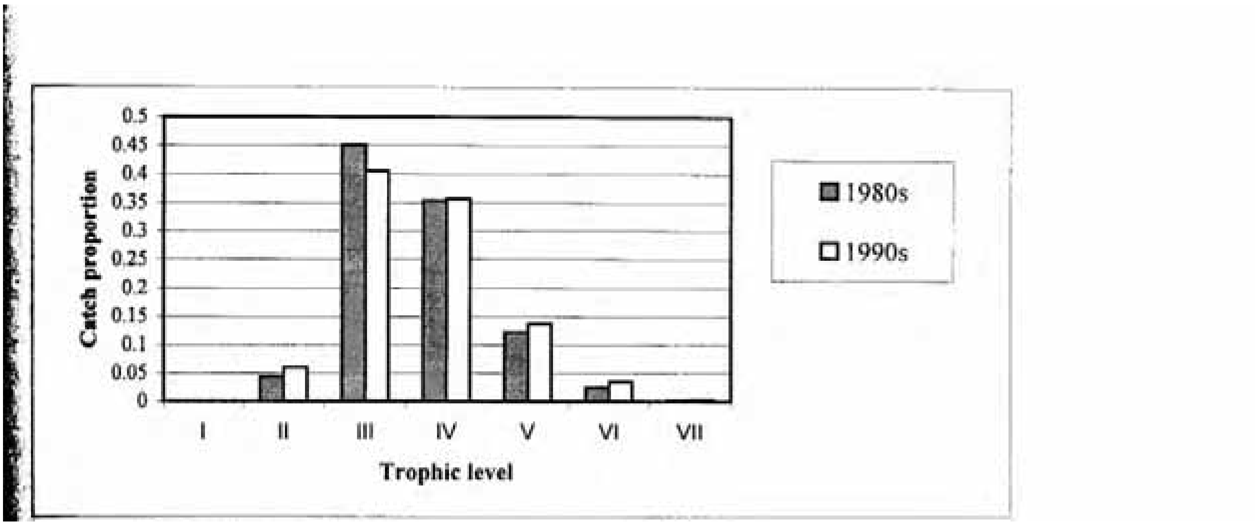


Fig. 5.5 Proportion of catches taken from discrete trophic levels in models of the southern Benguela ecosystem during the 1980s and 1990s.

5.6.2 Fishing mortality

It has been estimated that the total finfish biomass consumed globally by finfish is three times **larger** than the global catches of finfish (Christensen 1996b). A generalisation from more than

by predators, even in heavily exploited systems (Bax 1991, Jarre *et al.* 1991, Christensen and Pauly 1995). This is true for most species in the southern Benguela **ecosystem** (Fig. 5.6). Exceptions are predators such as snoek, other large pelagic fish and

mortality (Fig. 5.6). In the 1970s, fishing mortality for hake in the Peruvian, northwest African upwelling systems was similar to natural mortality (Jane-

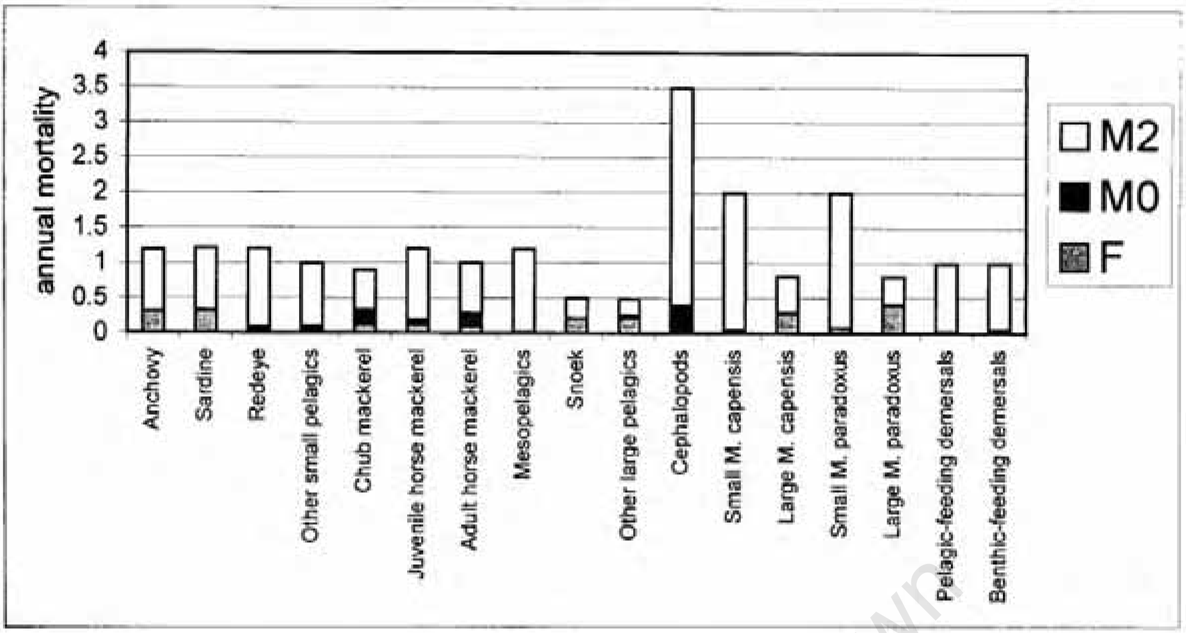


Fig. 5.6a Relative mortality by fishing (F), predation (M2) and other causes (MO) in the **southern** Benguela ecosystem during the 1980s. Mortalities were calculated using *Ecopath.*

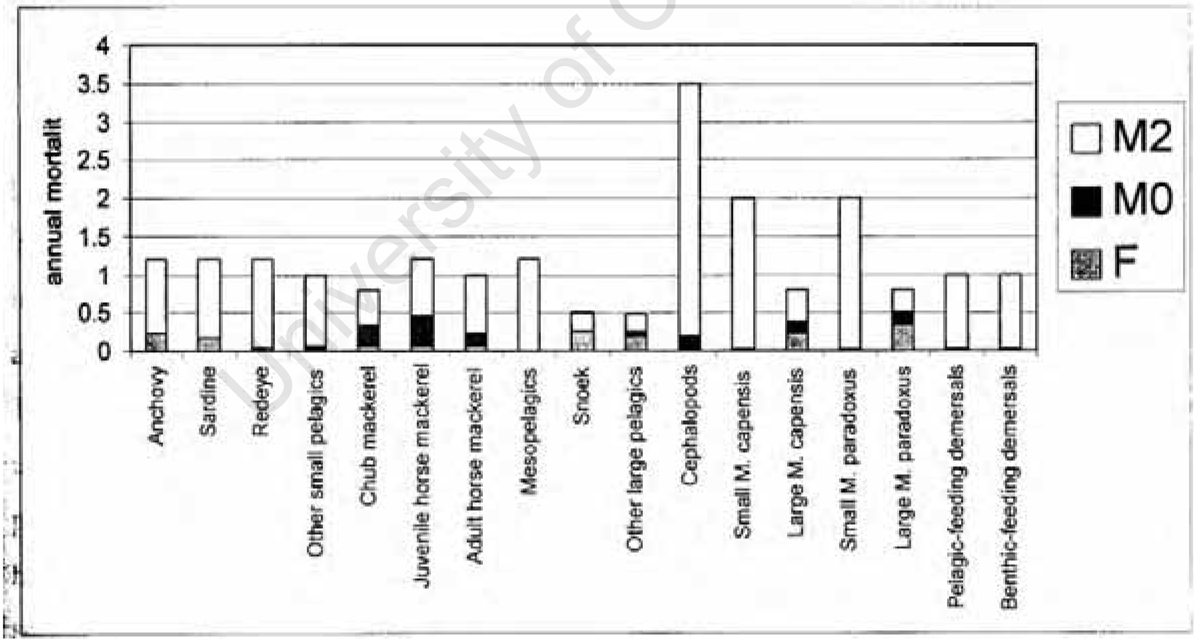


Fig. 5.6b Relative mortality by fishing (F), predation (M2) and other causes (MO) in the **southern** Benguela ecosystem during the 1990s. Mortalities were calculated using *Ecopath.*

(unpublished data, Marine and Coastal Management). Industry requested a larger sardine bycatch so that the anchovy fishery was viable, whereas scientists were concerned that this would impact negatively on the adult sardine fishery, upon which the valuable canning industry is based. Economically, it would probably be best to concentrate on the sardine directed fishery at the expense of the anchovy fishery (Cochrane *et al.* 1997). Apart from the bycatch issue, the procedure has other problems related to, amongst other factors, the large uncertainty in acoustic estimates of biomass and recruitment of anchovy and sardine, the fact that the current mid-year sardine recruitment estimate may not be the most suitable index from which to set the revised bycatch TAC, and the unknown natural mortality of juveniles between May and November surveys.

Hake

Because *M capensis* and *M paradoxus* are morphologically very similar, catch and effort statistics from the fishery are not able to distinguish between the two species. Therefore, the two hake species are managed together. The MP for hake involves setting separate TACs for hake on the west and south coasts. The TAC incorporates an observation error estimator from *a* dynamic age-aggregated surplus production model that assumes a Schaefer form for the production function (Payne and Punt 1995). This "Butterworth-Andrew estimator" uses biomass estimates and coefficients of variation from swept-area surveys as an index of abundance, commercial CPUE data and total annual commercial catches. The TAC is calculated by means of an $F_{0.2}$ constant effort strategy in which effort is calculated from the surplus production model as that level for which the slope of the equilibrium yield versus effort plot is 20% of the slope of the curve at the origin (Payne and Punt 1995), i.e. F is Maintained below the estimated level at which maximum sustainable yield (MSY) would be /cached, encouraging rebuilding of the stock (Cochrane *et al.* 1997).

The "single-species" approach to hake management is now experiencing some problems (Cochrane *et al.* 1997), of which three are mentioned briefly here. Recovery of the hake stock has not been as rapid as initially thought. In addition, there are unexplained discrepancies between the GLM-standardized CPUE trend and the commercial fishery trend (Brown *et al.* `1996). Thirdly, the uncertainty about the estimate of natural mortality of hake is problematic for assessing the pros and cons of longlining versus trawling for hake (Geromont *et al.* 1995).

Horse mackerel

Juvenile horse mackerel are caught in the pelagic purse-seine fishery on the South African west coast and adult horse mackerel are caught in a directed trawl fishery on the south coast of South Africa. Horse mackerel are also bycatch of the hake- and sole-directed demersal trawl fisheries. For almost all the years included in the 1980s and 1990s models of this thesis, TAC recommendations for horse mackerel were based on a dynamic production model using CPUE and biomass estimates from demersal swept-area research surveys to give replacement yield, the estimated catch that will maintain the resource at its present biomass level (Punt 1989 and 1992, Butterworth *et al.* 1992). Hydro-acoustic estimates of the horse mackerel stock size show that this model underestimated horse mackerel biomass. It has been recommended that both survey methods (i.e. swept-area demersal research surveys and hydro-acoustic surveys) should be used simultaneously to assess the horse mackerel resource as they assess different parts of the resource (Barange *et al.* 1998). Since 1996 a modified Beddington-Cooke yield-per-recruit model has been used to recommend a precautionary catch limit for the setting of a TAC. Horsten (1999) is testing a simple age-structured production model, which takes into account demersal and purse seine fleets. This model uses catch-by-mass data from demersal and pelagic landings and is fitted using estimates (and CVs) of horse mackerel biomass from research surveys. The new model should be able to assist in determining the maximum catch level producing the maximum sustainable yield of the horse mackerel resource.

Linefish

In 1985, the first linefish management framework was proposed (Penney *et al.* 1989). Stock assessments were not possible because there was a lack of biological and fisheries data, especially long-term catch and effort and size composition data. Therefore, the level of protection for each species was set fairly subjectively. A decade later, Griffiths *et al.* (1999) proposed a new Linefish Management Protocol (LMP) to set regulations based on clear objectives and quantifiable reference points. Using yield-per-recruit and spawner biomass-per-recruit models, Griffiths *et al.* (1997a and b) have shown that two species of kob in southern African waters are severely exploited. In the future, most linefish stocks are to be assessed using per-recruit analyses as there are not long-term data series suitable for more complicated analyses. The LMP states that a stock showing a historical reduction in CPUE or catch contribution of greater than 75% should be viewed as overexploited and that interim regulations should be put in place and necessary research initiated. Griffiths (2000) concluded that CPUE trends showed that almost all linefish species in South Africa are overexploited and that commercial extinction is possible, with implications for other components of the ecosystem. Griffiths *et al.* (1999) recommend that commercial effort be reduced, that marine reserves be enlarged and that recreational fisheries management regulations be put into place and heavily enforced.

5.7 MIXED TROPHIC IMPACT ASSESSMENT

The reduction in anchovy biomass and the increase in abundance of sardine in the 1990s is reflected in their relative net impacts on predatory fish such as snoek and other large pelagic fish, seabirds, seals and cetaceans. In the 1990s, redeye was abundant and had a positive impact on marine mammals. In this decade, the chub mackerel stock included large fish that have a more piscivorous diet than smaller chub mackerel. A quarter of the diet of chub Mackerel consisted of mesopelagic fish during the 1990s and this is reflected in the positive Impact of mesopelagic fish on chub mackerel (Fig. 5.7b). Fishing had larger mixed trophic impacts on many boxes in the 1980s than in the 1990s, as a consequence of larger annual catches in the 1980s (Table 5.2, Fig. 5.7 a and b).

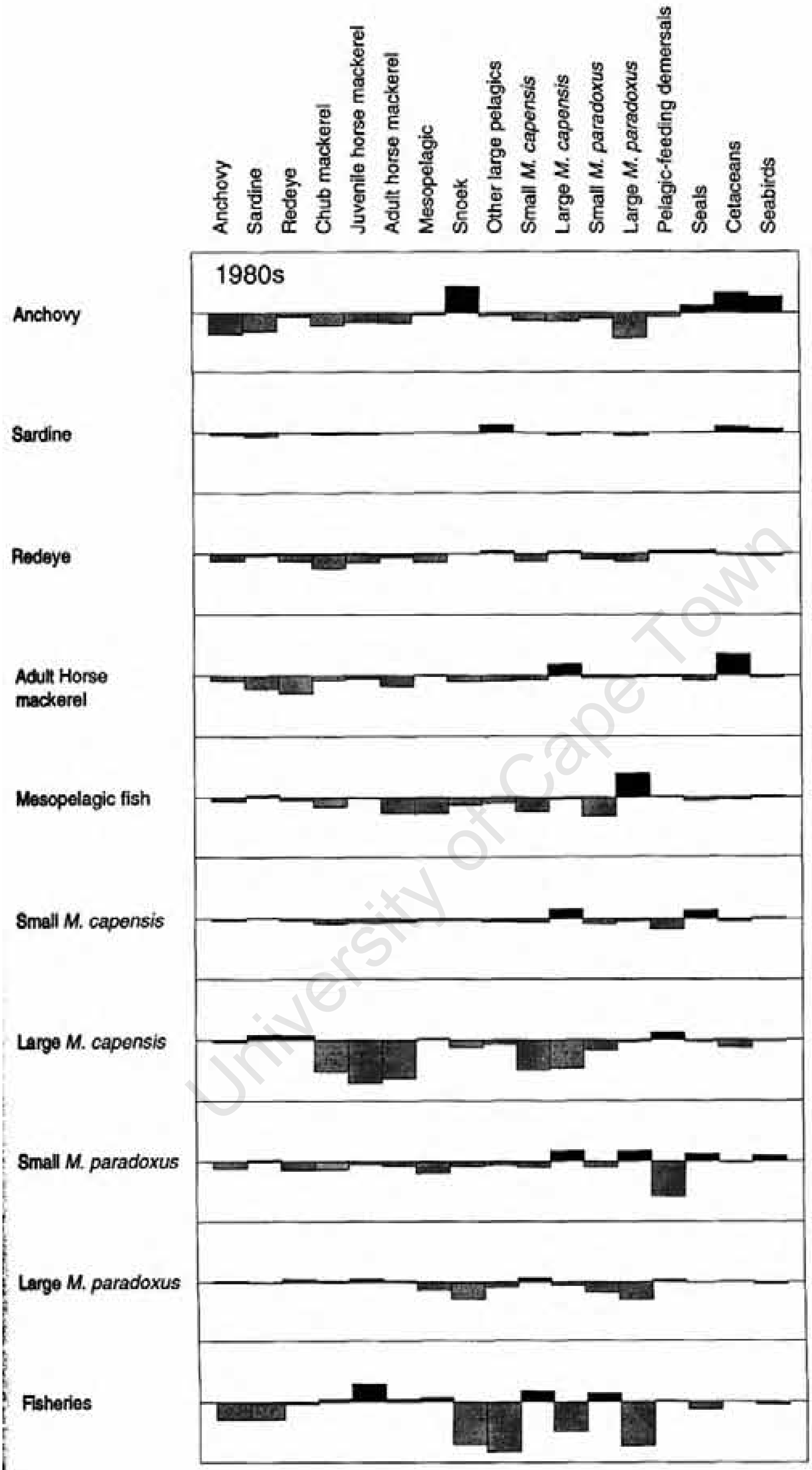


Fig. 5.7 (a) Mixed trophic impacts of selected groups in the southern Benguela ecosystem during the 1980s (outputs of *Ecopath* models). The bars indicate relative net impact (scaled between 0 and unity), where positive impacts are shown above the zero line for each impacting group,and negative impacts below. Impacted groups are arranged along the horizontal axis and impacting groups down the vertical axis.

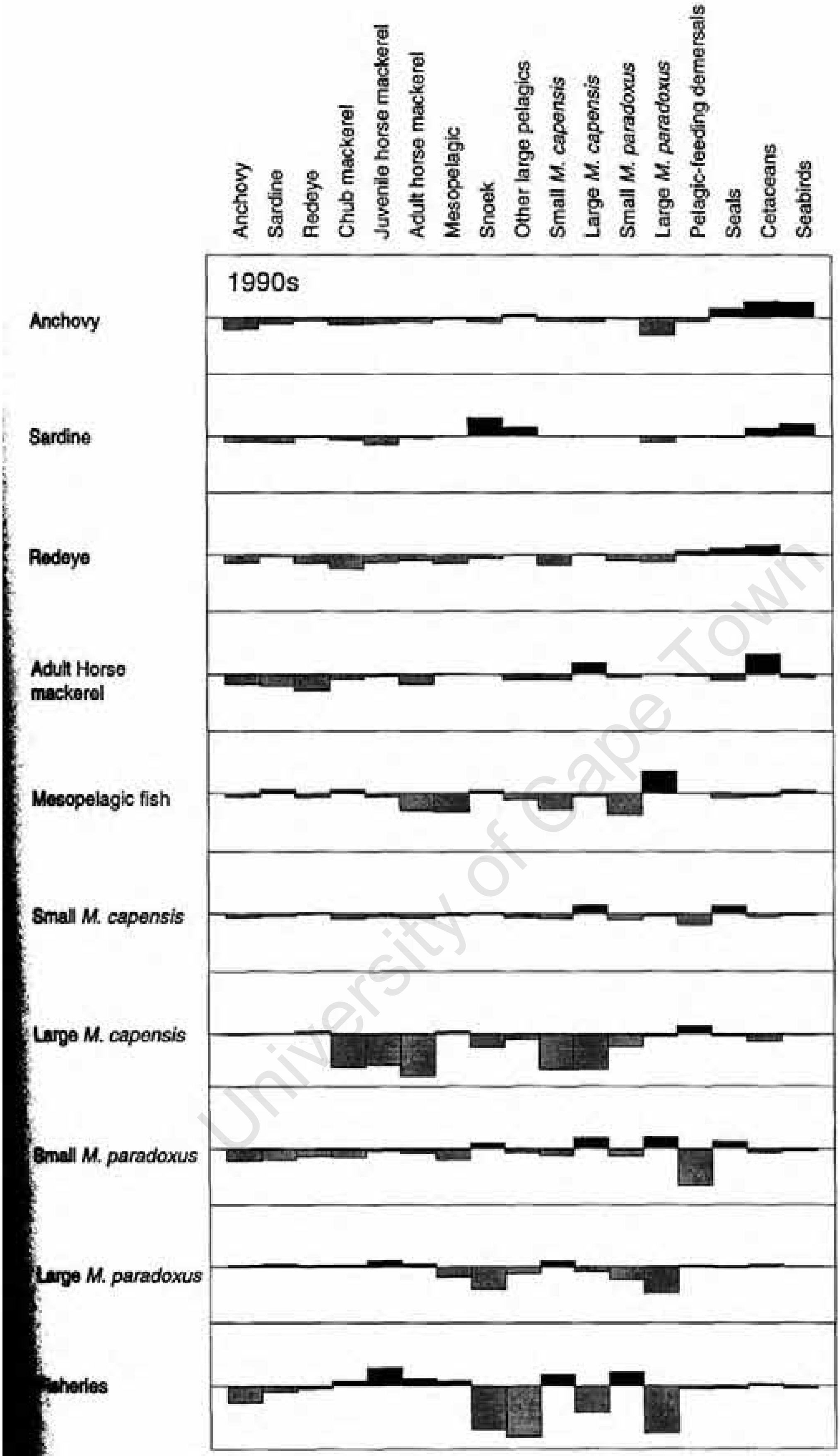


Fig. 5.7 (b) Mixed trophic impacts of selected groups in the southern Benguela ecosystem during the 1990s (outputs of *Ecopath* models). The bars indicate relative net impact (scaled between 0 and unity), where positive impacts are shown above the zero line for each impacting group,and negative impacts below. Impacted groups are arranged along the horizontal axis and impacting groups down the vertical axis.

5.8 PREDATOR AND PREY NICHES

The prey niche overlap index of Pianka (1973) may be used to determine the degree of overlap between species utilising common prey resources. A value of 1 indicates complete overlap in shared prey resources, whereas 0 indicates that the predators do not share common prey resources. A similar predator overlap index is used to determine the degree of overlap between species being consumed by common predators, with a similar interpretation of the 0-1 range of values. In the southern Benguela ecosystem, anchovy, sardine, redeye, other small pelagic fish and juvenile horse mackerel showed large degrees of overlap in both the prey they consumed and in the predators that consumed them (Table 5.4). These five small pelagic fish showed identical prey overlaps in the 1980s and 1990s because diet compositions of these groups are assumed constant between the two decades. However, there were greater overlaps in shared predators of small pelagic fish during the 1990s than the 1980s (Table 5.4). This may be related to the smaller total catches in the 1990s than the 1980s and the larger biomass of small pelagic fish predators (Chapter 4, Fig. 4.2).

Table 5.4 Predator and prey overlap indices for the five groups of small pelagics and mesopelagic fish in the southern Benguela ecosystem.

Group	Prey overlap index										Predator overlap index									
	Anchovy		Sardine		Redeye		Other small pelagics		Juvenile horse mackerel		Anchovy		Sardine		Redeye		Other small pelagics		Juvenile horse mackerel	
	80s	90s	80s	90s	80s	90s	80s	90s	80s	90s	80s	90s	80s	90s	80s	90s	80s	90s	80s	90s
Anchovy	1.00	1.00									1.00	1.00								
Sardine	0.59	0.59	1.00	1.00							0.67	0.90	1.00	1.00						
Redeye	0.99	0.99	0.50	0.50	1.00	1.00					0.55	0.57	0.33	0.52	1.00	1.00				
Other small pelagics	0.92	0.92	0.50	0.50	0.91	0.91	1.00	1.00			0.50	0.63	0.65	0.73	0.14	0.21	1.00	1.00		
Juvenile horse mackerel	0.96	0.96	0.51	0.51	0.96	0.96	0.99	0.99	1.00	1.00	0.42	0.48	0.27	0.60	0.13	0.15	0.36	0.66	1.00	1.00
Mesopelagic fish	0.90	0.90	0.39	0.39	0.92	0.92	0.70	0.70	0.79	0.79	0.50	0.45	0.17	0.42	0.85	0.82	0.32	0.26	0.09	0.14

5.9 CONCLUSIONS

Some differences have been shown between the anchovy-dominated system of the 1980s and the 1990s when sardine biomass increased. Nevertheless, the differences between the trophic models are not as large as expected from the differences in biomass and catches of many species. Trophically, the southern Benguela ecosystem seems to have functioned in a similar way during both decades, as shown by the similarity in transfer efficiencies, biomass per trophic level, mixed trophic impacts and many of the ecosystem maturity attributes. This is in line with results from comparisons of models of upwelling systems, where the systems tend to group by "system" rather than by decade or dominance regime (Jarre-Teichmann and Christensen 1998a). Biomass and catches of the small pelagic fish component differ between the two periods. However, production by small pelagic fish is close to 3 million tons in both decades (Chapter 4, section 4.6.1), at least partly as a result of management of the pelagic fisheries. Further, the combined ecotrophic efficiency of small pelagic fish (calculated as the ratio of the sum of catches and their consumption by predators to production by the group) is constant over the two decades (0.977 in 1980s and 0.976 in 1990s). In addition, the proportion of small pelagic fish production consumed by predators is similar in the two decades. The apparently small differences between the generalised trophic structure of the anchovy- and sardine-dominated ecosystems suggest some trophic similarity of small pelagic fish in the southern Benguela ecosystem. This concept is explored further in Chapter 9. In Chapter 10, the effects of fishing on the southern Benguela ecosystems during the two periods are compared and examined in more detail.

CHAPTER SIX

INVESTIGATING SENSITIVITY TO INPUT MODEL PARAMETERS AND CONSIDERING THEIR VARIABILITY

ABSTRACT

The effects of variability about input parameters in models of the southern Benguela ecosystem are investigated. Firstly, a simple sensitivity analysis in which input parameters are varied in steps of 10% from —50% to +50% shows that for many groups, the model is very sensitive to changes in biomass and/or productivity estimates, highlighting the importance of careful parameterization. The model is particularly sensitive to changes in input parameter estimates for benthic and planktonic groups. A second sensitivity analysis, *Ecoranger,* evaluates the effects of variability about the mean/mode of each input parameter according to set criteria (e.g. limits to output parameters, maximum possible P/Q values). Few "acceptable" alternative balanced models were found, indicating that there are tight constraints on southern Benguela models of the 1980s and 1990s, particularly in pathways via fish groups at intermediate trophic levels. The ecosystem was more tightly constrained in the 1980s than in the 1990s. Thirdly, sensitivities of seven input parameters for which alternative estimates are available were tested. Results support the use of initial values of these input parameters in the models.

6.1 INTRODUCTION

In order to balance the models of the southern Benguela ecosystem during the 1980s and 1990s, it was necessary to modify some of the input parameters (Chapter 4, section 4.5). To achieve this, information on the likely ranges of input parameters or the variability about them was taken into account. However, what were considered to be the "best" combinations of input parameters for the two balanced models are not the only possible combinations of parameter values. There is some degree of subjectivity involved in fitting models in this way, and this is a major criticism of ecosystem models in general. Here, this is addressed (key question 1c) by means of two forms of sensitivity analysis to investigate the effects of variability about input parameters, and to find the "best" set of input parameters. These analyses make the results of ecosystem models more rigorous and should be considered when advice on ecosystem management is to be given.

6.2 METHODS

6.2.1 Sensitivity analyses

Using a simple sensitivity analysis routine in which all input parameters are varied in steps of 10% from —50% to +50%, the resulting relative changes in all "missing" model parameters are calculated (i.e. in all parameters estimated by the model and regarded as output parameters). Results are presented relative to the original value i.e. as (new parameter estimate-original parameter estimate)/(original parameter estimate).

6.2.2 Exploring other parameter combinations for which models are balanced

The second type of sensitivity analysis is more sophisticated and is provided by *Ecoranger* (Pauly *et al.* 2000a). For each input parameter (e.g. biomass, P/B, Q/B, EE), the mode/mean and variability about it are selected (the 95% confidence interval for each parameter entered as a percentage above and below the mean). Alternatively, the range (minimum and maximum) of likely values may be entered for an input parameter. Similarly, for diet compositions, variability about each initial input value may be set (e.g. 10%). Using these ranges, values for each input parameter (including diet) are drawn at random from user-defined probability distributions (e.g. uniform, normal, triangular, log-normal). Each model run is then evaluated according to user-defined criteria (upper or lower limits to output parameters, maximum possible value for P/Q etc.). In Monte-Carlo fashion, the process is repeated a number of times (e.g. 50 000 in this study) to find "acceptable" models that fit the user-defined criteria.

Probability distributions of "acceptable" models are likely to be narrower than the input distributions estimated originally. Therefore, the process provides additional information on the likely values for input parameters (Christensen and Walters 2000). The shapes of the probability distributions provide information about the most likely parameter estimates giving "acceptable" models. For example, it is most likely that acceptable models will have parameter values near the mode for a parameter with a normal distribution. The best-fitting model is found using the method of least squares (minimization of residuals) to obtain parameter values closest to the original means. Alternatively, the model that maximizes biomass, system throughput or ascendancy can be found. In this study, *Ecoranger* is used to test possible combinations of parameters in balanced models by drawing from uniform distributions.

A certain degree of scientific judgement is required when interpreting *Ecoranger's* "best" combination of parameter values in any model. One of the weaknesses of *Ecoranger* is that parameters are varied independently of one other. In many cases, to be biologically feasible or at least reasonable, a reduction in one parameter should be coupled to an increase or decrease in another related parameter. In other words, there are additional constraints (e.g. on the maximum reasonable difference between two parameter values, or on the ratio of any two parameters) that are not taken into account fully using *Ecoranger.* This concern is partly addressed by setting lower and upper bounds for the production/consumption ratios for each group.

6.2.3 Alternative estimates

In addition to the previous two forms of sensitivity analysis, a few selected simulations are included where alternative estimates of some of the lesser-known parameters in the southern Benguela models are considered. These parameters include biomass of gelatinous zooplankton, P/B of sardine, chub mackerel, hakes and seals, P/B of chub mackerel, P/Q of large hakes and discards of small hakes.

6.2.4 Mixed trophic impact assessment

Finally, in addressing sensitivity and variability, mixed trophic impact assessment can be useful when interpreting the results of simulations; the net impact of a change in biomass of one group on the biomasses of other groups is assessed. Results are similar to those for biomass changes using the sensitivity analysis routine. Both methods have their merits. Mixed trophic impact assessment is clearly represented graphically and is a very useful means of highlighting which species interactions are important in the system. Results of mixed trophic impact assessment are presented in Chapter 5 (section 5.7).

6.3 RESULTS AND DISCUSSION

6.3.1 Sensitivity analysis

Models of the southern Benguela ecosystem during both the 1980s and 1990s were tested using the sensitivity analysis routine of *Ecopath* 3.1. Relative changes of 20% or more in output parameters are reported for a 20% decrease and a 30% increase in input parameters (Table 6.1). Changes of this magnitude are realistic considering the large interannual fluctuations in abundance for many species in the southern Benguela ecosystem (e.g. anchovy and sardine in Hampton 1992 and Hutchings *et al.* 1998), catches (e.g. horse mackerel in Barange *et al.* 1998, pelagic fish in Roel and Armstrong 1991), diets and daily rations *(e.g.* hakes in Punt *et al.* 1992, anchovy in Armstrong *et al.* 1991, seals in Punt *et al.* 1995). These results are selected for tabulation because a 20% decrease and a 30% increase in input parameter values are the smallest increments of 10% causing changes of 20% or more in several of the output parameters.

For the remainder of this section, "strong effects" will be defined as those causing a 20% or greater change in output model parameters. For most boxes, strong effects are restricted to the output parameters of the box being tested.

In many cases, a 20% reduction in an input parameter such as biomass (B) or the production/biomass ratio (P/B) causes the ecotrophic efficiency (EE) of the box to exceed 1, indicating that production of a box is no longer sufficient to support consumption of that group (Table 6.1, shaded cells). Thus, for many boxes the model is very sensitive to changes in estimates of biomass and/or productivity. This both emphasizes the need for good estimates, and also the constraints that are imposed on these estimates by information from the rest of the ecosystem.

Sensitivity analyses show that changes in the lower trophic levels, i.e. the planktonic and benthic boxes have strong impacts on other groups. This was also shown using mixed trophic impact assessment (Chapter 5, Fig. 5.7), where these groups have large effects on most other groups in the system. The most sensitive parameters are the production/biomass (P/B) and consumption/biomass (Q/B) ratios of microzooplankton. Even a 10% decrease in the P/B ratio or a 10% increase in the Q/B ratio of microzooplankton respectively causes a large increase in phytoplankton ecotrophic efficiency and microzooplankton biomass (Table 6.1), and it was not possible to obtain results for larger changes in these parameters. Using an ecotrophic efficiency less than 10% of the original 95% for microzooplankton was unsustainable (Table 6.1). Parameterization of mesozooplankton is important; mesozooplankton graze heavily on phytoplankton, in particular on chain-forming diatoms (Moloney 1992), affecting the ecotrophic efficiency of phytoplankton. Microzooplankton is another important prey of mesozooplankton, therefore changes in the P/B and Q/B ratios of mesozooplankton affect microzooplankton biomass.

Biomasses of the benthic boxes are sensitive to an increase in the Q/B ratio of benthic-feeding demersal fish. The ecotrophic efficiencies of both seals and cetaceans are sensitive to changes in biomass and the Q/B ratio of apex chondrichthyans feeding on them. The apex chondrichthyan group is a poorly parameterized component of the model. However, even strong impacts of this group on seals and cetaceans do not require that the consumption of seals and cetaceans exceeds their production.

Table 6.1 Results of sensitivity analyses performed on the southern Benguela models for the 1980s and 1990s. Parameters are tabulated for which a 20% reduction or a 30% increase in size caused a 20% or larger change in other model parameters. Values are percentage change in affected parameters. Where changes differ between decades, the percentage change for the 1990s is indicated. Where the reduction/increase of a parameter is unsustainable, cells are shaded.

		20% REDUCTION			30% INCREASE		
Group tested	**Parameter tested**	**Group affected**	**Parameter affected**	**Value (% change)**	**Group affected**	**Parameter affected**	**Value (% change)**
Phytoplankton	B	Phytoplankton	EE	+25%	Phytoplankton	EE	-23%
Phytoplankton	P/B	Phytoplankton	EE	+25%	Phytoplankton	EE	-23%
Benthic producers	P/B	Benthic producers	B	+25%	Benthic producers	B	-23%
Benthic producers	EE	Benthic producers	B	+25%	Benthic producers	B	-23%
Microzooplankton	P/B	Phytoplankton	EE	+144% at 10% level of reduction; unsustainable at >10% reduction	Phytoplankton	EE	-55%
Microzooplankton	P/B	Microzooplankton	B	+173% at 10% level of reduction; unsustainable at >10% reduction	Microzooplankton	B	-66%
Microzooplankton	Q/B	Phytoplankton	EE	-51%	Phytoplankton	EE	+113% at an increase of 10%; unsustainable at >10% increase
Microzooplankton	Q/B	Microzooplankton	B	-52%	Microzooplankton	B	+114% at an increase of 10%; unsustainable at >10% increase
Microzooplankton	EE	Phytoplankton	EE	+144% at 20% reduction; unsustainable at >20% reduction	Phytoplankton	EE	-55%
Microzooplankton	EE	Microzooplankton	B	+173% at 10% reduction; unsustainable at >10% reduction	Microzooplankton	B	-66%
Mesozooplankton	P/B	Phytoplankton	EE	+23%; +22% in 1990s	Phytoplankton	EE	-21%
Mesozooplankton	P/B	Microzooplankton	B	+25%	Microzooplankton	B	-23%
Mesozooplankton	P/B	Mesozooplankton	B	+25%	Mesozooplankton	B	-23%
Mesozooplankton	Q/B				Phytoplankton	EE	+27%
Mesozooplankton	Q/B	Microzooplankton	B	-20%	Microzooplankton	B	+30%; +29% in 1990s
Mesozooplankton	EE	Phytoplankton	EE	+23%; +22% in 1990s	Phytoplankton	EE	-21%
Mesozooplankton	EE	Microzooplankton	B	+25%	Mesozooplankton EE would exceed 1		
Mesozooplankton	EE	Mesozooplankton	B	+25%	Mesozooplankton EE would exceed 1		

		20% REDUCTION			30% INCREASE		
Group tested	**Parameter tested**	**Group affected**	**Parameter affected**	**Value (% change)**	**Group affected**	**Parameter affected**	**Value (% change)**
Macrozooplankton	P/B	Macrozooplankton	B	+25%	Macrozooplankton	B	-23%
Macrozooplankton	EE	Macrozooplankton	B	+25%	Macrozooplankton EE would exceed 1		
Gelatinous zooplankton	P/B	Gelatinous zooplankton	EE	+25%	Gelatinous zooplankton	EE	-23%
Gelatinous zooplankton	Q/B				Gelatinous zooplankton	EE	+22%; +23% in 1990s
Anchovy	B	Anchovy	EE	+25%	Anchovy	EE	-23%
Anchovy	P/B	Anchovy	EE	+25%	Anchovy	EE	-23%
Sardine	B	Sardine	EE	+25%	Sardine	EE	-23%
Sardine	P/B	Sardine	EE	+25%	Sardine	EE	-23%
Redeye	B (1980s)	Redeye	EE	+25%	Redeye	EE	-23%
Redeye	P/B	Redeye	EE	+25%	Redeye	EE	-23%
Redeye	EE (1990s)	Redeye	B	+25%	Redeye	B	-23%
Other small pelagics	B	Other small pelagics	EE	+25%	Other small pelagics	EE	-23%
Other small pelagics	P/B	Other small pelagics	EE	+25%	Other small pelagics	EE	-23%
Chub mackerel	B	Chub mackerel	EE	+25%	Chub mackerel	EE	-23%
Chub mackerel	P/B	Chub mackerel	EE	+25%	Chub mackerel	EE	-23%
Juvenile horse mackerel	B	Juvenile horse mackerel	EE	+25%	Juvenile horse mackerel	EE	-23%
Juvenile horse mackerel	P/B	Juvenile horse mackerel	EE	+25%	Juvenile horse mackerel	EE	-23%
Adult horse mackerel	B	Adult horse mackerel	EE	+25%	Adult horse mackerel	EE	-23%
Adult horse mackerel	P/B	Adult horse mackerel	EE	+25%	Adult horse mackerel	EE	-23%
Mesopelagic fish	P/B	Mesopelagic fish	B	+25%	Mesopelagic fish	B	-23%
Mesopelagic fish	EE	Mesopelagic fish	B	+25%	Mesopelagic fish EE would exceed 1		
Snoek	B	Snoek	EE	+25%; +26% in 1990s	Snoek	EE	-23%
Snoek	P/B	Snoek	EE	+25%; +26% in 1990s	Snoek	EE	-23%

		20% REDUCTION			30% INCREASE		
Group tested	**Parameter tested**	**Group affected**	**Parameter affected**	**Value (% change)**	**Group affected**	**Parameter affected**	**Value (% change)**
Other large pelagics	B	Other large pelagics	EE	+25%	Other large pelagics	EE	-23%
Other large pelagics	P/B	Other large pelagics	EE	+25%	Other large pelagics	EE	-23%
Cephalopods	P/B	Cephalopods	EE	+25%	Cephalopods	EE	-23%
Small *M. capensis*	P/B	Small *M. capensis*	B	+25%	Small *M. capensis*	B	-23%
Small *M. capensis*	EE	Small *M. capensis*	B	+25%	Small *M. capensis* EE would exceed 1		
Large *M. capensis*	B	Large *M. capensis*	EE	+20%; +18% in 1990s			
Large *M. capensis*	P/B	Large *M. capensis*	EE	+25%	Large *M. capensis*	EE	-23%
Small *M. paradoxus*	P/B	Small *M. paradoxus*	B	+26%	Small *M. paradoxus*	B	-24%
Small *M. paradoxus*	EE	Small *M. paradoxus*	B	+26%	Small *M. paradoxus* EE would exceed 1		
Large *M. paradoxus*	B	Large *M. paradoxus*	EE	+23%; +21% in 1990s	Large *M. paradoxus*	EE	-21%; -19% in 1990s
Large *M. paradoxus*	P/B	Large *M. paradoxus*	EE	+25%	Large *M. paradoxus*	EE	-23%
Pelagic-feeding demersals	P/B	Pelagic-feeding demersals	B	+33%	Pelagic-feeding demersals	B	-27%
Pelagic-feeding demersals	EE	Pelagic-feeding demersals	B	+33%	Pelagic-feeding demersals EE would exceed 1		
Benthic-feeding demersals	P/B	Benthic-feeding demersals	B	+29%	Benthic-feeding demersals	B	-25%
Benthic-feeding demersals	EE	Benthic-feeding demersals	B	+29%	Benthic-feeding demersals EE would exceed 1		
Benthic-feeding demersals	Q/B				Benthic producers	B	+20%
Benthic-feeding demersals	Q/B				Meiobenthos	B	+20%
Benthic-feeding demersals	Q/B				Macrobenthos	B	+20%
Pelagic chondrichthyans	P/B	Pelagic chondrichthyans	EE	+25%	Pelagic chondrichthyans	EE	-23%
Pelagic chondrich.	Q/B				Pelagic chondrich	EE	+27%

		20% REDUCTION			30% INCREASE		
Group tested	**Parameter tested**	**Group affected**	**Parameter affected**	**Value (% change)**	**Group affected**	**Parameter affected**	**Value (% change)**
Benthic chondrich.	P/B	Benthic chondrichthyans	EE	+25%	Benthic chondrich.	EE	-23%
Benthic chondrichth.	Q/B				Benthic chondrich.	EE	+23%
Apex chondrichthyan	B				Seals	EE	+24%; +25% in 1990s
Apex chondrichthyan	B	Cetaceans	EE	-20%	Cetaceans	EE	+30%
Apex chondrichthyans	Q/B				Seal	EE	+24%; +25% in 1990s
Apex chondrichthyans	Q/B	Cetaceans	EE	-20%	Cetacean	EE	+30%
Seals	B	Seals	EE	+25%	Seals	EE	-23%
Seals	P/B	Seals	EE	+25%	Seals	EE	-23%
Cetaceans	B	Cetaceans	EE	+25%	Cetaceans	EE	-23%
Cetaceans	P/B	Cetaceans	EE	+25%	Cetaceans	EE	-23%
Seabirds	P/B	Seabirds	EE	+25%	Seabirds	EE	-23%
Seabirds	Q/B	Seabirds	EE	-20%	Seabirds	EE	+30%
Meiobenthos	P/B	Meiobenthos	B	+25%	Meiobenthos	B	-23%
Meiobenthos	EE	Meiobenthos	B	+25%	Meiobenthos EE would exceed 1		
Macrobenthos	P/B	Benthic producers	B	+108% at 20% reduction; unsustainable at >30% reduction	Benthic producers	B	-44%
Macrobenthos	P/B	Meiobenthos	B	+108% at 20% reduction; unsustainable at >30% reduction	Meiobenthos	B	-44%
Macrobenthos	P/B	Macrobenthos	B	+108% at 20% reduction; unsustainable at >30% reduction	Macrobenthos	B	-44%
Macrobenthos	Q/B	Benthic producers	B	-39%	Benthic producers	B	+149%
Macrobenthos	Q/B	Meiobenthos	B	-39%	Meiobenthos	B	+149%
Macrobenthos	Q/B	Macrobenthos	B	-24%	Macrobenthos	B	+91%
Macrobenthos	EE	Benthic producers	B	+108% at 20% reduction; unsustainable at >30% reduction	Benthic producers	B	-44%
Macrobenthos	EE	Meiobenthos	B	+108% at 20% reduction; unsustainable at >30% reduction	Meiobenthos	B	-44%
Macrobenthos	EE	Macrobenthos	B	+108% at 20% reduction; unsustainable at >30% reduc.	Macrobenthos	B	-44%

		20% REDUCTION			30% INCREASE		
Group tested	**Parameter tested**	**Group affected**	**Parameter affected**	**Value (% change)**	**Group affected**	**Parameter affected**	**Value (% change)**
Benthic chondrich.	P/B	Benthic chondrichthyans	EE	+25%	Benthic chondrich.	EE	-23%
Benthic chondrichth.	Q/B				Benthic chondrich.	EE	+23%
Apex chondrichthyan	B				Seals	EE	+24%; +25% in 1990s
Apex chondrichthyan	B	Cetaceans	EE	-20%	Cetaceans	EE	+30%
Apex chondrichthyans	Q/B				Seal	EE	+24%; +25% in 1990s
Apex chondrichthyans	Q/B	Cetaceans	EE	-20%	Cetacean	EE	+30%
Seals	B	Seals	EE	+25%	Seals	EE	-23%
Seals	P/B	Seals	EE	+25%	Seals	EE	-23%
Cetaceans	B	Cetaceans	EE	+25%	Cetaceans	EE	-23%
Cetaceans	P/B	Cetaceans	EE	+25%	Cetaceans	EE	-23%
Seabirds	P/B	Seabirds	EE	+25%	Seabirds	EE	-23%
Seabirds	Q/B	Seabirds	EE	-20%	Seabirds	EE	+30%
Meiobenthos	P/B	Meiobenthos	B	+25%	Meiobenthos	B	-23%
Meiobenthos	EE	Meiobenthos	B	+25%	Meiobenthos EE would exceed 1		
Macrobenthos	P/B	Benthic producers	B	+108% at 20% reduction; unsustainable at >30% reduction	Benthic producers	B	-44%
Macrobenthos	P/B	Meiobenthos	B	+108% at 20% reduction; unsustainable at >30% reduction	Meiobenthos	B	-44%
Macrobenthos	P/B	Macrobenthos	B	+108% at 20% reduction; unsustainable at >30% reduction	Macrobenthos	B	-44%
Macrobenthos	Q/B	Benthic producers	B	-39%	Benthic producers	B	+149%
Macrobenthos	Q/B	Meiobenthos	B	-39%	Meiobenthos	B	+149%
Macrobenthos	Q/B	Macrobenthos	B	-24%	Macrobenthos	B	+91%
Macrobenthos	EE	Benthic producers	B	+108% at 20% reduction; unsustainable at >30% reduction	Benthic producers	B	-44%
Macrobenthos	EE	Meiobenthos	B	+108% at 20% reduction; unsustainable at >30% reduction	Meiobenthos	B	-44%
Macrobenthos	EE	Macrobenthos	B	+108% at 20% reduction; unsustainable at >30% reduc.	Macrobenthos	B	-44%

6.3.2 Exploring other parameter combinations for which models are balanced

Defined ranges and variability about the means of possible balanced models of the southern Benguela ecosystem in the 1980s and 1990s are tabulated (Table 6.2). A particular combination of parameter values is "acceptable" if it satisfies the following criteria: EEs for all groups do not exceed 1, values for output parameters are within user-defined ranges (Table 6.2) and P/Q ratios do not exceed 60% (default setting for *Ecoranger).* Distributions of the parameter values that produce successful runs are examined. Of the successful combinations of parameter values, the model that maximizes biomass in each decade is compared to the original models of Chapters 4 and 5 to estimate how far the ecosystem is from one having maximum total biomass.

Because 20% of the diet of microzooplankton is assumed to consist of other microzooplankton ("cannibalism" or within-group predation), some combinations of input parameters result in consumption of microzooplankton exceeding production by the box. In particular, this occurs if more than 20% variability about phytoplankton biomass is used, and is affected through the assumption that microzooplankton diet consists of 40% phytoplankton. In the 1990s model, which requires larger biomasses for zooplankton boxes, microzooplankton cannibalism is even more problematic. It is necessary to reduce the variability about the diet of microzooplankton to 5% (Table 6.2). To investigate the variability about parameters in both decades, it is necessary to halve the mean fraction of microzooplankton in the diet of microzooplankton and add 5% to the mean fractions of phytoplankton and detritus consumed by microzooplankton. These results suggest that in order to model the planktonic boxes of the southern Benguela ecosystem in more detail, it would be best to further subdivide the microzooplankton box so that intra-box consumption is reduced. For purposes of this study, which focuses on pelagic fish, model aggregation is retained.

Similarly, intra-box consumption of macrobenthos causes problems when extreme values of parameters are tested, so that it is necessary to reduce variability about the diet of this box from 20% to 10% and to reduce the mean macrobenthos fraction from 0% to 5% in the diet of macrobenthos, with a corresponding increase of 2% in the iobenthos fraction. This further highlights the problems pertaining to aggregation :organisms into a single large box when intra-box consumption is large.

Only 54 of the 50 000 combinations of input parameters (0.11%) for the 1980s model were found to be "acceptable". There were 129 acceptable runs (0.26%) for the 1990s model. This is because ecotrophic efficiencies (EEs) of many boxes are lower in the original 1990s than 1980s model, allowing greater variability of input parameters. The low success rate of finding parameters within the best estimated ranges that gave balanced models shows that the southern Benguela models of the 1980s and 1990s are tightly-fitted and that there is little room for allocating alternative values to most input parameters. Trophic flows between boxes are more tightly-constrained in the 1980s than in the 1990s, as was hypothesized in Chapter 4 (section 4.6.2).

The first fifty combinations of parameter values that were unacceptable according to the set criteria were recorded. When testing the 1980s and 1990s models respectively, 42% and 40% of the first fifty failed runs were because the EE of anchovy exceeded 100%, and 20% and 14% of failures result from the EE of sardine exceeding 100%. In two of the fifty failures in the 1980s, the P/Q ratio of gelatinous zooplankton exceeded 0.6 y^{-1} , the default maximum, and in another two cases, the EE of the group was less than 10%, a conservative minimum estimate. In one of the fifty failed runs, mesopelagic fish biomass exceeds the estimated maximum of 2.4 million tons. The EEs of adult horse mackerel and other small pelagic fish both exceed 100% in 10% of the failed cases in the 1980s. Ecotrophic efficiencies in excess of 100% in the cases of chub mackerel, other large pelagic fish and redeye account for the four remaining failed runs in these first 50 for the 1980s. These results show that there is a high demand for prey fish in the southern Benguela ecosystem, and that the heavy fishing pressure on these fish boxes leaves little room for increased predation pressure. Therefore, as discussed in the previous paragraph, there is tight control of flow along trophic pathways in the southern Benguela ecosystem, particularly those paths via fish boxes at intermediate trophic levels.

One failure in the set of the first 50 runs for the 1990s resulted from the P/Q ratio of gelatinous zooplankton exceeding 0.6 y ^{1} . 6% of the failures recorded in the 1990s occurred because the EE of adult horse mackerel was unsustainably high. A further 4% of unacceptable combinations were because the estimated required biomass of mesozooplankton exceeded the estimated maximum of 5.2 million tons, 22% because macrozooplankton biomass exceeded the estimated maximum of 4.8 million tons, and 8% because redeye biomass exceeded 2.4 million tons. One of the first fifty failures occurred when the EE of cephalopods exceeded 100% and another when that of phytoplankton was 100%. Horse mackerel and cephalopods are important prey and catch species. There is a limit to their sustainability, given the increase in demand for these groups to support increasingly larger predator stocks and fisheries. Larger biomasses of meso- and macro-zooplankton and redeye can be supported in a balanced model of the southern Benguela ecosystem, but these lie beyond the maximum estimates considered in Table 6.2. In one unacceptable case, consumption of phytoplankton by a very large zooplankton stock was too large to be supported by the phytoplankton standing stock.

Table 6.2 Combinations of parameter values used to obtain balanced models of the southern Benguela ecosystem for the 1980s and 1990s. Ranges or variability (%) about means for input parameters (normal type) and output parameters (bold type), serve as criteria determining "acceptability" of runs.

Group	B t.km^{-2}	P/B y^{-1}	Q/B y^{-1}	EE	Catch t.km^{-2}.y^{-1}	Diet
Phytoplankton	20%	30%	-		-	-
Benthic producers	Unrestricted	20%	-	50%	-	-
Microzooplankton	**1.0-11.0** (maximum is 10% more than B estimated from Brown *et al.* (1991), using Verheye *et al.*'s (1992) C: wet mass conversion ratio of 25).	10%	10%	0.900-0.999	-	5%
Mesozooplankton	**1.0-23.5** (maximum is 10% more than B estimated from Hutchings *et al.* (1991) using Verheye *et al.*'s (1992) C: wet mass conversion ratio of 25).	50% (ranges from 20 y^{-1} in Hutchings *et al.* 1991) to over 50 y^{-1} in Verheye *et al.* 1992)	20%	0.900-0.999	-	20%
Macrozooplankton	**1.8-21.9** (H. Verheye, MCM, pers. comm.)	10%	10%	0.900-0.999	-	20%
Gelatinous zooplankton	30% (B is poorly known)	30%	30%	**0.100-0.999**	-	30%
Anchovy	10%	10%	10%	**0.100-0.999**	10%	10%
Sardine	10%	10%	10%	**0.100-0.999**	10%	10%
Redeye	5.0-11.1 (minimum is 10% below conservative estimate of Roel and Armstrong 1991, maximum is twice this).	10%	10%	**0.100-0.999**	10%	10%
Other small pelagics	20%	20%	20%	0.100-0.999	20%	20%
Chub mackerel	30%	10%	10%	**0.100-0.999**	10%	10%
Juvenile horse mackerel	**0.2-0.5** (1980s: juvenile B estimated to be between 10% and 25% of adult B in 1980s) **0.4-0.6** (1990s: B of juveniles estimated to be 20% of the minimum and maximum B estimate of the species)	10%	10%	0.100-0.999	10%	10%
Adult horse mackerel	20% (1980s) **1.6-2.5** (1990s: adult B estimated to be 80% of minimum and maximum B estimated for the species)	0.52 y^{-1} (Jarre-Teichmann *et al.* 1998)-1.1 y^{-1} (10% above value used in this study)	10%	0.100-0.999	10%	20%
Mesopelagics	**4.5-10.9** (Armstrong *et al.* 1991)	10%	10%	10%	10%	10%
Snoek	1980s: 20% 1990s: **estimated**, maximum set to 4.0	20%	20%	**0.100-0.999** 20% (1990s)	10%	10%
Other large pelagics	20%	10%	10%	**0.100-0.999**	10%	20%
Cephalopods	30%	20%	20%	**0.100-0.999**	10%	30%
Small *M. capensis*	**Minimum=0.3** (equivalent to B from production model and survey data; B likely underestimated in surveys), maximum set to 4.0	10%	10%	5%	10%	30%
Large *M. capensis*	10%	10%	10%	**0.100-0.999**	10%	30%
Small *M. paradoxus*	**Minimum=1.0 (1980s) and 1.3 (1990s)** (equivalent to B from production model and survey data; B likely underestimated in surveys) , maximum set to 4.0	10%	10%	5%	10%	30%
Large *M. paradoxus*	10%	10%	10%	**0.100-0.999**	10%	30%
Pelagic demersals	**Maximum set to 20**	20%	20%	20%	20%	30%

Benthic demersals	**Maximum set to 20**	**20%**	20%	20%	20%	30%
Pelagic chondrichthyans	**30% (B is poorly known)**	**20%**	20%	**0.100-0.999**	20%	30%
Benthic chondrichthyans	**30% (B is poorly known)**	**20%**	20%	**0.100-0.999**	20%	30%
Apex chondrichthyans	**30% (B is poorly known)**	**20%**	20%	**0.100-0.999**	-	30%
Seals	10%	0.03 y^{-1} (Heymans 1996) – 1.041 y^{-1} (10% larger than mean estimate of 1989 workshop)	10%	**0.100-0.999**	10%	30%
Cetaceans	30% (B estimate unavailable)	20%	20%	**0.100-0.999**	-	30%
Seabirds	10%	10%	10%	**0.100-0.999**	-	10%
Meiobenthos	**Maximum set to 200**	20%	20%	20%	-	20%
Macrobenthos	**Maximum set to 200**	20%	20%	20%	-	10%

6.3.3 Distributions of parameter values in "acceptable" models

Plankton

Biomass estimates of phytoplankton giving rise to "acceptable" models cover the full spread of values within the 20% confidence limits about the estimated mean (Appendix B, Fig. B 1). Biomass of phytoplankton, micro- and meso-zooplankton are biased towards the lower parts of their distributions in models of both decades (Appendix B, Figs B.1 —B.3). The distribution of macrozooplankton biomass in acceptable cases is dome-shaped (Appendix B, Fig. B.4). The maximum acceptable biomasses of micro-, meso- and macrozooplankton are less than those considered to be the upper limits (Table 6.3). In the case of microzooplankton, the largest biomass estimate required for acceptable models is half the set maximum. These results indicate that the southern Benguela ecosystem is unable to support very large biomasses of zooplankton, in particular microzooplankton which have high Q/B ratios, consume large quantities of phytoplankton and consume from within their own box. As expected from indications that zooplankton have become more abundant in recent years (Verheye *et al.* 1998), larger biomass estimates of micro-, meso- and macro-zooplankton give balanced models in the 1990s (Table 6.3). As a consequence of more abundant zooplankton in the 1990s, consumption of phytoplankton is greater than in the 1980s, explaining the maximum EE of 0.9 for "acceptable" models of the 1990s, compared to 0.6 for the 1980s. It is likely that the large maximum EE of phytoplankton during the 1990s is also partly because variability about simulated phytoplankton export was 10% in the 1990s and 20% in the 1980s.

Table 6.3 Estimated input ranges of zooplankton biomass used in *Ecoranger,* original mean biomasses from models presented in Chapters 4 and 5, and the ranges for which parameter combinations were "acceptable" *(Ecoranger* output). Units are t.km^{-2}.

	Estimated input ranges *(Ecoranger)*	1980s model		1990s model	
		Original mean estimated by *Ecopath*	Output range *(Ecoranger)*	Original mean estimated by *Ecopath*	Output range *(Ecoranger)*
Microzooplankton	1.0-11.0	7.473	1.0-5.0	8.195	1.2-5.6
Mesozooplankton	1.0-23.5	8.031	4.9-18.1	8.737	5.3-20.5
Macrozooplankton	1.8-21.9	13.301	11.4-17.8	14.562	11.0-19.2

Anchovy, sardine and redeye

Biomass estimates of anchovy and sardine are skewed towards the upper parts of their ranges (10% about the input means) in both decades (Appendix B, Figs B5 and B6), reflecting the importance of sufficient anchovy and sardine to support consumption by other groups in the system, and catches by the pelagic fisheries. If large amounts of small pelagic fish are discarded in the South African pelagic fishery, this finding would be further exaggerated. The ranges of EEs of these three most abundant small pelagic fish in "acceptable" models are similarly high in both decades, indicating that the proportions of their available production that are consumed or caught are large and remain constant from the 1980s to the 1990s.

Distributions of redeye biomass differ between decades (Appendix B, Fig. B7). In the 1980s, when the biomass estimate is input to the model, there is a bimodal distribution of "acceptable" biomasses. In the 1990s, when biomass required by the system is estimated, more "acceptable" runs are obtained when redeye biomass is close to the output value of the original model, i.e. in the lower half of the estimated range. Although the original mean redeye biomass is higher in the 1990s (Chapter 4, Table 4.6), means of acceptable cases and redeye biomass for which system biomass is maximized are smaller in the 1990s (Table 6.4 and 6.5). These results and distributions indicate that the southern Benguela ecosystem is less tightly controlled and therefore less restricted in the 1990s (see also Chapter 4, section 4.6.2).

Mesopelagic fish

One of the criteria for accepting models is that estimated mesopelagic fish biomass falls between 4.5 and 10.9 $t.km^{-2}$ (Table 6.2). In both decades, the bottom of the range of acceptable cases is larger than the set minimum. This is because mesopelagic fish are an important prey species in the system. There are more "acceptable" cases in the lower half of the range in the 1980s than in the 1990s (Appendix B, Fig. B8). These results are in agreement with original models, in which mesopelagic fish biomass was required to be larger in the 1990s. However, the mean biomass of mesopelagic fish in "acceptable" models is lower than original estimates in both decades (Tables 6.4 and 6.5). In the mean model, the proportions of mesopelagic fish in the diets of predators remain almost identical to the original model. The lower mesopelagic fish biomass of "acceptable" models is related to the larger mean P/B ratio and the smaller mean Q/B ratio than in the original models (Tables 6.4 and 6.5). At the time of the study, the *Ecopath* software did not allow one to save *Ecoranger* models in which mesopelagic fish biomass was particularly low. Therefore it is difficult to say whether the contribution of mesopelagic fish in the diets of predators was smaller when mesopelagic fish biomass was small, and if so, to which groups some of the predation pressure was shifted.

Snoek

In the 1990s, biomass of snoek required to sustain catches and consumption in the system is estimated. Snoek biomass in "acceptable" models of the 1990s ranges between 54 000 t and 98 000 t, compared to the original estimate of 53 000 t used for the 1980s. Therefore, as suspected from catch data (Chapter 4, Table 4.2), it is likely that either snoek abundance has increased over the later decade, or the availability of snoek to fisheries and predators within the southern Benguela ecosystem has increased. In contrast to catches of most other linefish species, there is no evidence of a declining catch trend for snoek (Griffiths 2000). In fact, Griffiths (2000) mentions that present catch per unit effort *(cpue)* estimates for snoek may be negatively biased because there is intense competition between vessels fishing on the same shoals. In the southern Cape, snoek *cpue* increased between 1986 and 1998 because offshore pinnacles of the central Agulhas Bank were exploited (Griffiths 2000).

Table 6.4 Comparison of parameters of the original model, means of acceptable models, and parameter values for which biomass of the southern Benguela ecosystem during the 1980s is maximized. Output parameters estimated by the original model are shaded.

Group	Biomass (B, $t.km^{-2}.y^{-1}$)			Production/B (P/B, y^{-1})			Consumption/B (Q/B, y^{-1})			Ecotrophic efficiency (EE)		
	Original	Mean	Max B	Original	Mean	Max B	Original	Mean	Max B	Original	Mean	Max B
Phytoplankton	76.938	75.541	71.418	154.40	155.80	150.11	n/a	n/a	n/a	0.583	0.307	0.390
Benthic producers	6.339	6.064	9.674	15.00	15.12	17.49	n/a	n/a	n/a	0.500	0.473	0.363
Microzooplankton	7.473	2.482	3.189	482.00	477.96	462.09	1928.00	1922.63	1790.57	0.950	0.950	0.944
Mesozooplankton	8.031	9.400	13.926	40.00	41.25	27.91	133.33	135.92	129.13	0.950	0.948	0.994
Macrozooplankton	13.301	13.928	15.801	13.00	12.81	13.55	31.71	31.73	32.14	0.950	0.958	0.998
Gelatinous zooplankton	4.545	4.451	4.399	0.58	0.58	0.71	1.67	1.70	1.71	0.155	0.168	0.116
Anchovy	5.216	5.382	4.946	1.20	1.24	1.20	12.30	12.41	12.58	0.997	0.911	1.020
Sardine	0.586	0.599	0.626	1.20	1.23	1.26	12.37	12.34	13.21	0.994	0.925	0.905
Redeye	5.555	8.296	11.079	1.20	1.19	1.22	12.00	11.90	10.89	0.961	0.641	0.655
Other small pelagics	0.364	0.380	0.389	1.00	1.05	1.13	10.00	9.84	9.49	0.907	0.794	0.729
Chub mackerel	0.284	0.297	0.225	0.90	0.90	0.85	9.00	9.16	9.31	0.768	0.726	0.876
Juvenile horse mackerel	0.200	0.325	0.324	1.20	1.20	1.29	12.00	11.95	12.72	0.936	0.602	0.549
Adult horse mackerel	1.618	1.624	1.936	1.00	0.94	0.96	10.00	10.05	10.78	0.806	0.803	0.667
Mesopelagics	8.642	7.874	10.684	1.20	1.22	1.30	12.00	11.90	11.99	0.990	0.989	0.994
Snoek	0.240	0.249	0.22	0.50	0.53	0.56	5.00	4.86	5.65	0.997	0.863	0.965
Other large pelagics	0.131	0.129	0.122	0.48	0.49	0.47	5.60	5.54	5.11	0.916	0.864	0.867
Cephalopods	1.364	1.383	1.285	3.50	3.51	3.66	10.00	9.89	11.01	0.892	0.833	0.985
Small *M. capensis*	0.592	0.595	0.578	2.00	1.99	2.09	13.33	13.22	13.64	0.999	0.999	0.999
Large *M. capensis*	0.823	0.822	0.798	0.80	0.82	0.76	4.40	4.33	4.11	0.984	0.890	0.956
Small *M. paradoxus*	1.698	1.616	1.663	2.00	2.02	2.06	13.33	13.18	12.51	0.999	0.999	0.999
Large *M. paradoxus*	0.684	0.684	0.717	0.80	0.81	0.78	4.70	4.65	4.28	0.974	0.888	0.877
Pelagic-feeding demersals	3.445	3.184	5.462	1.00	1.03	0.80	5.00	4.83	5.77	0.990	0.983	0.978
Benthic-feeding demersals	3.511	3.117	3.96	1.00	1.01	1.00	5.00	4.89	4.71	0.990	0.983	0.975
Pelagic-f. chondrichthyans	0.582	0.511	0.694	0.50	0.52	0.42	4.55	4.10	3.85	0.993	0.828	0.899
Benthic-f. chondrichthyans	0.873	0.793	0.861	1.00	1.03	0.89	10.00	9.86	11.96	0.725	0.697	0.987
Apex chondrichthyans	0.045	0.041	0.043	0.50	0.50	0.57	5.00	4.95	5.13	0.000	0.000	0.000
Seals	0.133	0.132	0.138	0.95	0.76	0.39	19.31	19.15	18.18	0.454	0.568	0.939
Cetaceans	0.074	0.072	0.061	0.60	0.62	0.71	10.00	9.76	8.29	0.760	0.694	0.732
Seabirds	0.015	0.015	0.015	0.12	0.13	0.12	118.27	113.49	113.41	0.962	0.913	0.938
Meiobenthos	11.812	11.377	15.386	4.00	3.95	4.57	33.00	33.01	28.43	0.950	0.938	0.937
Macrobenthos	56.109	40.248	63.263	1.20	1.17	1.05	10.00	10.07	10.52	0.950	0.938	0.954

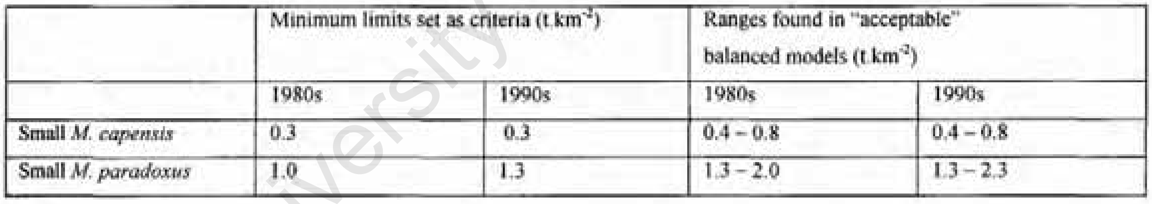
Table 6.5 Comparison of parameters of the original model, the means of acceptable models, and parameter values for which biomass of the southern Benguela ecosystem during the **1990s** is maximized. Output parameters estimated by the original model are shaded.

Group	Biomass (B, t.km^{-2}.y^{-1})			Production/B (P/B, y^{-1})			Consumption/B (Q/B, y^{-1})			Ecotrophic efficiency (EE)		
	Original	Mean	Max B	Original	Mean	Max B	Original	Mean	Max B	Original	Mean	Max B
Phytoplankton	76.938	76.254	83.53	154.40	154.55	178.76	n/a	n/a	n/a	0.636	0.326	0.333
Benthic producers	6.548	5.826	9.057	15.00	14.74	13.97	n/a	n/a	n/a	0.500	0.48	0.429
Microzooplankton	8.195	2.66	4.103	482.00	484.01	453.15	1928.00	1927.745	1814.274	0.950	0.949	0.909
Mesozooplankton	8.737	10.332	14.471	40.00	38.52	26.58	133.33	134.629	129.719	0.950	0.951	0.912
Macrozooplankton	14.562	14.731	14.734	13.00	12.98	13.71	31.71	31.738	29.155	0.950	0.949	0.994
Gelatinous zooplankton	5.000	4.956	6.105	0.58	0.58	0.72	1.67	1.703	2.160	0.152	0.169	0.155
Anchovy	3.573	3.628	3.875	1.20	1.23	1.14	12.30	12.281	11.214	0.990	0.915	0.982
Sardine	2.091	2.132	2.167	1.20	1.23	1.17	12.37	12.347	12.306	0.990	0.908	0.962
Redeye	6.226	8.037	9.444	1.20	1.20	1.27	12.00	11.969	12.180	0.990	0.749	0.738
Other small pelagics	0.364	0.378	0.402	1.00	1.06	0.97	10.00	9.925	9.581	0.934	0.822	0.934
Chub mackerel	0.455	0.447	0.392	0.80	0.80	0.76	8.00	7.993	8.101	0.663	0.677	0.751
Juvenile horse mackerel	0.484	0.515	0.453	1.20	1.20	1.18	12.00	11.904	11.389	0.663	0.613	0.698
Adult horse mackerel	1.937	2.114	2.145	1.00	0.91	0.92	10.00	10.021	10.453	0.818	0.808	0.791
Mesopelagics	10.242	9.391	10.112	1.20	1.20	1.17	12.00	12.078	11.890	0.990	0.989	0.99
Snoek	0.337	0.324	0.342	0.50	0.52	0.47	5.00	4.781	4.784	0.990	0.984	0.995
Other large pelagics	0.131	0.133	0.143	0.48	0.49	0.51	5.60	5.582	5.182	0.900	0.844	0.876
Cephalopods	1.364	1.372	1.552	3.50	3.68	3.57	10.00	9.532	11.506	0.953	0.858	0.837
Small *M. capensis*	0.638	0.599	0.747	2.00	2.03	1.99	13.33	13.235	12.571	0.999	0.999	0.999
Large *M. capensis*	1.127	1.113	1.215	0.80	0.81	0.85	4.40	4.352	4.112	0.831	0.809	0.794
Small *M. paradoxus*	1.878	1.756	1.969	2.00	2.03	1.84	13.33	13.168	12.200	0.999	0.999	0.999
Large *M. paradoxus*	1.067	1.058	1.155	0.80	0.79	0.75	4.70	4.695	4.536	0.791	0.791	0.776
Pelagic-feeding demersals	3.693	3.341	4.578	1.00	1.02	0.81	5.00	4.909	5.165	0.990	0.985	0.981
Benthic-feeding demersals	3.719	3.465	4.076	1.00	1.01	0.85	5.00	4.848	4.635	0.990	0.984	0.991
Pelagic-f. chondrichthyans	0.582	0.555	0.718	0.50	0.52	0.56	4.55	4.228	3.825	0.993	0.84	0.943
Benthic-f. chondrichthyans	0.873	0.852	0.755	1.00	1.02	1.19	10.00	9.908	11.56	0.731	0.696	0.731
Apex chondrichthyans	0.045	0.042	0.032	0.50	0.50	0.46	5.00	4.885	4.033	0.000	0.000	0.000
Seals	0.133	0.133	0.144	0.95	0.68	0.84	19.31	19.043	19.614	0.427	0.593	0.271
Cetaceans	0.082	0.081	0.075	0.60	0.60	0.56	10.00	9.953	9.873	0.686	0.629	0.479
Seabirds	0.012	0.012	0.012	0.12	0.13	0.13	118.27	114.806	121.68	0.962	0.914	0.934
Meiobenthos	12.201	10.679	16.125	4.00	4.01	4.26	33.00	32.991	30.936	0.950	0.940	0.939
Macrobenthos	57.957	39.753	69.247	1.20	1.21	0.97	10.00	9.932	9.312	0.950	0.937	0.912

Hakes

Small *M capensis* biomass is distributed in a dome-shape about the mean of "acceptable" cases, whereas biomass of large *M capensis* is more evenly distributed across its full range within 10% of the original means (Appendix B, Figs B.9 and B.10). Biomass estimates of small *M paradoxus* required to sustain catches and support consumption are skewed to the left in both decades (Appendix B, Fig. B 11). As in the case of mesopelagic fish, lower mean biomass is the result of slightly larger mean P/B ratios and mostly slightly smaller mean Q/B ratios of "acceptable" models compared to those in the original models of the two decades (Tables 6.4 and 6.5). Diets in the mean "acceptable" model remain very similar to those of original models. In the 1980s, mean parameters of hakes in "acceptable" models are closer to the means used in original models (Tables 6.4) than in the 1990s (Table 6.5). Estimates of maximum biomass of small hake are more than twice the survey biomass estimates. Surveys are likely to underestimate the stock size of small hake (Chapter 4, section 4.5.2). Therefore survey estimates are considered as minimum estimates of small hake biomass (Table 6.6).

Table 6.6 Ranges of biomass estimates of small hake



	Minimum limits set as criteria (t.km^{-2})		Ranges found in "acceptable" balanced models (t.km^{-2})	
	1980s	1990s	1980s	1990s
Small *M. capensis*	0.3	0.3	0.4 – 0.8	0.4 – 0.8
Small *M. paradoxus*	1.0	1.3	1.3 – 2.0	1.3 – 2.3

Groups for which biomass is poorly known

Variability about biomass estimates of cephalopods, chondrichthyans and cetaceans is assumed to be high (30%, Table 6.2) because estimates for these groups are poor. Despite selecting from uniform distributions about the original means of these groups, mean biomass estimates in "acceptable" models are close to the original values (Tables 6.4 and 6.5), underlining the fact that the models of the southern Benguela ecosystem during the 1980s and 1990s are tightly constrained.

6.3.4 Maximizing total biomass of the system

Mature systems are characterized by large biomasses (relative to total system throughput) and low P/B ratios (Odum 1969). In turn, systems subject to frequent disturbances are dominated by species with fast turnover rates (high P/B ratios), favourable for recolonization. In such a case, total system biomass is likely also to be large, but due to the high turnover rate in the system, the total biomass relative to total system throughput is small. The latter may be true for upwelling systems, which by their very nature are a fluctuating environment, frequently perturbed and characterized by a few, small, highly productive and abundant species. In this section of the study, parameter combinations for which system biomass is maximized are explored. The closer the actual system biomass is to that in the maximized biomass model, the closer the system is to realizing its potential to respond to and cope with perturbations, as genetic diversity in the populations is likely to be large if biomasses are high. The maximised biomass is then related to the relative biomasses at low trophic levels in the respective model to address the extent to which conclusions on system maturity can be drawn.

It should be noted that there are likely to be confounding effects between estimates of biomass, ecotrophic efficiencies and production/biomass, and these should be taken into account when examining the results of the maximized biomass model.

Biomass

Maximum biomass of "acceptable" models of the southern Benguela ecosystem is 10% more than the original 1980s model, and 15% more than the original 1990s model (Table 6.7). The "acceptable" model in which system biomass is maximized in the 1980s is one in which phytoplankton biomass is smaller than the biomass of phytoplankton in the original model and the mean phytoplankton biomass of the 54 "acceptable" models (Table 6.4). Conversely, in the 1990s model, maximum system biomass is reached when phytoplankon biomass is larger than the original estimate (Table 6.5). Surprisingly, biomass estimates of some other boxes are lower in the maximized biomass models than in original models. These include apex predators such as chub mackerel and apex chondrichthyans, but more surprisingly also benthic chondrichthyans and microzooplankton. In the 1990s, estimates of juvenile horse mackerel and mesopelagic fish are smaller in the maximized model (Table 6.5). Additional boxes having biomass values smaller than those in the original model of the 1980s include gelatinous zooplankton, anchovy, snoek, other large pelagic fish, cephalopods, hakes and cetaceans (Table 6.4). When biomass is maximized in the 1980s, biomasses of many boxes, expressed as a proportion of the combined biomass of planktonic and benthic boxes, are larger than in the original model (Fig. 6.1). Expressing biomasses in this way considers the efficiency of resource use rather than a simple increase in absolute biomasses that are supported when biomasses of "base food" boxes are larger. The boxes accounting for most of the maximization of system biomass in the 1980s are redeye, juvenile horse mackerel and pelagic-feeding demersal fish (Fig. 6.1). In contrast, when system biomass is maximized in the 1990s, biomasses of most boxes, relative to the biomass of planktonic and benthic boxes, are smaller than in the original 1990s model. Therefore, the boxes at low trophic levels are being more efficiently utilized in the original 1990s model than they would be if the system supported a larger total biomass in this decade. This is because increased system biomass is largely as a result of increased zooplankton biomass. Conversely, in the 1980s, larger system biomass could be attained through increases across most boxes.

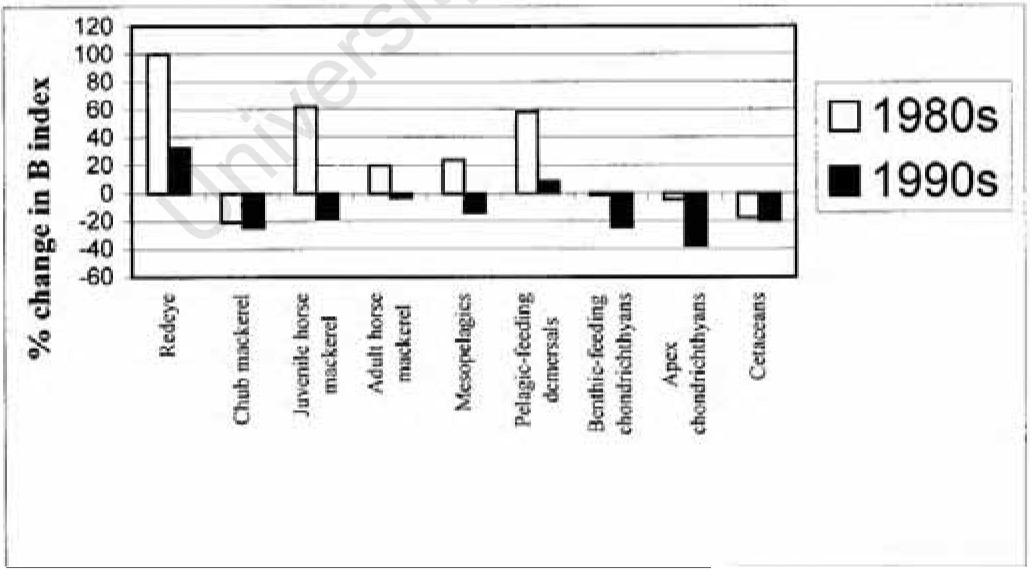
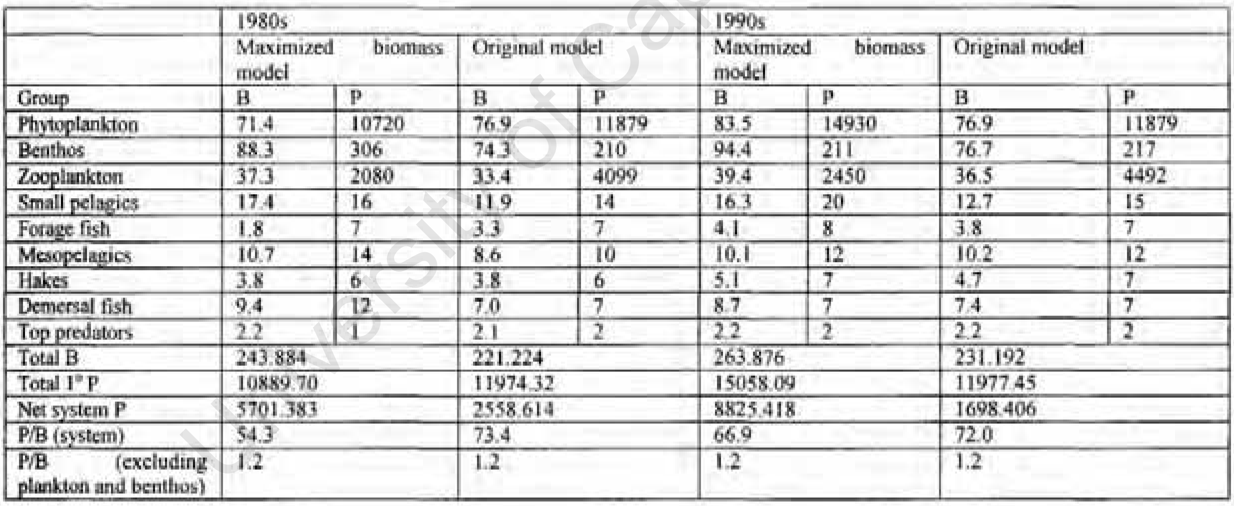


Figure 6.1 Proportional changes (%) in biomass indices of selected groups in the maximized models of the southern Benguela ecosystem during the 1980s and 1990s, compared to biomass indices of original models. Biomass indices are the biomass of the group expressed as a proportion of the total biomass of the planktonic and benthic

groups. Only groups having a relative index of + or — 20% in at least one decade are included.

Table 6.7 Biomass (B, t.km^{-2}) and production (P, t.km^{-2}.y^{-1}) of aggregated trophic boxes and total system biomass (B, t.km^{-2}), primary production (1° P, t.km^{-2}.y^{-1}) and net system production (t.km^{-2}.y^{-1}) of all boxes in the southern Benguela ecosystem, estimated by original models and those for which total system biomass is maximized. Groups are aggregated as follows: benthos (benthic producers and meio- and macro-benthos), zooplankton (micro-, meso- and macro-zooplankton and gelatinous zooplankton), small pelagics (anchovy, sardine, redeye, other small pelagic fish, juvenile horse mackerel), forage fish (chub mackerel, adult horse mackerel, cephalopods), mesopelagics (mesopelagic fish), hakes (large and small *M capensis* and *M paradoxus),* demersal fish (other pelagic-feeding and benthic-feeding demersal fish), and top predators (snoek, large pelagic fish, chondrichthyans, cetaceans, seals and seabirds).



	1980s				1990s			
	Maximized biomass model		Original model		Maximized biomass model		Original model	
Group	B	P	B	P	B	P	B	P
Phytoplankton	71.4	10720	76.9	11879	83.5	14930	76.9	11879
Benthos	88.3	306	74.3	210	94.4	211	76.7	217
Zooplankton	37.3	2080	33.4	4099	39.4	2450	36.5	4492
Small pelagics	17.4	16	11.9	14	16.3	20	12.7	15
Forage fish	1.8	7	3.3	7	4.1	8	3.8	7
Mesopelagics	10.7	14	8.6	10	10.1	12	10.2	12
Hakes	3.8	6	3.8	6	5.1	7	4.7	7
Demersal fish	9.4	12	7.0	7	8.7	7	7.4	7
Top predators	2.2	1	2.1	2	2.2	2	2.2	2
Total B	243.884		221.224		263.876		231.192	
Total 1° P	10889.70		11974.32		15058.09		11977.45	
Net system P	5701.383		2558.614		8825.418		1698.406	
P/B (system)	54.3		73.4		66.9		72.0	
P/B (excluding plankton and benthos)	1.2		1.2		1.2		1.2	

For maximized biomass in the 1980s model, system production is only 81% of that in the original model because of lower zooplankton production when zooplankton biomass is maximized (Table 6.7). Conversely, in the 1990s, phytoplankton production increases when biomass is maximized, so that although zooplankton production decreases with increased zooplankton biomass, total system production is 6% larger than in the original 1990s model (Table 6.7). Overall, this means that for biomass to be maximized in the southern Benguela ecosystem, slower turnover rates (smaller P/B ratios of the system) are required than when the model was based on observed biomass (Table 6.7).

Production at higher trophic levels increases when system biomass is maximized, but overall system turnover rates (P/B ratios) are the same as those when the original parameters are used. When variability about parameters of groups at the lower trophic levels (planktonic and benthic boxes) is severely restricted, and variability about parameters of other groups is retained (as in Table 6.2), maximum total biomass (excluding detritus) supported in the 1980s increases by only 2%, compared to a 17% increase in the 1990s. This shows that as alluded to previously (Chapter 4, Section 4.6.2, this chapter, section 6.1), trophic flows through the southern Benguela ecosystem are more constrained in the 1980s than in the 1990s. This reflects that the limited scope for increased biomass to be supported in the 1980s is not restricted to planktonic and benthic groups at low trophic levels. Therefore, the differences between the trophic functioning in the maximized biomass and actual situations are mainly due to differences in the planktonic groups and not to major differences in biomasses or productivity of groups at higher trophic levels (fish and their predators). This has implications for the interpretation of system maturity and maximized biomass of upwelling systems. The traditional classification of system maturity may not be entirely applicable to upwelling systems, which can be limited in their ability to respond to increased food supplies by interactions at high trophic levels.

Ecotrophic efficiencies

The EE of anchovy is slightly greater than 1 in the maximized biomass model of the 1980s, but when rounded to one decimal place, does not exceed 1.0, which accounts for the model being accepted. Therefore, in this case, production by anchovy is slightly less than anchovy consumption and harvesting, suggesting that anchovy were over-utilized.

When total biomass is maximized in the southern Benguela ecosystem, the EE of phytoplankton is a third less than in the original 1980s model, and almost half that of the original 1990s model (Tables 6.4 and 6.5). This is largely because consumption of phytoplankton by microzooplankton is much reduced in the maximized models (microzooplankton biomass was smaller because intra-box consumption of microzooplankton was reduced — see second paragraph of section 6.3.1). Mesozooplankton biomass is larger in the maximized biomass model than in the original or mean models, because mesozooplankton is an important prey group of predators such as redeye, mesopelagic fish and horse mackerel. Larger stocks of these mesozooplanton feeders are supported in the maximized biomass situation.

Because biomass estimates of juvenile horse mackerel in the 1980s, and adult horse mackerel and redeye in both decades are required to be larger in the maximized models, the EEs of these groups are much lower than in original models (Tables 6.4 and 6.5).

Production/biomass ratios

In maximized models, the P/B ratios of three groups are noticeably different from those in original models (Tables 6.4 and 6.5).

i) For both decades, the P/B ratio of mesozooplankton is only two thirds that originally assumed (40 y^{-1}). However, given the larger biomass of mesozooplankton, production is actually 20% more in the 1980s and 9% more in the 1990s than in original models.

ii) There is uncertainty about the P/B ratio of seals, and a wide range of values is acceptable. In the maximized biomass model of the 1980s, the seal P/B ratio is less than half the original ratio of 0.95 y^{-1}. Seal biomass is almost the same, corresponding to production only 40% of that in the original model, so that EE is high in the maximized model (Table 6.4). The difference between P/B ratios in maximized biomass and original models is much smaller in the 1990s (Table 6.5), when seal culling had ceased and variability about this parameters was reduced.

iii) For both decades, the P/B ratio of pelagic-feeding demersal fish is at the bottom of its range of 20% about the mean (Tables 6.4 and 6.5). Because biomass is larger in the maximized model of the 1990s, production of pelagic-feeding demersal fish is similar to that in the original model. However, in the 1980s, production is 27% larger in the maximized biomass model.

6.3.5 Alternative estimates

Using a larger estimate of gelatinous zooplankton biomass

Originally, biomass of gelatinous zooplankton was estimated to be 55 million tons (A.J. Boyd, MCM, pers. comm.), whereas the estimate used in Chapter 4 is 1 million tons (L. Hutchings, MCM, pers. comm.). The southern Benguela ecosystem is unable to sustain the 55 million t because the increased consumption of "detritus" by gelatinous zooplankton caused the EE of detritus to exceed 200% in both decades. In addition, twice the original estimates of biomass of microzooplankton and mesozooplankton, and 27% (1990s) and 30% (1980s) more macrozooplankton biomass would be needed to support consumption by the increased gelatinous zooplankton standing stock.

Assuming a smaller Production/Biomass ratio for sardine in the 1990s

Assuming the P/B ratio is equivalent to total mortality (Z) under steady-state, i.e. the sum of fishing mortality (F) and natural mortality (M), the P/B ratio for sardine is calculated to be 1.2 31^{-1} in the 1980s and 1.0 $3T^{-1}$ in the 1990s (Table A.2, Appendix A). This estimate is obtained from F calculated to be 0.37 y^{-1} in the 1980s and 0.18 y^{-1} in the 1990s (unpublished data of MCM), and M estimated to be 0.8 37^{-1} (De Oliveira *et al.* 1998a). It compares to the estimate of 1.1 $3/^{1}$ for sardine in the northern Benguela (Hewitson and Cruikshank 1993). For the model in Chapter 4, the P/B ratio of sardine is assumed to be 1.2 $3T^{-1}$ in both decades to account for the increase in sardine biomass between the 1980s and 1990s. When the southern Benguela model is re-run with a P/B ratio of 1.0 37^{-1} for sardine in the 1990s, production of sardine is insufficient to sustain consumption of sardine by other groups in the system (EE=119%). Reduced consumption by sardine causes a small reduction in the EE of phytoplankton from 63.6% to 63.2%, and 0.4% less micro-, meso- and macrozooplankton biomass are required. Therefore, M is likely to be larger than 0 8 y^{-1} used in stock-assessment models in which only post-recruits are considered. It is also linked to a change in predator composition and biomass, which changed between the 1980s and 1990s.

Using smaller Production/Biomass ratios for chub mackerel

Originally, Jarre-Teichmann *et al.* (1998) used P/B ratios of 0.6 $3T^{-1}$ and 0.5 y^{-1} respectively for the 1980s and 1990s. These are smaller than values of 0.9 $3/^{-1}$ and 0.8 y^{-1} used in Chapter 4, the larger values being in line with estimates for chub mackerel off Northwest Africa. When the smaller P/B ratios are used, consumption of chub mackerel by its predators exceeds chub mackerel production and the EE of the group is 115%. Biomasses and EEs of groups consumed by chub mackerel are reduced. Estimates of biomass of micro-, meso- and macrozooplankton required to support consumption are 1-2% smaller than previously. In the 1980s, the EE of anchovy decreases from 99.7% to 99.4%, and that of redeye from 96.1% to 96.0%. In the 1990s, the EEs of anchovy and sardine both decrease from 99.0% to 98.4%. Biomass of mesopelagic fish required to support consumption by chub mackerel is 1% less in the 1980s and 3% less in the 1990s, and biomass of redeye estimated for the 1990s is 4% less when reduced chub mackerel P/B ratios are assumed.

Assuming smaller Production/Biomass ratios for small hake

In this study, the P/B ratios of small hakes (0-2 years) are assumed to be high, in agreement with Bergh *et al.* (1985) who estimated rapid turnover of small hake as a result of high mortality. However, it is possible that P/B ratios of small hake may be similar to those of small pelagic fish such as anchovy and sardine, as considered by Jarre-Teichmann *et al.* 1998. Here, P/B ratios of small *M capensis* and *M paradoxus* of 1.2 y^{1} are tested (compared to 2.0 y^{-}' used in Chapter 4). In both decades, biomass of small hake of both species would be required to be 1.7 times that when P/B ratios are 2.0 y^{-1}, equivalent to between 2.7 and 4.6 times the biomasses estimated from production models using survey data (Fig. 6.2). Although it is probable that small hake have been undersampled in surveys (see Chapter 4, section 4.5.2), such large biomasses are probably overestimates. Therefore, it is likely that P/B of small hake as high as the value of at least 2.0 $y^{\cdot}$ used in this study (Chapter 4).

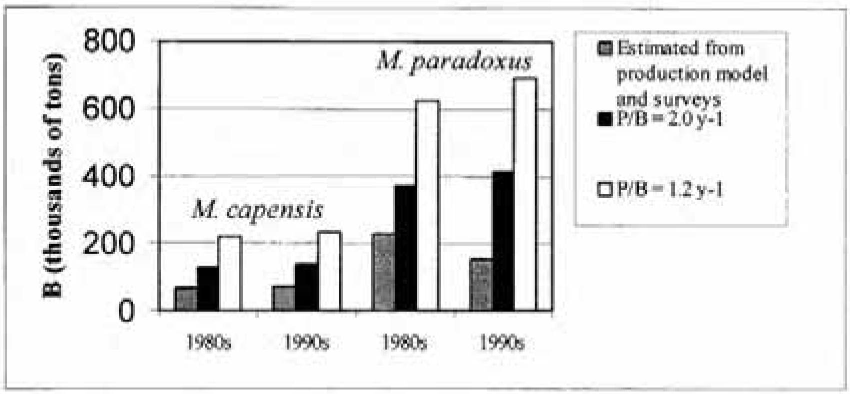


Fig. 6.2 Biomass of small hakes in the southern Benguela ecosystem during the 1980s and 1990s, as estimated from production models and surveys, and as estimated here using indicated values for P/B ratios *(31')*.

Incorporating estimates of discards of small hake

It has been estimated that discarded small hake (<35 cm) amount to 24% of the hake caught by inshore trawlers on the south coast (Anonymous 1997, Chapter 4, Table 4.2). This is equivalent to 30% and 50% more small *M capensis* caught in the 1980s and 1990s respectively, and 2% and 10% more small *M paradoxus* in the 1980s and 1990s respectively. An additional 660 t small *M capensis* and 440 t small *M paradoxus* are required to sustain these discards in both decades. Slightly larger stocks of zooplankton, redeye, mesopelagic fish and demersal fish are required to support consumption of these groups by the increased hake stocks (Fig. 6.3). EEs are unaffected, indicating only a small change to the overall system if discards of this magnitude are included. However, effects may well be larger if hake are discarded in fisheries other than inshore trawls on the south coast. Only 6-7% of total catches of hake (excluding discards) are taken by the inshore trawl fishery on the south coast of South Africa (Chapter 4, Table 4.2).

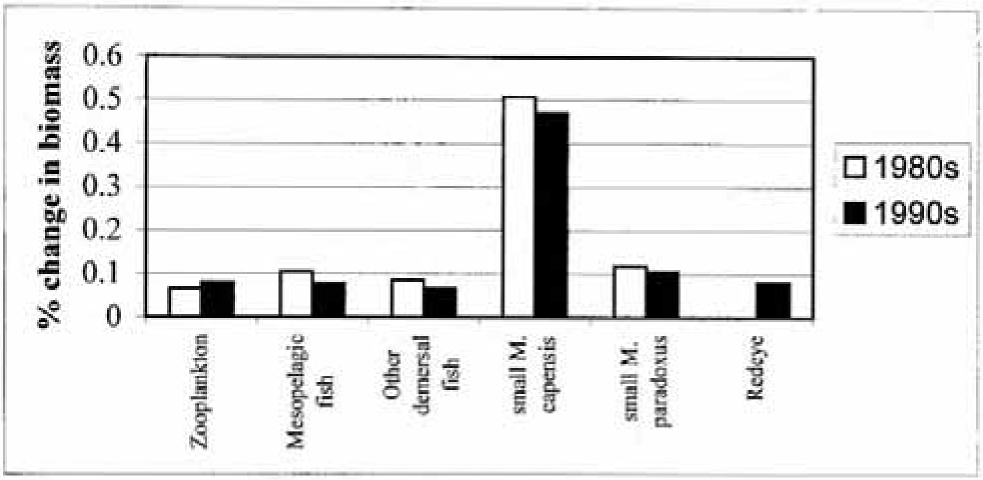
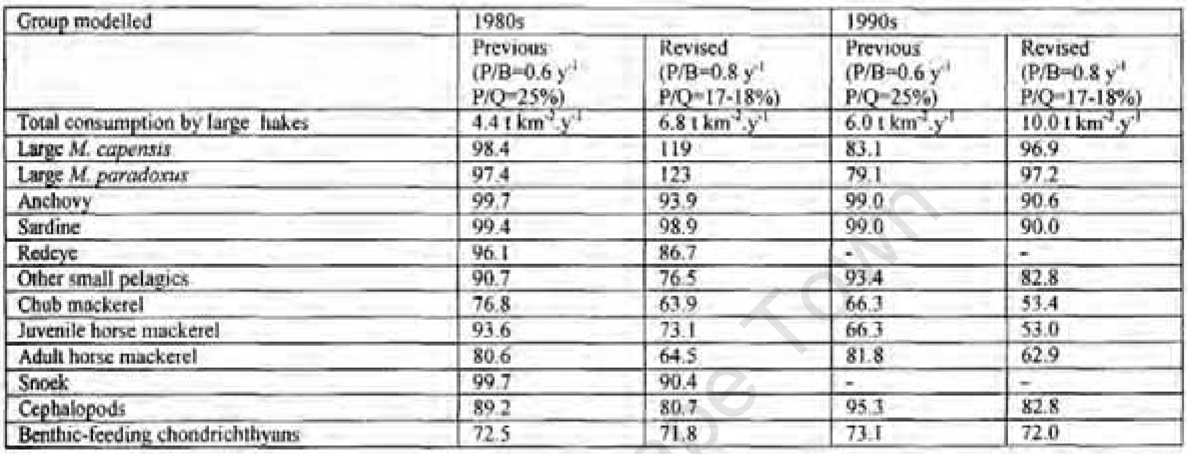


Fig. 6.3 Relative change (percentage) in estimated biomass required when discards of small hake in inshore trawls on the South African south coast are included in hake catches.

Exploring the use of different Production/Biomass and Production/Consumption ratios for large hake

In Chapter 4, a P/B ratio of 0.8 y' is used for large hake, and a P/Q ratio is estimated to be 18% for large *M paradoxus* and 17% for large *M capensis*, based on Q/B rates estimated by Punt and Leslie (1995). These values differ from those used previously; P/B and P/Q ratios for large hakes are assumed to be 0.6 y^{-1} and 25% respectively (Jarre-Teichmann *et al.* 1998). Using these reduced P/B and increased P/Q values, estimated biomasses of zooplankton, mesopelagic fish, small hakes, pelagic- and benthic-feeding demersal fish and macro- and meio-benthos are all reduced. This is because consumption of these groups by large hake is half that when the P/B ratio is 0.8 y' and the P/Q ratio is 17 or 18%. Larger differences in estimated biomasses are obtained in the 1990s than the 1980s because biomasses of large hakes were greater than for the 1980s. Reduced consumption by large hakes results in smaller EEs for groups on which large hake prey (Table 6.8). The 1980s model is unbalanced when the combination of small P/B and large P/Q values are used for large hake. EEs exceed 100% (Table 6.8), suggesting that production may be insufficient to support human exploitation and consumption by predators.

Table 6.8 Comparison of EEs (%) of large hakes and their prey when two combinations of P/B and P/Q are used. "Previous" values were P/B=0.6 y^{-1} and P/Q=25% (resulting in 2.2 $t.km^{-2}.y^{-1}$ and 3.0 $t.km^{-2}.y^{-1}$ consumed by each large hake group in the 1980s and 1990s respectively). "Revised" values are those used in this study (Chapter 4) i.e. P/B=0.8 y^{-1}, and P/Q=17-18% (resulting in 3.6 $t.km^{-2}.y^{-1}$ and 3.2 $t.km^{-2}.3/^{1}$ consumed by large *M capensis* and *M paradoxus* respectively in the 1980s, and 5.0 $t.km^{-2}.y^{-1}$ consumed by each large hake group in the 1990s).



Group modelled	1980s		1990s	
	Previous (P/B=0.6 y^{-1} P/Q=25%)	Revised (P/B=0.8 y^{-1} P/Q=17-18%)	Previous (P/B=0.6 y^{-1} P/Q=25%)	Revised (P/B=0.8 y^{-1} P/Q=17-18%)
Total consumption by large hakes	4.4 $t\ km^{-2}.y^{-1}$	6.8 $t\ km^{-2}.y^{-1}$	6.0 $t\ km^{-2}.y^{-1}$	10.0 $t\ km^{-2}.y^{-1}$
Large *M. capensis*	98.4	119	83.1	96.9
Large *M. paradoxus*	97.4	123	79.1	97.2
Anchovy	99.7	93.9	99.0	90.6
Sardine	99.4	98.9	99.0	90.0
Redeye	96.1	86.7	-	-
Other small pelagics	90.7	76.5	93.4	82.8
Chub mackerel	76.8	63.9	66.3	53.4
Juvenile horse mackerel	93.6	73.1	66.3	53.0
Adult horse mackerel	80.6	64.5	81.8	62.9
Snoek	99.7	90.4	-	-
Cephalopods	89.2	80.7	95.3	82.8
Benthic-feeding chondrichthyans	72.5	71.8	73.1	72.0

Using a smaller Production/Biomass ratio for seals

There was some concern that the estimate used at the 1989 workshop for P/B of seals was too large (0.946 y^{-1}, nearly as big as the P/B used for demersal fish and other small pelagic fish). In one of their *Ecopath* models, Heymans *et al.* (in prep.) used a P/B for seals as small as 0.03 y^{-1}, the minimum value allocated to seal P/B in my experiments of section 5.3 above. Further, it is felt that the P/B ratio should be at most half of the 1989 workshop estimate (A. Jane, Danish Institute of Fisheries, Denmark, and J.-P. Roux, Ministry of Fishery, Namibia, pers. comm.). Therefore, P/B=0.5 y^{-1} is tested. This value is close to that of 0.6 y^{-1} estimated for cetaceans (Chapter 4). In agreement with sensitivity analysis showing that the only parameter sensitive to a change in seal P/B ratio is the EE of seals (Table 6.1), modelling using this smaller P/B for seals has little effect besides increasing the EE of seals from 45.4% to 85.9%. The proportion of natural predation on hake and anchovy that is caused by seals remains unchanged, and when rounded to the nearest decimal place, total system throughput, sum of production and net system production are the same as when the larger P/B ratio is used.

CHAPTER SEVEN

MODELLING TROPHIC FLOWS THROUGH THE NORTHERN BENGUELA ECOSYSTEM: 1980-1989

ABSTRACT

A model of the trophic flows through the northern Benguela ecosystem between 1980 and 1989 was constructed using *Ecopath,* and is fully described. The model closes the temporal gap between models of the system in the 1970s and 1990s. The aim is to provide a workable model that can be a basis for discussion and can be compared to a similar one of the southern Benguela ecosystem for the same period. Ultimately, this type of model may form a basis for multispecies management approaches in the region. By the 1980s, sardine and hake stocks in the northern Benguela ecosystem had decreased, yet were still heavily fished. Horse mackerel had increased over the previous decade, and was the dominant pelagic species during the 1980s, with large catches. Production by some groups was insufficient to sustain consumption by other components of the system. 1.5 million tons of pelagic goby, 1.7 million tons of mesopelagic fish and 0.7 million tons of demersal fish (excluding hake) were required to support predators in the northern Benguela sub-system. By examining the effects of alternative estimates for some parameters, uncertainty in parts of the model is highlighted and our confidence in other parameter estimates is improved.

7.1 INTRODUCTION

In order to summarize results of the Benguela Ecology Programme (BEP), experts working on different groups in the Benguela region brought together both published and unpublished data at a workshop held in Cape Town in 1989. The workshop resulted in simple input-output carbon budgets of the northern and southern Benguela sub-systems for the period 1980-1989. Based on these results, together with more recently published data and other unpublished data, *Ecopath* models have been prepared of the two systems during the 1980s, and of the southern Benguela sub-system during the 1990s. The model for the northern Benguela sub-system is presented in this chapter.

To date, a number of attempts have been made to model the trophic flows through the Northern Benguela sub-system. Using the ***Ecopath*** modelling approach (Christensen and Pauly 1992), trophic functioning of the northern Benguela sub-system has been examined for three periods, namely 1971-1977 and 1978-1983 (Jarre-Teichmann 1998, Jarre-Teichmann and Christensen 1998a, Jarre-Teichmann and Christensen 1998b) and 1990-1995 (Heymans 1996, Heymans and Baird 2000). This chapter presents the first attempt at modelling trophic flows in the northern Benguela ecosystem between 1980 and 1989, closing the temporal gap between the previous models.

What were perceived to be the most relevant and useful data for the 1980s were used in this model. The aim of the chapter is not to compare in detail this model to others developed for the ecosystem; this is being undertaken separately as part of a large collaborative multi-national programme on multispecies management. Rather, the model presented here was constructed to facilitate comparisons with the southern Benguela model over the same period (Chapter 8). In this chapter key question 2a is addressed: what are the biomass, production, consumption and catches of the components of the northern Benguela ecosystem during the 1980s?

7.2 DATA USED FOR THE TROPHIC MODEL OF THE NORTHERN BENGUELA ECOSYSTEM

7.2.1 Input data

The northern Benguela model covers the shelf region to approximately the 500m depth contour, extending from 15 °S (just north of the Cunene River, near the boundary between Angola and Namibia) to 29°S (Orange River, near the boundary between Namibia and South Africa), over an area of 179 000 km ^{2}. Input data and their sources are tabulated in Appendix C, Tables C 1 -C7. Where values used differ from original values, revised values and explanatory comments are provided.

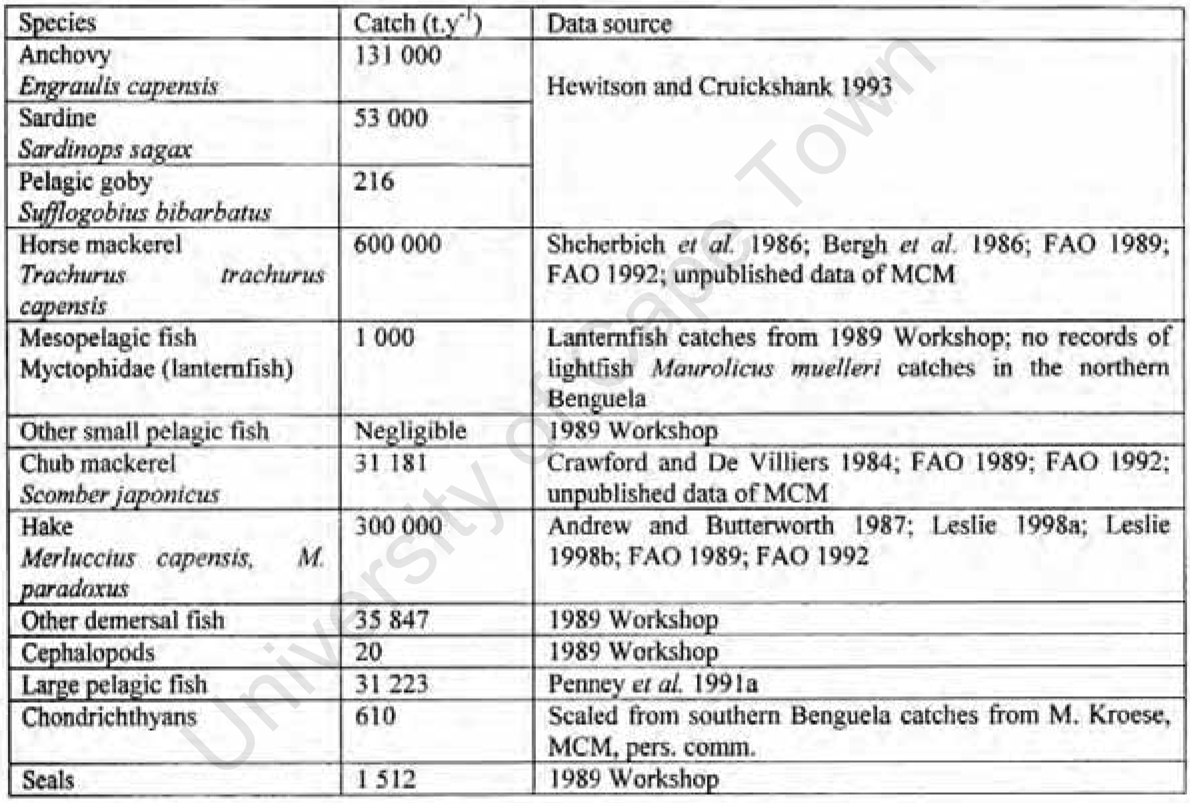
In the model, the detritus box receives faecal material, or material through residual mortality from other boxes. Using the method of Pauly *et al.* (1990), Regier *et al.* (1990) and Pauly *et al.* (1993), for a euphotic zone depth of 35m and primary production of 510.23g $C.m^{-2}$, the biomass of detritus off Namibia was calculated to be 59.027g $C.m^{-2}$ (corresponding in wet mass to 841 $tons•km^{-2}$). No other parameters for detritus are required in *Ecopath* models.

As in the southern Benguela models, bacteria are not an explicit part of the model because insufficient information on bacterial activity is available for the northern Benguela ecosystem. Therefore bacterial activity and consumption of bacteria remain "hidden" in the detritus compartment, as has been the case in many other models (e.g. Christensen and Pauly 1993).

7.2.2 Catch data

Catches in the northern Benguela sub-system during the 1980s are reported in Table 7.1.

Table 7.1. Mean annual catches in the northern Benguela ecosystem during the 1980s. "1989 Workshop" refers to estimates made during the Benguela ecosystem modelling workshop held in 1989 (see section 7.1).



Species	Catch ($t.y^{-1}$)	Data source
Anchovy *Engraulis capensis*	131 000	Hewitson and Cruickshank 1993
Sardine *Sardinops sagax*	53 000	
Pelagic goby *Sufflogobius bibarbatus*	216	
Horse mackerel *Trachurus trachurus capensis*	600 000	Shcherbich *et al.* 1986; Bergh *et al.* 1986; FAO 1989; FAO 1992; unpublished data of MCM
Mesopelagic fish Myctophidae (lanternfish)	1 000	Lanternfish catches from 1989 Workshop; no records of lightfish *Maurolicus muelleri* catches in the northern Benguela
Other small pelagic fish	Negligible	1989 Workshop
Chub mackerel *Scomber japonicus*	31 181	Crawford and De Villiers 1984; FAO 1989; FAO 1992; unpublished data of MCM
Hake *Merluccius capensis, M. paradoxus*	300 000	Andrew and Butterworth 1987; Leslie 1998a; Leslie 1998b; FAO 1989; FAO 1992
Other demersal fish	35 847	1989 Workshop
Cephalopods	20	1989 Workshop
Large pelagic fish	31 223	Penney *et al.* 1991a
Chondrichthyans	610	Scaled from southern Benguela catches from M. Kroese, MCM, pers. comm.
Seals	1 512	1989 Workshop

7.2.3 Diet data

Data on the diet of species in the northern Benguela ecosystem during the 1980s are estimated from a number of sources (Table 7.2). The diet composition matrix compiled for the northern Benguela ecosystem is in Appendix C (Table C.8).

Table 7.2 Sources of data on the diets of boxes in the northern Benguela model for the 1980s.

Species group	Data source
Microzooplankton	Assumed same as in southern Benguela ecosystem; Jarre-Teichmann *et al.* 1998.
Mesozooplankton	Hutchings *et al.* 1991.
Macrozooplankton	Hutchings *et al.* 1991.
Gelatinous zooplankton	Assumed same as in southern Benguela ecosystem; Jarre-Teichmann *et al.* 1998.
Anchovy	King and MacLeod 1976, Hewitson and Cruickshank 1993.
Sardine	King and MacLeod 1976.
Pelagic Goby	Crawford *et al.* 1985.
Horse mackerel	Andronov 1983, Andronov 1985, Konchina 1986.
Small pelagic fish	1989 Workshop, J. Hewitson, formerly MCM, pers. comm.
Chub mackerel	Large fish assumed to have been depleted by heavy fishing in 1970s. Used relative proportions of small and medium fish from VPA by O. Centurier-Harris, formerly MCM, unpublished data to estimate diet from Baird 1978.
Hake	Andronov 1983, Roel and MacPherson 1988, Konchina 1986. Estimated diet from these sources using relative proportion of biomass in size classes from Schumacher 1987, Gordoa and MacPherson 1989 and Abelló 1988.
Other demersal fish	Estimated for 1989 Workshop by J. Hewitson, A. Badenhorst and K. Cochrane, formerly MCM.
Cephalopods	Estimated for 1989 Workshop by M. Lipinski, MCM. Lipinski 1992.
Large pelagic fish	Penney *et al.* 1991b (tuna and kob), Dudley 1987 (snoek). Used data for southern Benguela ecosystem.
Chondrichthyans	Assumed same as adjusted diet for southern Benguela ecosystem in Jarre-Teichmann *et al.* 1998.
Marine birds	Crawford *et al.* 1991
Seals	David 1987
Cetaceans	Sekiguchi 1992 (dolphins), 1989 Workshop.
Meiobenthos	Assumed same as estimate for southern Benguela ecosystem by Jarre-Teichmann *et al.* 1998.
Macrobenthos	Assumed same as estimate for southern Benguela ecosystem by Jarre-Teichmann *et al.* 1998.

7.3 BALANCING THE NORTHERN BENGUELA ECOSYSTEM MODEL

For many of the model groups, the input data described in Appendix C (Table C.1-C.8) results in ecotrophic efficiencies (EE, the fraction of the total production that is consumed by predators or exported from the system) greater than one. This indicates that model production of these groups is insufficient to support the model consumption by other groups, and in some cases the catches. Since much uncertainty surrounded many of the parameter estimates, the model was balanced by altering the lesser-known estimates for some groups.

7.3.1 Biomass estimates

Mesopelagic fish

If biomass of lightfish is assumed to be 10 000 tons, as estimated at the 1989 workshop, biomass of mesopelagics in the northern Benguela sub-system is insufficient to support feeding by other groups. The model was used to estimate the required biomass, given an EE of 99%. The modelled system requires 1.66 million tons of mesopelagic fish. If, as in the southern Benguela sub-system (Armstrong *et al.* 1991), lightfish are assumed to be present in equal proportion to lanternfish, then this equates to a biomass of 830 000 tons each of lanternfish and lightfish. At least for lanternfish, this is acceptable, as Hewitson and Cruickshank (1993) mention that 800 000 tons of lanternfish is a reasonable lower limit to the population in the northern Benguela sub-system. Further, Hutchings (unpublished) estimates mesopelagic fish to be at 1.5 million tons off Namibia.

Pelagic goby

There is insufficient goby to support consumption by other groups in the model. The model estimates biomass at 1.45 million tons, more than double that estimated by Hewitson and Cruickshank (1993), who caution that little was known about the goby stock during the period examined. It is possible that pelagic goby, like horse mackerel, was able to take advantage of plankton food made available when its competitors, anchovy and sardine, became less abundant during the 1980s. This is in agreement with the suggestion of Crawford (1987), that more than one species may benefit from energy made available when another resource collapses.

Other demersal fish

It was necessary to use the model to estimate the biomass of this poorly known group, assuming an EE of 99%, given the heavy feeding pressure on this group in the Benguela system (Jarre-Teichmann *et al.* 1998). Modelled biomass of other demersal fish is required to be 657 000t, i.e. half that of hake. This is considered to be a reasonable estimate.

Other small pelagic fish

The initial model did not include sufficient small pelagic fish to support the system. Therefore biomass is estimated by the model, assuming a high EE of 99%. Biomass required is about four times that initially used, i.e. 135 000 tons.

7.3.2 Diets

Zooplankton

Although phytoplankton biomass in the northern Benguela sub-system is 2.5 times that in the southern Benguela sub-system during the same period, phytoplankton P/B is larger in the southern sub-system (Tables 8.1 and 8.2). Therefore, average phytoplankton production is not greater in the northern sub-system. Nevertheless, because small pelagic fish have been found to consume larger proportions of phytoplankton in the northern sub-system (e.g. King and MacLeod 1976) than in the southern sub-system (e.g. L. Hutchings, MCM, pers comm. and Van der Lingen 1998), it is generally felt that phytoplankton consumption by micro- and meso-zooplankton is likely to be larger than originally estimated for the northern sub-system.

Consumption of small pelagic fish

Making use of dietary composition data for large pelagic fish, seals and chondrichthyans in the southern Benguela sub-system causes problems for small pelagic species in the northern Benguela model. The relative proportions of small pelagic fish in the modelled diets of these groups were recalculated to reflect the relative proportion of anchovy and sardine production in the northern Benguela sub-system during the 1980s. Consumption of anchovy by marine birds exceeded anchovy production, and the relative proportions of anchovy and sardine in their diet were adjusted to reflect relative abundance in the system.

Cephalopods

EE for cephalopods was estimated in the initial realisation of the model as greater than 700%, indicating that requirements by other components in the model substantially exceeded simulated cephalopod production. This is caused by large quantities of cephalopods being consumed by hake, other demersal fish, cephalopods, seals, chondrichthyans and to a smaller extent, large pelagic fish. Given that hake were much more abundant in the northern than in the southern Benguela sub-system in the 1980s, and that many of the diets assumed for the northern Benguela model were taken from the southern Benguela model, much of the consumption of cephalopods was instead attributed to hake.

Other demersal fish

Diet of other demersal fish is not very well known. This group causes high predation mortality on itself and on small pelagics and cephalopods, and requires some modification to balance the model. Macrobenthos in the diet of demersal fish was increased so that the group comprised 38.1%, equivalent to about half the proportion of macrobenthos in the diet of demersal fish in the southern Benguela sub-system. This is plausible given the oxygen deficient benthic environment of the northern Benguela region.

7.4 BIOMASS AND MAJOR FLOWS

Total biomass (excluding detritus) in the northern Benguela ecosystem during the period 1980-1989 was 360 t.lcm^{-2} (Table 7.3), comparable to that off Peru in the 1960s, and very large in comparison to other upwelling systems modelled by Jane-Teichmann and Christensen (1998 a). Total biomass off Namibia in the 1980s was larger than that in earlier periods (1971-77, 1978-83, Jarre-Teichmann and Christensen 1998 a) but similar to that in the early 1990s (Heymans *et al.* in prep., Table 7.3). This reflects the assumption in the earlier models that the productivity, rather than the biomass, of small pelagics needed to be increased in line with observed productivities in other upwelling systems, so that the large food demand of predatory fish is met (A. Jane, Danish Institute for Fisheries Research, pers. comm.). However, the opposite assumption is made here that the northern Benguela ecosystem has large biomasses, but is less productive than other regions (L. Hutchings, MCM, pers. comm.). Total consumption, production, throughput and respiration were all larger in the 1980s than in the periods before and immediately after this decade (Table 7.3). The large differences in these flows, particularly throughput, between the 1980s model and those for the 1970s and 1990s, are at least partly related to data availability and use in the three models (Heymans *et al.* in prep.). Total biomass increased over the three decades modelled whereas there was a decrease in net primary production between the 1970s and 1990s (Heymans *et al.* in prep.). Total fish biomass in the northern Benguela sub-system was noticeably larger in the 1980s than in the previous and following decades (Heymans *et al.* in prep).

Table 7.3 Summary statistics for the trophic model of the northern Benguela ecosystem in the 1980s (shaded) compared to those in periods before and after this decade (Heymans *et al.* in prep.) Biomass is in tons·km^{-2} and flows are in t.km^{-2}.y^{-1}.

	1971-1977	1980-1989	1990-1995
Total biomass (excluding detritus)	282	360	381
Sum of all consumption	3214	11743	4477
Sum of all exports	6124	1254	4452
Sum of all flows to detritus	6555	4265	5591
Total system throughput	17443	23327	16252
Sum of all production	8264	10034	7479
Net system production	6124	1254	4452
Sum of all respiratory flows	1550	6065	1731
Total net primary production	7675	7319	6183
Total catches	7	7	3

7.5 PRIMARY PRODUCTION EQUIVALENTS

In the northern Benguela ecosystem, catches of horse mackerel and hake are large, both requiring substantial proportions of total primary production (Fig. 7.1). However, harvesting hake at a high trophic level requires more primary production per unit of yield than harvesting horse mackerel at a low trophic level (Fig. 7.1). Therefore, fishing hake is ecologically more expensive than fishing horse mackerel. Hake is economically more valuable than horse mackerel. For example, from data presented in Stuttaford (1997) for 1994, N$ 3 500 were obtained per ton of hake exported, compared to only N$ 1 300 per ton horse mackerel exported.

Catches of large pelagic fish are smaller than those of other demersal fish, but because large pelagics are at a higher trophic level, fishing this group requires a larger proportion of primary production (Fig. 7.1). The percentage of primary production required to sustain all fisheries off Namibia during the 1980s was 5.8% (annual catches totalled 7 $t.km^{-2}.y^{-1}$, Table 7.3). This is about half that required to sustain catches in the previous decade (Jarre-Teichmann *et al.* 1998 a), when total catches were closer to 10 $t.km^{-2}.y^{-1}$ and there was severe fishing pressure on hake and horse mackerel.

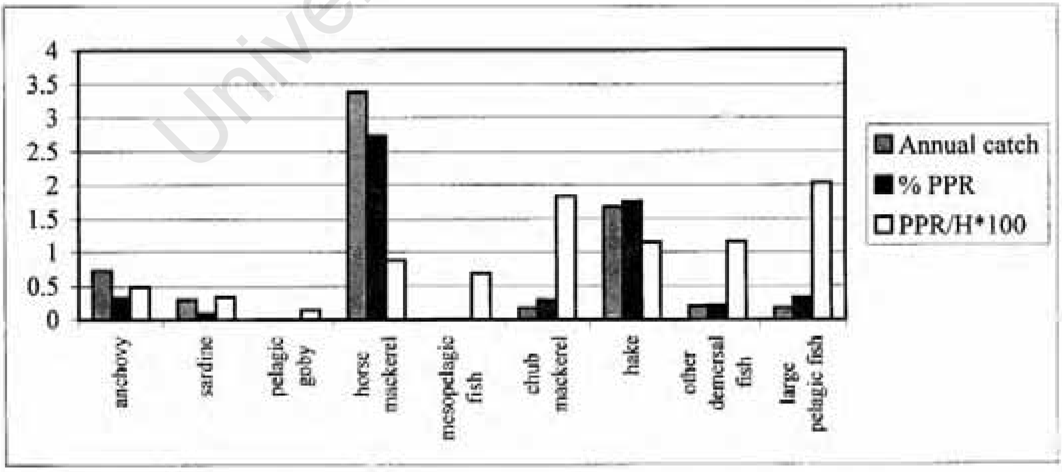


Fig. 7.1: Comparison of catches in the northern Benguela ecosystem during the 1980s, showing mean annual catches ($t.km^{-2}.y^{-1}$), % total primary production required (PPR) to sustain catches and PPR per unit harvested (PPR/H). PPR/H is scaled for ease of graphic presentation and is dimensionless.

7.6 INVESTIGATING ALTERNATIVE ESTIMATES OF SOME PARAMETERS

There is uncertainty about many of the parameter estimates used in the initial realization of the balanced model. A selection of alternative model scenarios explores the influences of some of the parameters which are likely to be important in structuring the model, and for which estimates may deviate from those initially used. Because it was largely dietary compositions that were altered in the initial balancing of the model, alterations to diets are not explored further. However, it should be noted that the allocation of diet compositions in the model has a major influence over how the model system functions trophically.

7.6.1 Alternative estimate of phytoplankton productivity

A scenario is modelled in which the phytoplankton Production/Biomass ratio is estimated to be 30.3 y^{-1} from original P and B estimates given in Brown *et al.* (1991). With the lower P/B, the EE of phytoplankton is 108%, indicating insufficient production to support modelled consumption of phytoplankton by other groups in the system.

7.6.2 Alternative estimate of gelatinous zooplankton biomass

If, instead of our estimate of 5 million tons for gelatinous zooplankton in the northern Benguela ecosystem during the 1980s, we assume a larger value of 28 million tons (as suggested by A.J. Boyd at the 1989 workshop, and in agreement with the large biomass estimates of *Aequorea aequorea* and *Chrysaora hysoscella* in Fearon *et al.* (1992)), the only model outputs that change much are total system biomass and parameters directly dependent on it. This is because gelatinous zooplankton are made up mostly of liquid and have low P/B and Q/B ratios. Further, as only a small quantity of gelatinous zooplankton is consumed in the system, availability has little impact on other components. Similarly, there is little difference from the initial model if, instead of consuming equal portions of phytoplankton, bacteria, microzooplankton and mesozooplankton, gelatinous zooplankton are assumed to consume these prey groups in proportion to their relative biomasses. However, preliminary analyses using revised diet compositions of gelatinous zooplankton from E. Beucher (pers. comm.) show that the model is relatively sensitive to the input of dietary data. Further, predation by jellyfish may cause mass mortalities of pelagic fish larvae and may impact other groups competing with gelatinous zooplankton for food (Gibbons *et al.* 1992).

7.6.3 Alternative estimate of horse mackerel biomass

There is large variability about the biomass estimates of horse mackerel in the literature and a fairly conservative biomass of 2.5 million tons was used in the initial realisation of the model. The model was re-run using the upper estimate of 5.67 million tons (Shcherbich *et al.* 1986). The model is unbalanced, showing an EE of 129% for macrozooplankton, indicating that there is insufficient production of macrozooplankton to support that required as food. The largest possible biomass of horse mackerel that could be supported by the balanced model system is 3.04 million tons (17.00 tons•km^{-2}). This biomass allows an increase in pelagic goby and mesopelagic fish biomass estimated in the model (Table 7.4). This increase is caused by greater consumption of cephalopods by horse mackerel, thereby increasing macrozooplankton prey available to mesopelagic fish and pelagic goby. Corresponding to these changes are increases in the EEs of macrozooplankton and cephalopods.

7.6.4 Alternative estimate of the Production/Biomass ratio for hake

A smaller P/B ratio ($0.9.y^{-1}$) for hake was used to model trophic flows in the southern Benguela ecosystem (Jarre-Teichmann *et al.* 1998) than for the northern Benguela ecosystem (Appendix C, Table C.5). It is possible that natural mortality of hake in the northern Benguela ecosystem is over-estimated, so that P/B is smaller than the value of $1.0 \cdot y^{-1}$ initially assumed. The model was re-run assuming an alternative P/B of $0.9 \cdot y^{-1}$ but keeping P/Q at 22% as before. Hake production is then insufficient to support cannibalism of small hake by large hake, giving an EE of 106%. Consumption by hake is reduced from $36.3\ t.km^{-2}.y^{-1}$ to $29.1\ tons.km^{-2}.y^{-1}$, because Q/B is adjusted down to account for the reduced P/B, if P/Q remains constant. Consequently, predation by hake on pelagic goby, mesopelagic fish and demersal fish is reduced and increased amounts of food will be required to support these prey stocks. Alternatively, smaller stocks of hake prey can be supported by the modelled system (Table 7.4).

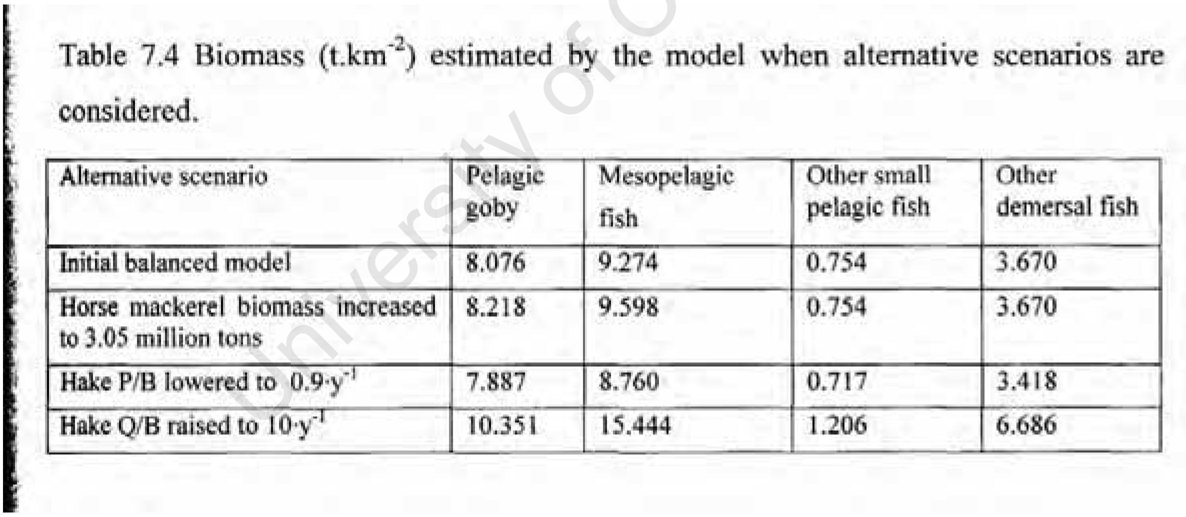


Table 7.4 Biomass ($t.km^{-2}$) estimated by the model when alternative scenarios are considered.

Alternative scenario	Pelagic goby	Mesopelagic fish	Other small pelagic fish	Other demersal fish
Initial balanced model	8.076	9.274	0.754	3.670
Horse mackerel biomass increased to 3.05 million tons	8.218	9.598	0.754	3.670
Hake P/B lowered to $0.9 \cdot y^{-1}$	7.887	8.760	0.717	3.418
Hake Q/B raised to $10 \cdot y^{-1}$	10.351	15.444	1.206	6.686

7.6.5 Alternative estimate of the Consumption/Biomass ratio for hake

The possible range for Consumption/Biomass (Q/B) of hake is large (see input data section). The model was re-run assuming Q/B of $10\ y^{-1}$ (compared to $5\ y^{-1}$ in the initial model) for P/B of both $1.0\ y^{-1}$ and $0.9\ y^{-1}$. Because consumption is identical in both runs, both show increases of the same magnitudes in the biomasses of other groups (Table 7.4). Larger stocks of pelagic goby, mesopelagic fish and demersal fish are required to support the increased consumption of hake. Similarly, an increased biomass of demersal fish requires an increase in biomass of small pelagic fish (prey for demersal fish) in the system. However, the model is not balanced for these higher standing stocks, reflected in EEs exceeding 100% for macrozooplankton, anchovy, horse mackerel, cephalopods and large pelagic fish. If Q/B is in fact much higher than the value of 5 y^{-1} assumed for both the northern and southern Benguela sub-systems (Jarre-Teichmann *et al.* 1998), the diet of hake would need to be revisited and extensively altered from that for which the model was initially balanced.

7.7 CONCLUSIONS

It is necessary to estimate the biomass of some groups to balance the model. This ensures that production is sufficient to support the consumption of predatory groups in the ecosystem. For example, it is necessary to double the biomass of pelagic goby estimated by Hewitson and Cruickshank (1993). Cephalopod production is insufficient to support consumption reported for many of the groups, and this component is reduced in the diets of several groups. Biomass of the demersal fish group is required to be half that of hake. There are few data available on benthos and the model is used to estimate the biomass required to sustain other components of the system. Meiobenthos, macrobenthos and benthic producers are required to be 25% of the biomasses of these groups in the southern Benguela ecosystem. This is reasonable given the frequent occurrence of hypoxic conditions along the Namibian shelf (Bailey 1991) and the fact that the southern Benguela sub-system not only includes the upwelling region, but also extends over the Agulhas Bank with its wider shelf. Exploring the impacts of changing the estimates of some parameters serves to highlight areas of uncertainty in the model, but also improves our confidence in the estimates of others.

CHAPTER EIGHT

COMPARING MODELS OF THE SOUTHERN AND NORTHERN BENGUELA SUB-SYSTEMS DURING THE 1980S

ABSTRACT

There are structural and functional differences between the northern and southern Benguela sub-systems. Despite large total biomass and large catches in the northern Benguela sub-system during the 1980s, all other major trophic flows are larger in the southern Benguela sub-system. Primary production required to support catches in the north is greater than that required in the south. However, fishing is ecologically more expensive in the south than in the north. Top predators are more important components in the southern than in the northern Benguela sub-system. Demersal fish are more abundant in the southern Benguela sub-system, related to the fact that the southern model included the Agulhas Bank in addition to the upwelling area of the west coast. Mesopelagic fish, together with redeye in the southern Benguela sub-system and pelagic goby in the northern Benguela sub-system, were of little commercial value but served as important prey items for many groups in the two ecosystems. Increased fishing has different effects in the two sub-systems, caused by complex responses to indirect and direct competition. Large pelagic fish are more severely affected by fishing strategies that reduce their small pelagic prey in the south than in the north. Horse mackerel and hake are closely linked in the south, so that reducing hake biomass has a more pronounced effect on horse mackerel in the southern than in the northern Benguela sub-system.

8.1 INTRODUCTION

The work presented in the Chapter 7 details a model of the northern Benguela ecosystem for the period 1980-1989. Many of the model outputs become more meaningful when compared to those of similar models for other systems or periods. In this chapter, the northern Benguela model for the 1980s is compared with a similar one for the southern Benguela sub-system, with the same ecosystem components and for the same period (key question 2b). In this way, the chapter places the trophic structure of the southern Benguela sub-system on which the thesis focuses, into the context of the larger Benguela ecosystem. It also serves as a basis for a preliminary comparison of the effects of different fishing strategies in the northern and southern Benguela sub-systems (key question 3c).

8.2 METHODS

Steady-state trophic models of the northern and southern Benguela ecosystems are described and compared in terms of biomasses and parameter estimates. Total flows, flow diagrams, consumption by groups, primary production equivalents required (Chapter 3, section 3.3.3) to sustain catches and support top predators, aggregation of biomass at discrete trophic levels (Chapter 3, section 3.3.2) and mixed trophic impacts (Chapter 3, section 3.4.1) are compared between the two models.

Using *Ecosim* (Chapter 3, section 3.5), the effects of altered fishing on the northern and southern Benguela ecosystems are simulated. At the time of the study, *Ecosim* was only available in its alpha form. All settings were default, with interactions assumed to be of the mixed control type (i.e. top-down and bottom-up control were given equal weightings by setting the "vulnerability" of groups to 0.5). Vunerability settings and different types of flow control are explored further in Chapter 9 using southern Benguela models.

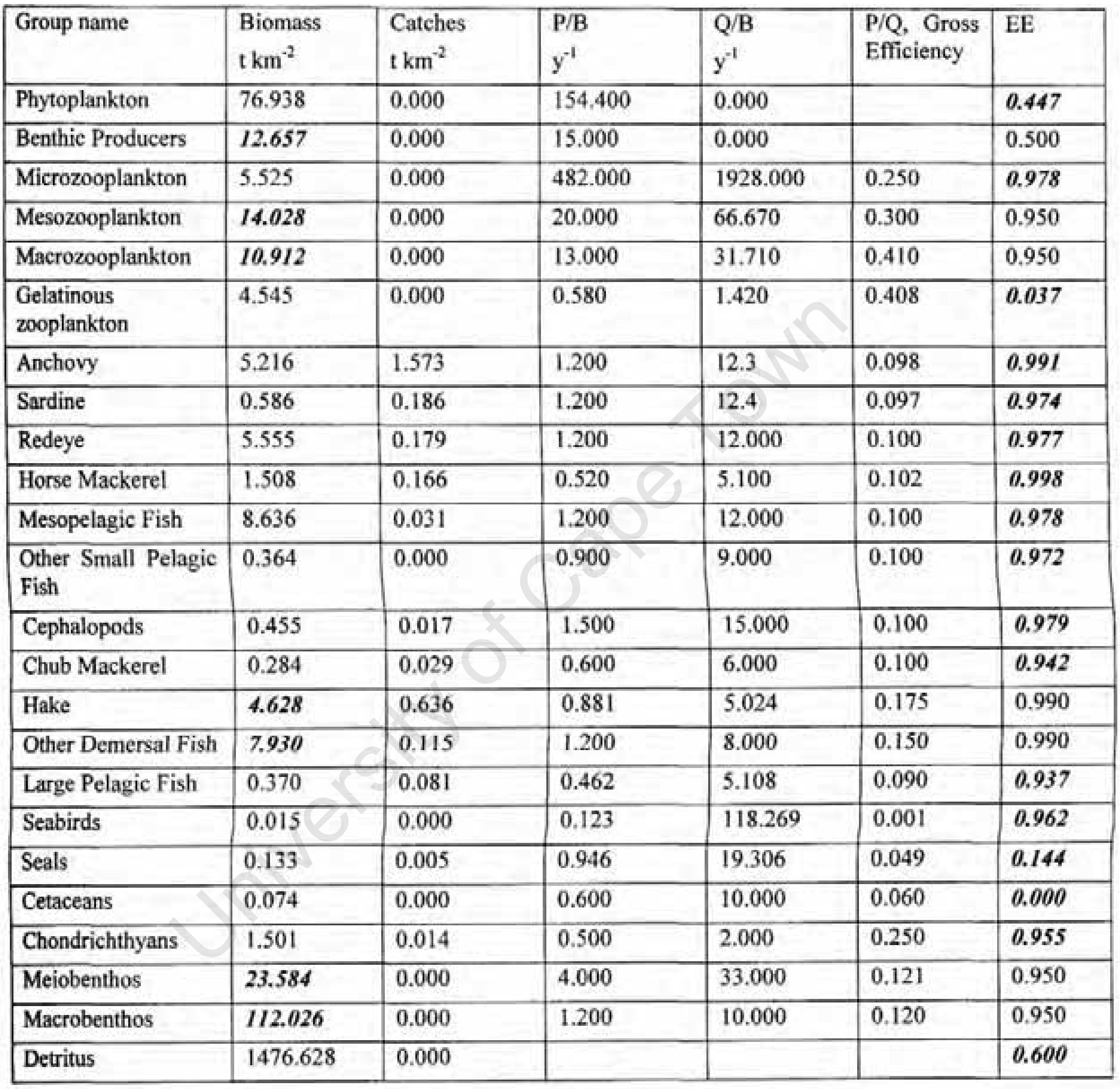
8.3 NORTHERN AND SOUTHERN BENGUELA MODELS FOR THE 1980S

The model of the northern Benguela sub-system is described in detail in the previous chapter. It covers the shelf region to about 500m depth, extends from 15 ˚S to 29˚S and covers an area of 179 000 km^2. The model of the southern Benguela ecosystem covers the shelf region to about 500m depth, extends from 29 ˚S, around the southern tip of Africa and eastwards to 28˚E, covering an area of 220 000 km^2. A model of trophic flows has been constructed for the southern Benguela sub-system during the 1980s (Jarre-Teichmann *et al.* 1998). This model was modified here to separate some components for clarity, and to incorporate new hake data, which only became available after preparation of the first model. This second model was still further revised for more elaborate analysis in other parts of this thesis and is the one detailed in Chapter 4. The model used here differs from that in Chapter 4 because hakes, other demersal fish, horse mackerel and chondrichthyans are not subdivided into different size categories. To avoid repetition of the methods described in Chapter 4, details of data extraction, manipulation and revision of estimates are not included here. Instead, all parameters and dietary data used in this balanced version of the southern Benguela model are summarised in Tables 8.2 and 8.4, for comparison with those for the northern Benguela model (Tables 8.1 and 8.3).

Table 8.1 Parameters of the northern Benguela model during the 1980s. P/B is the ratio of production to biomass, Q/B is consumption per unit biomass, gross efficiency is the ratio of production to consumption, and EE is ecotrophic efficiency. Italicized and bold parameters indicate output model parameters estimated using *Ecopath*.

Group name	Biomass t km^{-2}	Catches T km^{-2}	P/B y^{-1}	Q/B y^{-1}	P/Q, Gross Efficiency	EE
Phytoplankton	203.664	0.000	35.700	0.000		***0.912***
Benthic Producers	***3.210***	0.000	15.000	0.000		0.500
Microzooplankton	3.990	0.000	354.000	1770.000	0.200	***0.977***
Mesozooplankton	25.000	0.000	40.000	133.333	0.300	***0.437***
Macrozooplankton	15.000	0.000	13.000	31.707	0.410	***0.843***
Gelatinous zooplankton	27.933	0.000	0.371	0.905	0.410	***0.115***
Anchovy	1.408	0.732	1.160	11.717	0.099	***0.997***
Sardine	0.749	0.296	1.100	11.000	0.100	***0.934***
Pelagic Goby	***8.076***	0.001	0.900	9.000	0.100	0.990
Horse Mackerel	13.966	3.382	0.520	5.200	0.100	***0.917***
Mesopelagic Fish	***9.274***	0.006	1.230	12.300	0.100	0.990
Other Small Pelagic Fish	***0.754***	0.000	0.900	9.000	0.100	0.990
Cephalopods	0.279	0.000	1.500	15.000	0.100	***0.956***
Chub Mackerel	0.349	0.174	0.600	6.000	0.100	***0.911***
Hake	7.263	1.676	1.000	4.545	0.220	***0.998***
Other Demersal Fish	***3.670***	0.200	1.000	6.667	0.150	0.990
Large Pelagic Fish	0.860	0.174	0.490	2.450	0.200	***0.977***
Seabirds	0.010	0.000	0.160	120.300	0.001	***0.000***
Seals	0.289	0.008	0.940	19.184	0.049	***0.044***
Cetaceans	0.028	0.000	1.000	12.658	0.079	***0.000***
Chondrichthyans	0.375	0.003	0.500	2.000	0.250	***0.952***
Meiobenthos	***5.957***	0.000	4.000	33.333	0.120	0.950
Macrobenthos	***28.296***	0.000	1.200	10.000	0.120	0.950
Detritus	840.000	0.000				***0.761***

Table 8.2 Parameters of the southern Benguela model during the 1980s. P/B is the ratio of production to biomass, Q/B is consumption per unit biomass, gross efficiency is the ratio of production to consumption, and EE is ecotrophic efficiency. Italicized and bold parameters indicate output model parameters estimated using *Ecopath.*



Group name	Biomass t km^{-2}	Catches t km^{-2}	P/B y^{-1}	Q/B y^{-1}	P/Q, Gross Efficiency	EE
Phytoplankton	76.938	0.000	154.400	0.000		***0.447***
Benthic Producers	***12.657***	0.000	15.000	0.000		0.500
Microzooplankton	5.525	0.000	482.000	1928.000	0.250	***0.978***
Mesozooplankton	***14.028***	0.000	20.000	66.670	0.300	0.950
Macrozooplankton	***10.912***	0.000	13.000	31.710	0.410	0.950
Gelatinous zooplankton	4.545	0.000	0.580	1.420	0.408	***0.037***
Anchovy	5.216	1.573	1.200	12.3	0.098	***0.991***
Sardine	0.586	0.186	1.200	12.4	0.097	***0.974***
Redeye	5.555	0.179	1.200	12.000	0.100	***0.977***
Horse Mackerel	1.508	0.166	0.520	5.100	0.102	***0.998***
Mesopelagic Fish	8.636	0.031	1.200	12.000	0.100	***0.978***
Other Small Pelagic Fish	0.364	0.000	0.900	9.000	0.100	***0.972***
Cephalopods	0.455	0.017	1.500	15.000	0.100	***0.979***
Chub Mackerel	0.284	0.029	0.600	6.000	0.100	***0.942***
Hake	***4.628***	0.636	0.881	5.024	0.175	0.990
Other Demersal Fish	***7.930***	0.115	1.200	8.000	0.150	0.990
Large Pelagic Fish	0.370	0.081	0.462	5.108	0.090	***0.937***
Seabirds	0.015	0.000	0.123	118.269	0.001	***0.962***
Seals	0.133	0.005	0.946	19.306	0.049	***0.144***
Cetaceans	0.074	0.000	0.600	10.000	0.060	***0.000***
Chondrichthyans	1.501	0.014	0.500	2.000	0.250	***0.955***
Meiobenthos	***23.584***	0.000	4.000	33.000	0.121	0.950
Macrobenthos	***112.026***	0.000	1.200	10.000	0.120	0.950
Detritus	1476.628	0.000				***0.600***

Table 8.3 Balanced diet composition (%) in the northern Benguela model for the 1980s. Prey groups are listed in rows, predators in columns. An asterisk indicates that a prey group comprises less than 0.5% of the predator's diet.

Prey/ predator	Microzoo.	Mesozoo.	Macrozoo.	Gel. Zoo.	Anchovy	Sardine	Goby	H. Mack.	Mesopel.	Small Pel.	Cephalo.	Chub Mack.	Hake	Demersals	Large Pel.	Seabirds	Seals	Cetaceans	Chondrich.	Meioben.	Macroben.
Phytoplankton	50	75	60	25	33	56	93														
Benthic producers																				5	5
Microzooplankton	10	20		25	4	8															
Mesozooplankton		5	40	25	31	18	1	18	40	81		1	2	8		*					
Macrozooplankton					32	18	6	79	60	14	10	80	49	32	19	4					
Gelatinous zooplankton										3			3								
Anchovy												2	1		7	18	2	1	7		
Sardine															7	5	4	1	4		
Pelagic Goby								1			10		4	2	39	47	53	7			
Horse Mackerel											10		5		2	1	24		1		
Mesopelagics								3			59	16	18	2	5	5	1	19			
Small pelagics												1		2	4	4		12			
Cephalopods								*			1		*	*	*	4	1	32	*		
Chub mackerel															*	*			2		
Hake											10		5	10	6	10	12	28	11		
Other demersal fish													5	5	11	2			42		
Large pelagic fish													*		*	*	4		*		
Seabirds																			0		
Seals																					
Cetaceans																					
Chondrichthyans																			23		
Meiobenthos																					8
Macrobenthos										2			9	38	1				10		7
Detritus	40			25																95	80

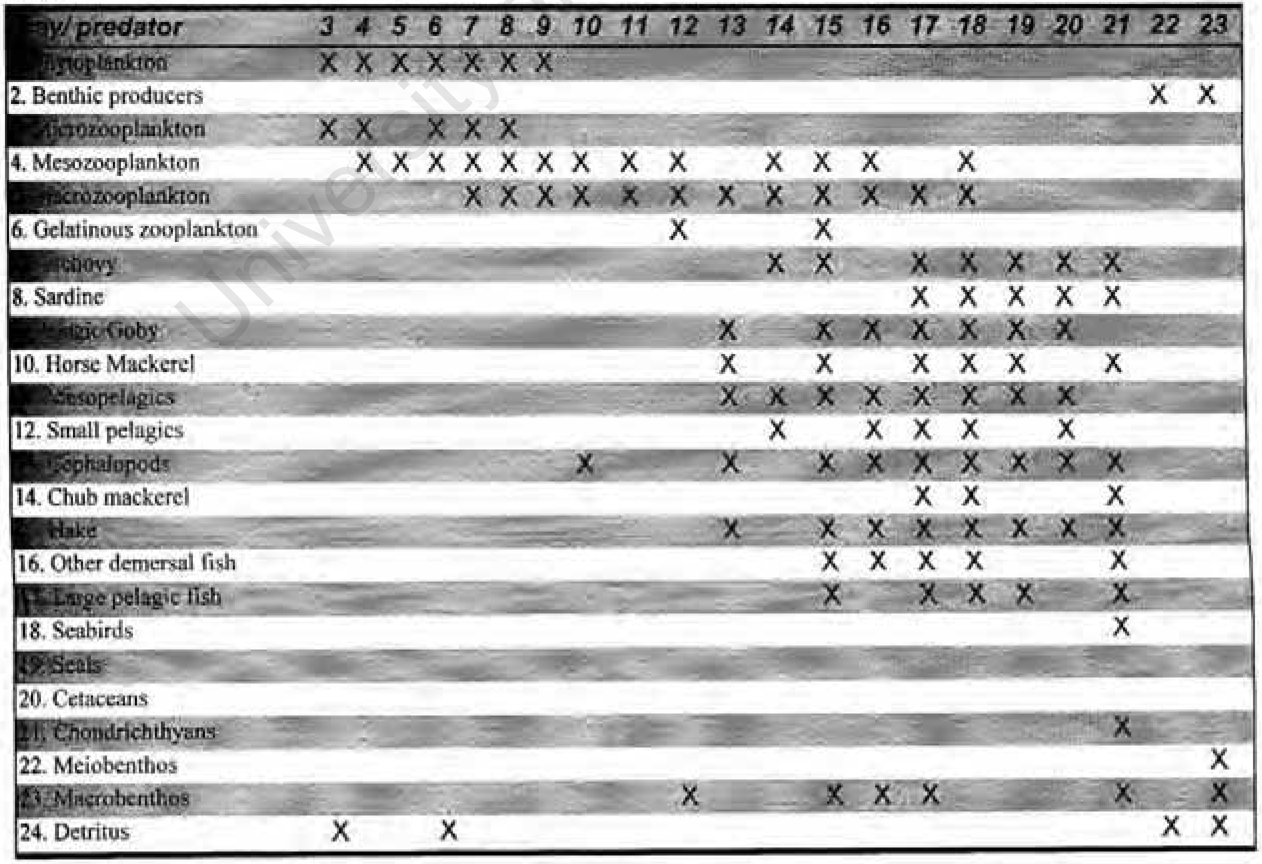
Table 8.4 Balanced diet composition (%) in the southern Benguela model for the 1980s. Prey groups are listed in rows, predators in columns. An asterisk indicates that a prey group comprises less than 0.5% of the predator's diet.

Prey/ predator	Microzoo.	Mesozoo.	Macrozoo.	Gel. Zoo.	Anchovy	Sardine	Chub Mack.	H. Mack.	Cephalo.	Redeye	Small Pel.	Large Pel.	Meioben.	Macroben.	Hake	Demersals	Seabirds	Seals	Cetaceans	Mesopelagics	Chondrich.
Phytoplankton	40	50	60	25	5	32															
Benthic producers													5	5							
Microzooplankton	20	50	40	25	4	32															
Mesozooplankton				25	57	29	1	15		60	81					4	1			40	
Macrozooplankton					34	7	80	82	8	40	16	14			44	7	10		8	60	
Gelatinous zooplankton											3										
Anchovy							2		15			39			5		37	25	30		9
Sardine									1			5					8	3	7		1
Club Mackerel												1			*		*	1			2
Horse Mackerel									4			3					1	3	27		1
Cephalopods								*	1			4			*	*	7	5	16		1
Redeye							1	3	5			11			7	5	2	24	1		9
Other small pelagics												2			*	*	6	1	3		1
Large pelagics												*			*		*	1			*
Meiobenthos														8							
Macrobenthos									22			1		7		75		7			10
Hake									5			7			6	1	17	19	4		*
Demersal fish									16			10			9	7	1	11			42
Seabirds																	*				
Seals																	*				*
Cetaceans																					
Mesopelagics							16		23			4			30	2	10	1	4		
Chondrichthyans																					23
Detritus	40			25									95	80							

8.4 COMPARISONS OF ECOSYSTEM STRUCTURES

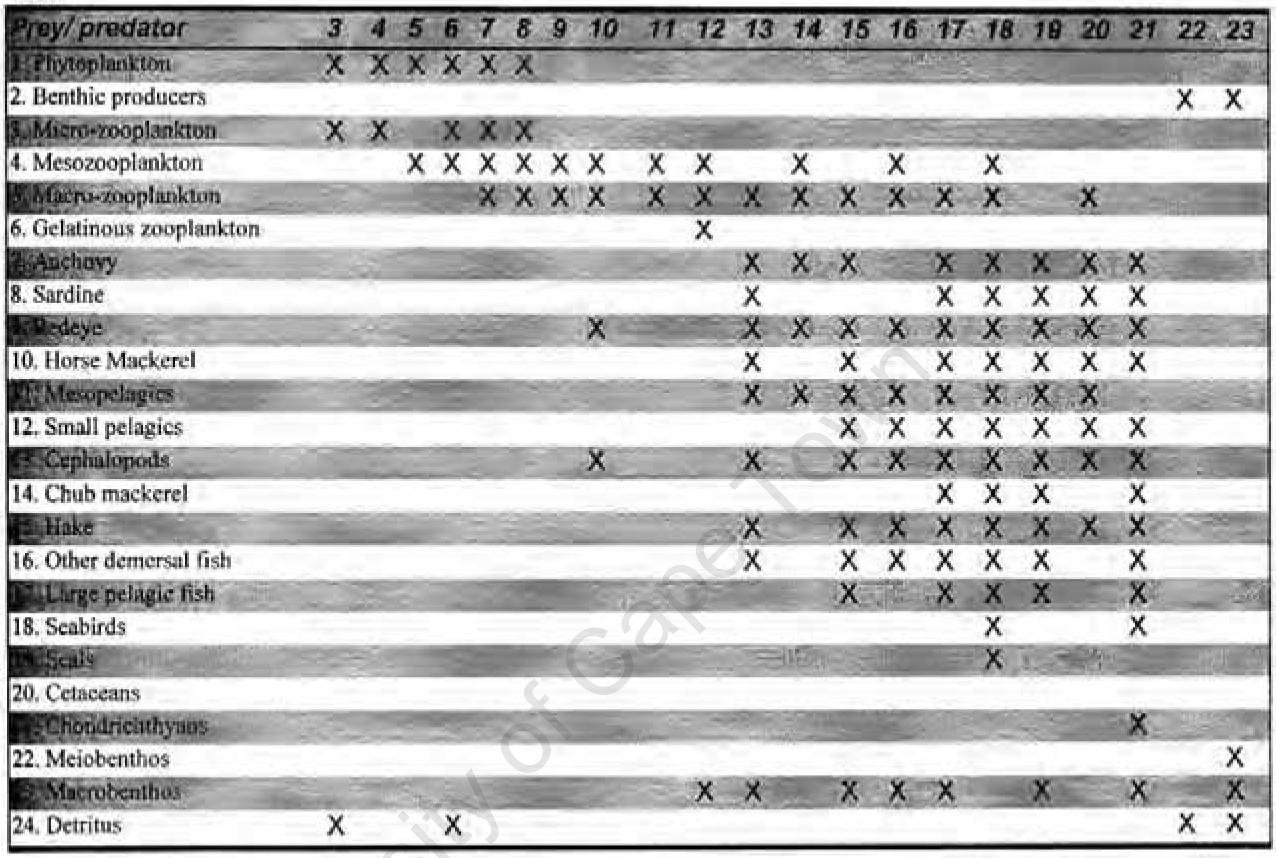
Connectivity matrices summarising the predator-prey interactions in the northern and southern Benguela ecosystems are included for comparative purposes (Fig. 8.1). Similar niches are occupied by pelagic goby in the northern Benguela sub-system and redeye in the southern Benguela sub-system, but neither is abundant in the other ecosystem, and their diets differ. Phytoplankton are an important part of the diet of pelagic goby off Namibia, whereas redeye in the south are zooplanktivorous. There are also differences in predator-prey interactions between the two ecosystems for mesozooplankton, cephalopods, hake, seals, cetaceans and chondrichthyans (Fig. 8.1). These are related to differences in abundance of fish species between the two ecosystems.

Fig. 8.1a A connectivity matrix (after Cochrane *et al.* 1991a) summarising the flows from predators to prey in the northern Benguela sub-system during the 1980s. A cross indicates a flow from a row component to a column component. Prey groups are listed in rows, predators in columns (corresponding to the row number used for prey), so that flows to predators are indicated along the x-axis and flows from prey along the y-axis.



y/ predator	*3*	*4*	*5*	*6*	*7*	*8*	*9*	*10*	*11*	*12*	*13*	*14*	*15*	*16*	*17*	*18*	*19*	*20*	*21*	*22*	*23*
ytoplankton	X	X	X	X	X	X	X														
2. Benthic producers																				X	X
crozooplankton	X	X		X	X	X															
4. Mesozooplankton		X	X	X	X	X	X	X	X	X		X	X	X		X					
acrozooplankton					X	X	X	X	X	X	X	X	X	X	X	X					
6. Gelatinous zooplankton										X			X								
chovy												X	X		X	X	X	X	X		
8. Sardine															X	X	X	X	X		
lagic Goby											X		X	X	X	X	X	X			
10. Horse Mackerel											X		X		X	X	X		X		
esopelagics											X	X	X	X	X	X	X	X			
12. Small pelagics												X		X	X	X		X			
ephalopods								X			X		X	X	X	X	X	X	X		
14. Chub mackerel															X	X			X		
Hake											X		X	X	X	X	X	X	X		
16. Other demersal fish													X	X	X	X			X		
17. Large pelagic fish													X		X	X	X		X		
18. Seabirds																			X		
19. Seals																					
20. Cetaceans																					
21. Chondrichthyans																			X		
22. Meiobenthos																					X
23. Macrobenthos										X			X	X	X				X		X
24. Detritus	X			X																X	X

Fig. 8.1b A connectivity matrix (after Cochrane *et al.* 1991a) summarising the flows from predators to prey in the southern Benguela sub-system during the 1980s. A cross indicates a flow from a row component to a column component. Prey groups are listed in rows, predators in columns (corresponding to the row number used for prey), so that flows to predators are indicated along the x-axis and flows from prey along the y-axis.



Prey/ predator	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
1. Phytoplankton	X	X	X	X	X	X															
2. Benthic producers																				X	X
3. Micro-zooplankton	X	X		X	X	X															
4. Mesozooplankton			X	X	X	X	X	X	X	X		X		X		X					
5. Macro-zooplankton					X	X	X	X	X	X	X	X	X	X	X	X		X			
6. Gelatinous zooplankton										X											
7. Anchovy											X	X	X		X	X	X	X	X		
8. Sardine											X				X	X	X	X	X		
9. Redeye								X			X	X	X	X	X	X	X	X	X		
10. Horse Mackerel											X		X		X	X	X	X	X		
11. Mesopelagics											X	X	X	X	X	X	X	X			
12. Small pelagics													X	X	X	X	X	X	X		
13. Cephalopods								X			X		X	X	X	X	X	X	X		
14. Chub mackerel															X	X	X		X		
15. Hake											X		X	X	X	X	X	X	X		
16. Other demersal fish											X		X	X	X	X	X		X		
17. Large pelagic fish													X		X	X	X		X		
18. Seabirds																X			X		
19. Seals																X					
20. Cetaceans																					
21. Chondrichthyans																			X		
22. Meiobenthos																					X
23. Macrobenthos										X	X		X	X	X		X		X		X
24. Detritus	X			X																X	X

8.4.1 Northern Benguela Model

In the northern Benguela sub-system, there was heavy fishing on both sardine and hake during the 1970s. Sardine, the dominant pelagic species between 1971 and 1977 (Jarre-Teichmann and Christensen 1998a), was severely reduced from 1.5 million tons to 134 000 tons in the 1980s. Anchovy also decreased in abundance from 593 000 tons in the 1970s to 252 000 tons in the 1980s. The dominant pelagic species in the 1980s was horse mackerel, at 2.5 million tons. Biomass of hake (both species combined) was 1.3 million tons. Biomasses of meiobenthos, macrobenthos and benthic producers were required to be 25% of the sum of those in the southern Benguela sub-system. This is reasonable given the frequent hypoxic events along the Namibian shelf (Bailey 1991) and the wider shelf of the Agulhas Bank included in the southern Benguela model.

8.4.2 Southern Benguela Model

During the 1980s, anchovy was the dominant pelagic fish, with a biomass of 1.1 million tons. Sardine was at a low level of only 129 000 tons, mesopelagic fish were at 1.7 million tons, and hake (both species combined) were at about 624 000 tons. In order that the model balanced, some of the parameters of a few groups had to be re-evaluated. Hake and other demersal fish caused major problems in the model, particularly related to diet composition of the various size groups. The proportion of these groups in the diet of others was reduced in many cases and it was necessary to use the model to estimate the predatory biomass of these groups, based on the amount required as prey and catches. Hake biomass was required to be about 64% higher than estimated, and that of other demersal fish, 7.5 times higher. These adjustments in turn had repercussions throughout the system, as prey species were consumed in larger amounts than initially estimated. As in the northern Benguela sub-system, cephalopods were not sufficiently abundant to support demands by other components, and the proportions in diets of some groups had to be reduced considerably.

8.5 COMPARING FLOWS

8.5.1 Summary statistics

For the period 1980-1989, total biomass (excluding detritus) was smaller in the southern Benguela sub-system (297 $t.km^{-2}$) than in the northern Benguela sub-system (360 $t.km^{-2}$). Annual catches in the southern Benguela sub-system (3 $t.km^{-2}.y^{-1}$) were less than half those in the northern Benguela sub-system (7 $t.km^{-2}.y^{-1}$). All major flows (defined in Chapter 3) were greater in the southern Benguela sub-system (Fig. 8.2), indicating that it is more productive than the northern Benguela sub-system. Mean path lengths (defined in Chapter 5, section 5.5.2) in the two sub-systems were short, at 3.02 in the southern and 3.19 in the northern Benguela sub-system.

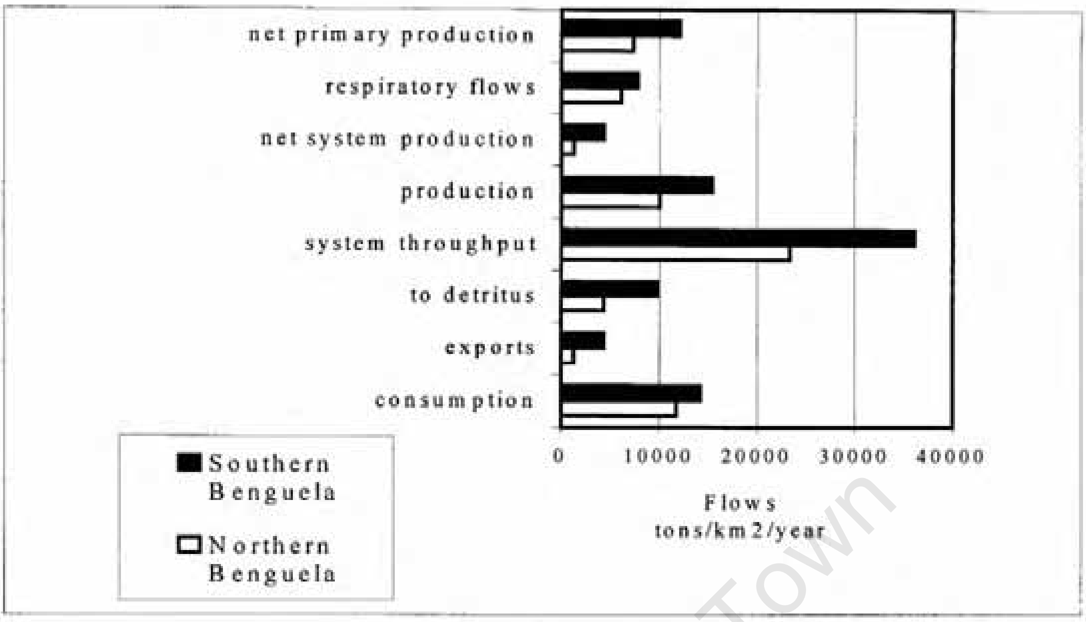


Fig. 8.2 Comparison of whole system properties in the northern and southern Benguela sub-systems in the 1980s. Flows are in t.km^{-2}.y^{-1}.

8.5.2 Trophic structure

Trophic levels of the components of the two systems are compared (Fig. 8.3). In both systems, zooplanktivorous mesopelagics, and horse mackerel, the latter supplementing its zooplanktivorous diet with a small proportion of fish, are at high trophic levels. Hake and other demersal fish occupy even higher trophic levels and are abundant. Most components in the southern Benguela ecosystem occupy higher trophic levels than the same groups in the northern Benguela ecosystem. In particular, anchovy, hake, large pelagics, marine birds and seals occupy trophic levels 2.9, 3.8, 3.7, 3.7 and 3.8 in the northern Benguela ecosystem compared with trophic levels 3.5, 4.2, 4.5, 4.6 and 4.6 in the southern Benguela ecosystem.

There is a large difference between the trophic level (2.1) of pelagic goby (northern Benguela ecosystem) and that of redeye (3.6), considered to be its counterpart in the southern Benguela ecosystem. This is because pelagic goby is primarily phytoplanktivorous, whereas redeye is a zooplanktivore. Both compete with anchovy and sardine in their respective systems, consuming larger proportions of phytoplankton off Namibia than off South Africa.

8.5.3 Major consumers

In both ecosystems, zooplankton consume more than 96% of the total production. For groups other than zooplankton, consumption by anchovy and redeye is important in the south, whereas horse mackerel and pelagic goby are important consumers in the north (Fig. 8.4). The fraction of production consumed by demersal fish in the north is less than that in the south because biomass is smaller in the north. Hake and mesopelagic fish are important consumers in both sub-systems (Fig. 8.4).

When the consumption of small pelagic fish (anchovy, sardine, redeye, pelagic goby and other small pelagic fish) is compared between the two ecosystems (Fig.8.5), it is clear that marine mammals are much more important as consumers in the north than in the south. This is explained by less than half the number of seals present in the southern Benguela ecosystem than off Namibia in the 1980s. There is also a greater fraction of small pelagic fish in the diet of seals in the north, where gobies make up over 50% of seal diet. There is heavier harvesting of small pelagic fish off South Africa (Fig. 8.5a) because horse mackerel were the dominant pelagic fish caught commercially off Namibia in the 1980s, and these are not classified as small pelagics here because horse mackerel adults and juveniles are aggregated into one box. Consumption of small pelagics by predatory fish is greater in the south than in the north, mainly by predatory hake and other demersal fish. In the north, hake are more than twice as abundant as in the south, but diet consists of only 5% small pelagic fish, compared to 12% in the south. Demersal fish are not as abundant in the north so consume less small pelagic fish production.

8.6 IMPACTS OF FISHERIES AND TOP PREDATORS

Large catches of horse mackerel and hake were taken in the northern Benguela sub-system during the 1980s (Fig. 8.7a) whereas anchovy and hake were the most important commercial species off South Africa (Fig. 8.7b). In the southern Benguela sub-system, the greatest proportions of total primary production were required to support catches of anchovy, large pelagic fish and hake (Fig. 8.7b). Catches of horse mackerel and hake required the greatest proportions of total primary production in the northern Benguela sub-system (Fig. 8.7a, and also Chapter 7, section 7.5). Large pelagic fish catches required a greater percentage of primary production in the south, although smaller catches were taken off South Africa than in Namibian waters (Fig. 8.7a and b). Therefore fishing large pelagics is more ecologically expensive in the southern Benguela sub-system than in the north because large pelagic fish are at a higher trophic level off South Africa than off Namibia.

Primary production required for all fisheries was 3.6% of total primary production in the southern Benguela and 5.8% of total primary production in the northern Benguela sub-system. The latter is smaller than estimates of 14% for the Namibian fishery in the early 1970s and 8% for the late 1970s (Jarre-Teichmann and Christensen 1998a). The fraction of primary production required to sustain catches in the southern Benguela ecosystem was small in comparison to the range from 8 to 14% for Peru and Northwest Africa, but similar to that required for fisheries off California between 1977 and 1985 (Jarre-Teichmann and Christensen 1998a). The small fraction could be explained by the mismatch in space and time of phytoplankton and zooplankton productivity (Verheye *et al.* 1992) and fish consumption, as discussed by Hutchings (unpublished). It has been suggested that for this reason, phytoplankton may be limiting to mesozooplankton, despite the total phytoplankton production in the southern Benguela sub-system being in excess of that required for mesozooplankton feeding (Verheye *et al.* 1992). Phytoplankton and zooplankton production may be more synchronous in the northern Benguela sub-system.

Primary production required by fisheries per unit yield was 95.9 in the northern sub-system compared to 178.9 in the southern sub-system, indicating that overall, fishing in the southern Benguela ecosystem was ecologically more expensive than in the northern Benguela ecosystem, despite lower catches in the south. The mean trophic levels of the fishery were similar in the southern (4.7) and northern (4.6) systems.

Primary production required to support the consumption of top predators (large pelagic fish, seals, chondrichthyans, seabirds, whales and dolphins) in the southern Benguela sub-system was 1 553 ty^{-1}, and in the northern Benguela sub-system 657 ty^{-1}, corresponding to 8.7% and 5.2% respectively of the total primary production. This indicates the important role played by top predators in the southern sub-system (Jarre-Teichmann *et al.* 1998), and is also reflected in the smaller catches of species serving as their prey in the southern than in the northern sub-system. This is probably partly related to the Agulhas Bank and south coast being incorporated into the southern Benguela model. The shallow bank and many sheltered bays of the south coast serve as ideal pupping and calving areas for many species of chondrichthyans and migratory whales. In addition, at certain times of the year, the Agulhas Bank is home to spawning small pelagic fish, which serve as prey for many top predators in the region.

8.7 AGGREGATED FOOD WEB STRUCTURES

An extremely interesting difference between the northern and southern Benguela ecosystems is that biomass is concentrated in trophic level I (the level of the producers) in the northern Benguela sub-system and trophic level II (herbivore level) in the southern Benguela sub-system (Table 8.5). At most trophic levels, transfer efficiencies are similar in the two systems, with the exception that transfer through trophic level III in the southern ecosystem is almost twice as efficient as that in the northern ecosystem. As expected for upwelling systems (Jarre-Teichmann 1992, Jarre-Teichmann and Pauly 1993, Christensen and Pauly 1993, Jarre-Teichmann and Christensen 1998a), the transfer efficiencies at high trophic levels are reduced, with large proportions being exported or returned to detritus. Transfer efficiencies are not reported for trophic level I because this level includes detritus, which is a non-living group for which transfer is not defined. However, considering transfer of primary production is helpful. The proportion of primary production transferred from trophic level I to II is close to 42% in the southern Benguela sub-system and more than twice this (88%) in the northern Benguela sub-system, indicating that the Namibian ecosystem relies more heavily on phytoplankton and emphasizing the greater importance of herbivory in the north than in the south. There are some long food chains in both systems, resulting in a total of 9 discrete trophic levels.

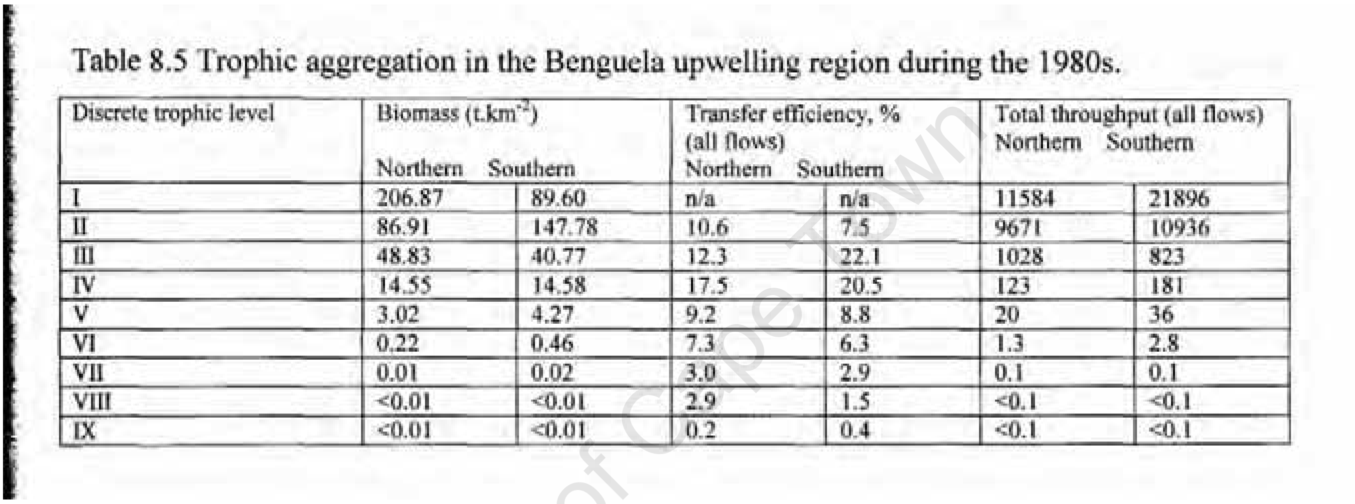


Table 8.5 Trophic aggregation in the Benguela upwelling region during the 1980s.

Discrete trophic level	Biomass ($t.km^{-2}$) Northern	Southern	Transfer efficiency, % (all flows) Northern	Southern	Total throughput (all flows) Northern	Southern
I	206.87	89.60	n/a	n/a	11584	21896
II	86.91	147.78	10.6	7.5	9671	10936
III	48.83	40.77	12.3	22.1	1028	823
IV	14.55	14.58	17.5	20.5	123	181
V	3.02	4.27	9.2	8.8	20	36
VI	0.22	0.46	7.3	6.3	1.3	2.8
VII	0.01	0.02	3.0	2.9	0.1	0.1
VIII	<0.01	<0.01	2.9	1.5	<0.1	<0.1
IX	<0.01	<0.01	0.2	0.4	<0.1	<0.1

8.8 MIXED TROPHIC IMPACT ASSESSMENT

In the northern Benguela ecosystem, microzooplankton competes with anchovy, sardine, other small pelagic fish and goby for phytoplankton food, thereby having a net negative impact on these groups. However, the phytoplankton box is not subdivided into size groups in this study. Had this been done, negative mixed trophic impacts would be reduced. By contrast, in the southern Benguela sub-system, microzooplankton benefits mesozooplankton, anchovy, sardine and redeye *Etrumeus whiteheadi*, by providing a food source for these groups and by serving as food for others upon which these groups prey (Fig. 8.8).

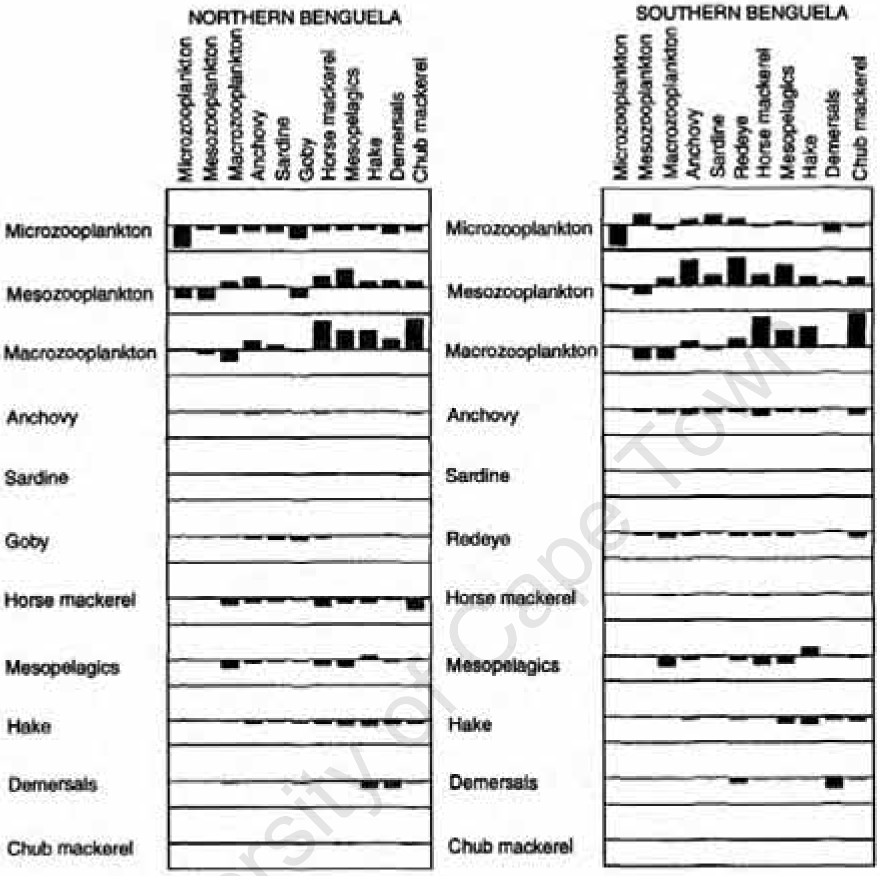


Fig. 8.8 Mixed trophic impacts of selected groups in the northern and southern Benguela sub-systems during the 1980s.The bars indicate relative net impact (scale between 0 and unity) where positive impacts are shown above the zero line for each impacting group, and negative impacts below. Impacted groups are arranged along the horizontal axis and impacting groups down the vertical axis.

Mesozooplankton compete with pelagic goby for phytoplankton food. Therefore, an increase in mesozooplankton would have a negative impact on goby off Namibia. However, mesozooplankton serve as prey for many other groups, which could benefit should mesozooplankton become more abundant. By comparison, mesozooplankton benefits the counterpart to goby in the southern Benguela sub-system, viz. redeye, which are not phytophagous.

Because of its greater biomass in the south, anchovy have more pronounced trophic impacts on other groups in the southern Benguela sub-system than in the north. Similarly, an increase in horse mackerel, the dominant pelagic species in the northern Benguela sub-system, would have large negative effects on other groups competing for zooplankton prey. In addition to being food for hake (positive effect), horse mackerel compete with hake for zooplankton prey (negative effect), and their net effect on hake in the northern Benguela sub-system is negative (Fig. 8.8). Sardine show small net effects in both ecosystems. As expected from larger catches in the northern Benguela sub-system, groups in this sub-system are more severely affected by fishing than the same groups in the south.

8.9 COMPARING ECOSYSTEM EFFECTS OF FISHING

Altered fishing mortality in simulation models has different effects in the two systems (Figure 8.9). Increasing fishing mortality (F) on the three most abundant small pelagic fish in each system (namely anchovy and sardine in both systems, and redeye in the south and goby in the north) has less pronounced effects on other components in the northern than in the southern Benguela sub-system (Figure 8.9a, top panel). Anchovy and sardine stocks in both systems crash when fishing on these species is increased fourfold (Fig. 8.9a). Further, in the southern Benguela sub-system, there is a sharper decline in large pelagic fish when their prey of anchovy and sardine are severely fished.

Redeye and goby catches are very low and therefore increasing these by a factor of four appears to have little effect. Despite such low fishing effort on redeye and goby in the southern and northern sub-systems respectively, the EEs of these two groups are very high (greater than 0.97, Tables 8.1 and 8.2), indicating that they are in high demand as food for other groups. Fishing at higher absolute levels would have major implications for the systems. In the southern Benguela sub-system, chub mackerel and horse mackerel are favoured by decreases in anchovy and sardine biomass, leaving more zooplankton available to their competitors (see negative mixed trophic impact of anchovy on chub mackerel and horse mackerel in the south, Fig. 8.8).

When fishing mortality is increased fourfold as above, but only for the first four years of the simulation, sardine in the northern Benguela sub-system begin to recover, although only reaching about one third of its original biomass by year ten (Figure 8.9b, middle panel). Anchovy does not recover. In the southern Benguela sub-system, both species recover by year ten.

Increasing fishing mortality of hake fourfold in the first four years of simulation reduces hake biomass, thereby favouring some of the prey species of hake, such as mesopelagic fish and cephalopods (Figure 8.9c, bottom panel). However, in the northern Benguela sub-system, other small pelagic fish (saury, flying fish, etc.) are reduced and do not recover once fishing on hake is restored to its original level. In both systems, horse mackerel are negatively affected by increased fishing on hake, stabilising at a lower level of abundance once fishing on hake is restored to its original level. The effect is more severe in the south than in the north and is explained by the greater net negative impact that mesopelagic fish have on horse mackerel in the south by competing with them for zooplankton food (Fig. 8.8).

An additional scenario considered the ecosystem effects of heavier fishing on horse mackerel. As horse mackerel are lightly fished in the southern Benguela sub-system, increasing F by a factor of four, for example, has little effect. However, in the northern Benguela sub-system, increasing F on horse mackerel fourfold for four years reduces horse mackerel biomass dramatically, so that by year ten, biomass is only at half its original level. Horse mackerel has a negative effect on chub mackerel by competing with them for zooplankton prey (refer to mixed trophic impacts in Fig.

8.8). Therefore chub mackerel are favoured by this scenario, levelling off at a biomass a factor of 1.7 that at the start.

8.10 CONCLUSIONS

There are clearly differences in the structure and functioning of the northern and southern Benguela sub-systems, related to abundances of the various components, as well as to the level of harvesting on these. Herbivory is more important in the northern Benguela sub-system than in the southern Benguela sub-system. Zooplankton are more abundant in the northern than southern Benguela sub-system in the 1980s, but not as efficiently transferred to higher trophic levels. Catches are larger in the north, despite the larger overall production in the southern Benguela sub-system. However, fishing is ecologically more expensive in the south. Top predators are important components in the southern Benguela sub-system, as indicated by twice the primary production required to support consumption by top predators in the south than in the north. Demersal fish biomass required to support consumption in the southern Benguela sub-system is twice that in the north. However, when hake biomass is taken into account, the overall demersal component is only slightly larger in the south, and is explained by the fact that the southern Benguela sub-system is a continuum from an upwelling region to a wide shelf ecosystem. Although only lightly fished in both sub-systems, mesopelagic fish, redeye and pelagic goby are required to sustain the production of other components within the systems, and their heavier exploitation should be considered with caution.

Simulations of altered fishing strategies show that increasing fishing mortality (in proportion to its original value) has different effects in the two systems, and that these are complex responses to indirect and direct competition. In the south, large pelagic fish are more severely affected by fishing strategies that reduce their small pelagic prey. Also, horse mackerel and hake are more closely linked, so that reducing hake biomass has a more pronounced effect on horse mackerel in the southern Benguela sub-system than in the north. It is planned that this work will form part of a fuller comparison of the trophic functioning of both the northern and southern Benguela sub-systems during periods dominated by different species. Using an approach such as this, it would be possible to compare the way in which harvest and conservation strategies impact the northern and southern sub-systems under different species dominance regimes. This would be of benefit to both South Africa and Namibia, particularly as the fisheries have been managed in different ways in the two systems over the last few decades. Researchers and managers in each system could learn from the other, and both could work together towards improving fisheries management and conservation in the future.

CHAPTER NINE

BOTTOM-UP, MIXED OR WASP-WAIST CONTROL IN THE SOUTHERN BENGUELA ECOSYSTEM

ABSTRACT

The effects of altered fishing on three abundant small pelagic fish, and on hake, are explored using the dynamic model *Ecosim* for three scenarios of top-down and bottom-up control of zooplankton, small pelagic fish and their predators. There are large differences between the ecosystem effects of altered fishing simulated under the three scenarios. Bottom-up control of zooplanktivorous fish by zooplankton dampens effects of altered fishing. Wasp-waist control (top-down control of zooplankton by their predators and bottom-up control of predators by small pelagic fish) causes vigorous effects to propagate through the ecosystem. Effects of mixed control are intermediate between the former two scenarios. Heavier fishing may be sustainable under one scenario of control, whereas fisheries may crash if another type of control is assumed between ecosystem components. The key to predicting ecosystem effects of fishing is understanding the way in which components of the ecosystem interact.

9.1 INTRODUCTION TO THE WASP-WAIST CONCEPT

Among the most productive marine ecosystems are those found in upwelling regions. These tend to be characterised by a large number of species at low trophic levels (phyto- and zooplankton), as well as a variety of species at high trophic levels (predatory fish, marine mammals and birds, sharks etc.). However, at intermediate trophic levels, there are usually few species, mainly small pelagic fish. Generally, upwelling regions are dominated by one or two species of anchovy and sardine during a particular period. An ecosystem with few intermediate species present at high abundances, and high species diversity of planktonic prey and predatory fish, mammals and birds, has been classified as a "wasp-waist" ecosystem (Rice 1995, Bakun 1996). Variations in mid-trophic level wasp-waist populations have been shown to dominate trophodynamic variability in many marine ecosystems (Rice 1995). The large fluctuations in pelagic fish population sizes may have large bottom-up effects on their predator species at higher trophic levels, and large top-down effects on species at lower trophic levels and on which the highly variable pelagic fish populations feed (Bakun 1996). Therefore, control is neither top-down nor bottom-up, but rather from the "waist", up and down (Bakun 1996).

Cury *et al.* (2000) present retrospective analyses of top-down control of zooplankton and bottom-up control of pelagic fish that support the wasp-waist concept in upwelling ecosystems. For example, off southern Africa, a shift in the zooplankton community structure has been observed and linked to the possible top-down effects of differential size-selective predation by anchovy and sardine (Verheye and Richardson 1998, Verheye *et al.* 1998). Jennings and Kaiser (1998) noted that top-down control of prey fish by their predators in marine ecosystems is not usually observed because most pelagic predators are generalists, feeding on a wide range of prey species and capable of prey switching. Instead, there may be cases of donor-control (bottom-up control) of some predatory species that are unable to change their diets when relative abundances of prey fish change. Cury *et al.* (2000) found much evidence for bottom-up control of predators by their pelagic fish prey. For example, certain seabirds species, such as the African Penguin in the Benguela ecosystem, have limited foraging ranges and are affected by long-term fluctuations in pelagic fish population sizes and geographical distribution. Collapses of forage fish resources have had dramatic impacts on predatory fish. For example, the snoek population off Chile collapsed four years after the collapse of the Chilean anchoveta *Engraulis ringens* in 1973, and snoek catches have remained low ever since (Cury *et al.* 2000).

We might ask if it is necessary to distinguish between types of control operating in an ecosystem. this chapter the ecosystem effects of fishing are investigated in situations where different kinds f control are assumed to operate (key question 3b). Control is assumed to be either bottom-up oups eating zooplankton are controlled by their prey), wasp-waisted (there is bottom-up ntrol of predators eating small pelagic fish, and top-down control of zooplankton by small logic fish) or mixed (all interactions between groups are a mixture of top-down and bottom-up ntrol). These three types of flow control (Fig. 9.1) are investigated using a dynamic trophic ulation model of the southern Benguela ecosystem.

9.2 METHODS

An early, steady-state mass-balanced *Ecopath* model of the southern Benguela ecosystem during the 1980s is run in the dynamic simulation mode *Ecosim* (Chapter 3, section 3.5). For this study, all settings in *Ecosim* assume default values, with the exception of "flow control", a term that describes the interactions between groups in an ecosystem, determining whether there is top-down, bottom-up or mixed control of predators by their prey and vice versa. In *Ecosim*, flow control is parameterized by allocating a value to "vulnerability ratios" for each predator-prey interaction modelled. For each box modelled, there are components that are vulnerable and invulnerable to predation (see Chapter 3, section 3.5, equations 3.7-3.9). User-defined "vulnerability" is the transfer rate between the behaviourally or structurally vulnerable and invulnerable components of prey to their predators, and determines whether flow is bottom-up, top-down or mixed/intermediate (Walters *et al.* 1997, Walters unpublished). Low values of "vulnerability" define bottom-up flow control, where an increase in the productivity of a prey box leads to its increased biomass and corresponds to its increased availability to predators. This usually causes resilience of the prey to fishing in *Ecosim* models (Walters unpublished).

On the other hand, high values for "vulnerability" define top-down flow control, where an increase in biomass of a predator can reduce the biomass of its prey, in turn allowing their prey to become more abundant (Walters *et al.* 1997). High "vulnerabilities" usually cause the model prey to be highly sensitive to changes in fishing mortality rates (Walters unpublished). Simulations of altered fishing mortalities have been found to be very sensitive to "vulnerabilities" in *Ecosim* (Bundy 1997, Christensen and Walters 2000, Walters unpublished).

Here, three scenarios of flow control are tested to illustrate its importance on the simulated effects of altered fishing:

a) Interactions with micro-, meso- and macro-zooplankton are assumed to be largely bottom-up controlled (i.e. food limited), with vulnerability set to 0.1. All other interactions are of the mixed control type (0.5).
b) Interactions between all groups are assumed to be of the mixed-control type (vulnerability set to 0.5) i.e. neither predator- nor donor-control operates.
c) Interactions between micro-, meso- and macro-zooplankton and their predators are assumed to be top-down controlled, with vulnerability set to 0.9. Interactions between small pelagic fish (anchovy, sardine, redeye, saury, flying fish etc.) and their predators are assumed to be bottom-up controlled (food limitation for predators of small pelagics), with vulnerability set to 0.1. All other interactions are of mixed control type (0.5). This scenario represents a wasp-waisted system and is referred to as wasp-waist control (Curt' *et al.* 2000).

Three scenarios are used to explore the impacts of altered fishing on three of the most abundant small pelagic fish groups (anchovy, sardine and redeye *Etrumeus whiteheadi)* and on the commercially most important fish (hake *Merluccius capensis* and *M paradoxus)* off South Africa. In all cases, the model is run for ten years in the absence of altered fishing, so that stability is reached prior to perturbation of the ecosystem. Altered fishing scenarios investigated are:

1) Increased fishing mortality (F) of anchovy, sardine and redeye fourfold from year ten to fifty,
2) Increased fishing mortality of anchovy, sardine and redeye fourfold from year ten to fifteen, thereafter Fs restored to original levels for a further 35 years, and
3) Increased fishing mortality of hake fourfold from year ten to fifteen, thereafter F restored to its original level for a further 35 years.

There are now three methods in which "vulnerabilities" can be estimated in *Ecosim* including routines that fit time series data and optimize the evolutionary optimum between feeding time and growth rates (Christensen and Walters 2000). However, these are new and were not used in this study.

9.3 RESULTS OF SIMULATING INCREASED FISHING MORTALITY

9.3.1 Increasing fishing mortalities on anchovy, sardine and redeye

In model projections, anchovy and sardine stocks decrease or collapse under all three flow control scenarios (Fig. 9.2 a). By contrast, redeye is little affected, as fishing mortality is small at the outset. When there is bottom-up control of small pelagic fish by zooplankton, the modelled system stabilises at new biomass levels. Biomass of anchovy stabilises at half that at the start, and sardine at 40% of its original biomass. Modelled populations of predators of small pelagic fish (seals, whales, dolphins, seabirds and large pelagic fish) stabilise at smaller sizes. By comparison, groups such as other small pelagic fish, horse mackerel and cephalopods, competing with anchovy and sardine for zooplankton prey, stabilise at population sizes greater than those before heavier fishing (Fig. 9.2a).

When wasp-waist control is modelled, chub mackerel, horse mackerel and other small pelagic fish benefit from the reduced anchovy and sardine stocks by reduced competition for zooplankton prey (Fig. 9.2a). When control is wasp-waisted, large pelagic fish are reduced to 43% of the group's original biomass, whereas modelled abundance decreases steadily over 50 years when there is mixed control.

When bottom-up flow control is modelled, anchovy and sardine catches are sustainable at about double those in the 1980s. However, the anchovy fishery collapses when control is mixed or wasp-waisted. Despite small catches of redeye, their EE is very high (greater than 90%), indicating that redeye are important prey in the sub-system. Fishing of redeye at four times the original F (still only at F=0.12) is sustainable for the fifty year simulation period under all three control types. Nevertheless, it is likely that heavier exploitation of redeye would have detrimental ffects on other groups feeding on the species.

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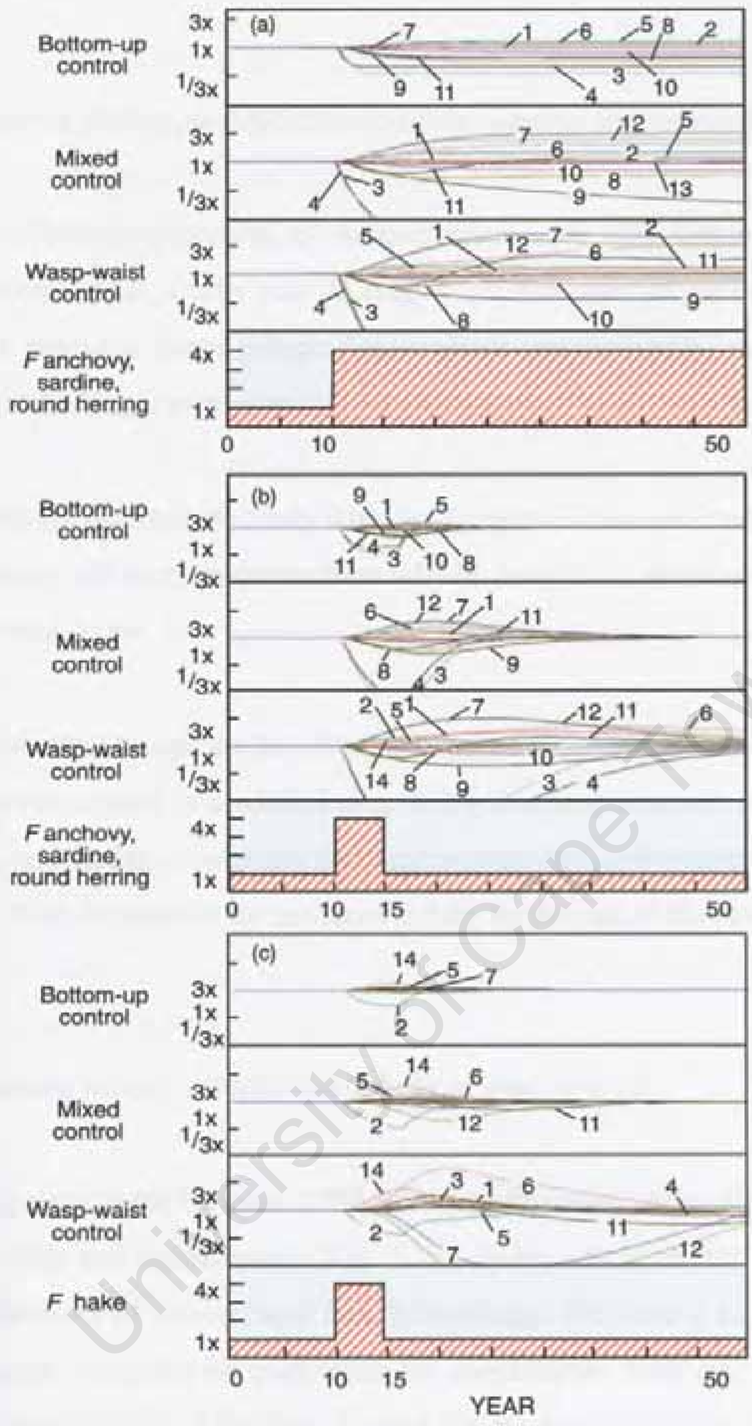


1 = Redeye
2 = Hake
3 = Sardine
4 = Anchovy

5 = Cephalopods
6 = Other small pelagics
7 = Chub mackerel
8 = Seals

9 = Large pelagics
10 = Seabirds
11 = Cetaceans
12 = Horse mackerel

13 = Chondrichthyans
14 = Mesopelagics

Fig.9.2 Effects of increased fishing mortality on biomasses in the southern Benguela ecosystem model, assuming bottom-up, mixed and wasp-waist control under the following scenarios:

a) a fourfold increase in fishing mortality *(F)* of anchovy, sardine and redeye from year ten onwards.

b) a fourfold increase in fishing mortality *(F)* of anchovy, sardine and redeye from year 10 to 15, after which Fs are restored to original levels.

c) a fourfold increase in fishing mortality *(F)* of hake from year 10 to 15, after which Fs are restored to original levels.

Biomass is plotted as a proportion of original biomass.

9.3.2 *Increasing fishing mortalities on anchovy, sardine and redeye from year10 to 15*

When there is bottom-up control, all components recover fully within ten years after fishing returns to normal levels, i.e. by year 25 (Fig. 9.2b). Recovery of anchovy and sardine is fast, whereas their predators (large pelagic fish, seabirds and mammals) and competitors (such as cephalopods) take longer to recover.

When flow control is mixed, recovery times are longer and there are more pronounced responses to altered fishing. All components recover fully by year 35 i.e. about twenty years after fishing returns to normal levels.

Populations of many groups do not return to original sizes by the end of the simulation period when wasp-waist control is modelled (Fig. 9.2b). Anchovy biomass only reaches 86% of its original size, and predators (seabirds and large pelagic fish) and competitors (redeye, saury and other pelagic fish) of anchovy do not recover fully by the end of the simulation period.

9.3.3 *Increasing fishing mortality on hake from year 10 to 15*

Heavy fishing reduces the biomass of hake, thereby favouring some of its prey species, such as mesopelagic fish and cephalopods (Fig. 9.2c). Horse mackerel are negatively affected by increased biomasses of mesopelagic fish. Mesopelagic fish have a large net negative trophic impact on horse mackerel by competing for zooplankton food (see mixed trophic impact assessment, Chapter 5, Fig. 5.7). When control is bottom-up, all groups modelled recover within about ten years after fishing on hake returns to normal levels, and within about twenty years when control is mixed.

Mesopelagic fish respond almost immediately to altered fishing on hake, whereas other groups such as chub mackerel, saury and other small pelagic fish have a delayed (3-4 years) response. This is explained by the fact that hake consume large quantities of mesopelagic fish (30% of the diet of hake) and by mesopelagic fish feeding exclusively on zooplankton, enabling them to respond quickly to the suddenly improved availability of zooplanktonic food and reduced predation. By comparison, chub mackerel and other small pelagic fish are slower to show signs of recovery because predation mortality by hake is less important than for mesopelagic fish (chub mackerel and other small pelagic fish make up only 0.1% and 0.2% of the diet of hake respectively).

When control is wasp-waisted, the fishing pattern greatly perturbs the system so that 35 years after return to normal fishing on hake, many groups have not yet returned to baseline levels of abundance (Fig. 9.2c). Since reduced hake abundance allows mesopelagic fish to become more abundant, and because mesopelagic fish compete with chub mackerel for zooplankton prey, heavier fishing on hake has a negative effect on chub mackerel. Therefore, contrary to what may be expected when considering only chub mackerel predation by hake (Bergh *et al.* 1985), increased hake fishing reduces the size of the chub mackerel stock in this simulation.

9.4 THE IMPORTANCE OF FLOW CONTROL IN DETERMINING THE EFFECTS OF ALTERED FISHING

When there is bottom-up control of predators by zooplankton (i.e. zooplankton availability is limiting), modelled effects of altered fishing are small. This results from intense competition among species eating zooplankton. However, when control of zooplankton by pelagic predators is top-down, and there is bottom-up control of predatory pelagic fish, marine birds, marine mammals and fishers by small pelagic prey species, major perturbations propagate through the systems. This occurs because there is reduced competition for zooplankton food under wasp-waist control, allowing the ecosystem components to respond readily to changes in fishing pressures. Modelling mixed control type interactions gives results intermediate between those of the bottom-up and wasp-waist control scenarios.

Modelling using *Ecosim* shows that when there is heavy fishing on small pelagic fish such as anchovy, sardine and redeye, competing species such as chub mackerel and horse mackerel benefit through enhanced availability of zooplankton prey. The increase in abundance of these competitors delays the recovery of anchovy and sardine once fishing returns to normal levels. Predators of small pelagics, in particular large pelagic fish, decline and are slow to recover.

It has been suggested that altering exploitation patterns of hake may have unpredictable effects (Bergh *et al.* 1985). Squid, an important prey of hake, may play a central role in the southern Benguela ecosystem (Bergh *et al.* 1985). As predicted by Bergh *et al.* (1985), heavy fishing of hake reduces predation mortality of squid, allowing an increase in cephalopod biomass. Larger fishing mortality of hake allows mesopelagic fish to become more abundant, thereby negatively impacting horse mackerel through increased competition for zooplankton prey. The effects of altered fishing are dampened when there is bottom-up control by zooplankton on its small pelagic predators, whereas top-down control of small pelagic fish on zooplankton (in the wasp-waist scenarios) causes more vigorous responses of components, and recovery is slower. These results are supported by the work of Mackinson *et al.* (1997), who used *Ecosim* to compare the trophic impacts of harvesting in three upwelling ecosystems. Heavy exploitation of small pelagics led to an increase in biomass of their prey and competitors, and a corresponding decline in biomass of predators (Mackinson *et al.* 1997). They found that bottom-up control of small pelagics by zooplankton could not account for the switch in species dominance from anchovy to sardine in Peru; when top-down control was modelled, components of the system fluctuated more wildly and underwent larger changes in biomass than when bottom-up control was modelled.

It is concluded that, to a large extent, ecosystem effects of fishing are determined by the way in which interactions between components within a system are linked. Results are very different under different selections of top-down and bottom-up control between selected groups. When there is bottom-up control by zooplankton, increasing fishing mortality of anchovy and sardine fourfold from year ten onwards was sustainable, although modelled stocks stabilise at lower *levels of abundance. This is an example of the response discussed by May et al. (1979), whereby* some systems experiencing a change in harvesting or environmental change respond in a catastrophic way so that the system stabilises at a new equilibrium, a process that is often not reversible. However, assuming mixed or wasp-waisted control causes a collapse of anchovy and sardine stocks and fisheries.

Populations take longer to recover after perturbation of the steady-state system through increased fishing when wasp-waist control is assumed, as opposed to bottom-up or mixed control. In particular, thirty five years after a five-year pulse of heavy fishing on small pelagic fish, modelled anchovy and sardine populations have not yet returned to original levels when control is wasp-waisted. This result is similar to the observed long (sixty five to seventy years) time scale upon which anchovy and sardine populations fluctuate naturally in both the Benguela and Californian systems (M^{c}Lachlan 1995, Baumgartner 1992, 1995). It is expected that a period of heavy fishing on small pelagic fish would have large effects on the ecosystem given their importance as predators of zooplankton and as prey for fish, avian and mammalian predators. It is unlikely that in the real world situation, the heavy fishing events modelled would have such small effects as those when bottom-up control is assumed. Retrospective analyses of data from upwelling ecosystems suggested that there is top-down control of zooplankton and bottom-up control of pelagic fish, supporting the wasp-waist concept (Cury *et al.* 2000). Although the dynamics of wasp-waist systems are not yet fully understood, it is clear that such food webs do not behave in the same way as others in which there are more species at mid-trophic levels than at high and low trophic levels (Rice 1995). It is likely that of the three flow control types modelled, the wasp-waist scenario represents best the flow of matter between components of the southern Benguela ecosystem. Therefore, for simulations in which effects of fishing are examined (Chapter 10), wasp-waist control is assumed to operate in the southern Benguela ecosystem. This may be advantageous; the wasp-waist nature of boreal food webs facilitates modelling that would be tricky should more complex interactions determine the trophic functioning of these ecosystems (Livingstone and Tj elmeland 2000). The work presented in this section highlights the importance of understanding the way an ecosystem functions in terms of internal control between components, which will be the key to improving predictions of the ecosystem effects of fishing.

CHAPTER TEN

POTENTIAL EFFECTS OF ALTERED FISHING STRATEGIES IN THE SOUTHERN BENGUELA ECOSYSTEM

ABSTRACT

Several theoretical fishing strategies are examined to explore the possible ecosystem effects of implementing these options in the southern Benguela ecosystem. Potential effects of altered fishing are larger in 1980s simulations than in those of the 1990s because the model ecosystem is more tightly constrained in the 1980s. Results often contradict those hypothesized, highlighting the importance of taking into account direct and indirect ecosystem interactions and the way in which they change over time when considering alternative fishing strategies. Simulations of the potential effects of altered fishing strategies will depend on assumptions upon which the models are based, particularly that fisheries and biological estimates input to the model are averages for eight-ten year periods. Heavier fishing on large hakes with the intention of reducing hake "cannibalism" does not appear to benefit hakes in the southern Benguela ecosystem. This study suggests that anchovy catches were optimal during the 1980s, that larger sardine catches are unlikely to be sustainable during the 1990s (although a pulsed increase in the sardine fishery had few long-term impacts), and that if the demersal trawl fishery were to be expanded, one would expect large decreases in hake stocks. Potential fishing strategies would have important implications for fisheries managers because trade-offs between fisheries are often required if larger catches in some fisheries are to be sustained. Careful consideration of socio-economic benefits and constraints and clearly defined management objectives are required when considering alternative fishing strategies.

10.1 INTRODUCTION

The potential effects of changed fishing strategies on different components of the southern Benguela ecosystem are investigated (key question 3a) so that advice can be provided for the management of fisheries that depend on sustainability of the system. There is pressure to expand and develop some fisheries off South Africa to provide employment opportunities. The current study explores the feasibility of some of these options by considering the potential effects of changes in fishing strategies on the whole ecosystem, as well as the implications for other fisheries.

Heavy fishing is modelled on species that are only lightly fished at present, such as redeye and mesopelagic fish. Although currently not of high commercial value, these species are important prey of other commercially valuable species such as hakes and pelagic-feeding demersal fish. How much redeye and mesopelagic fish can be caught without reducing the catches of hakes, for example?

Increases in catches of species such as anchovy, sardine and snoek, currently having large directed fisheries (Chapter 5, section 5.6.3), are modelled so that effects on other ecosystem components and fisheries can be monitored. It is likely that there will be trade-offs required to support larger fisheries on these species. For example, predators of small pelagic fish include seabirds and marine mammals, groups attracting growing interest for their potential to sustain a potentially lucrative ecotourism industry. Further, snoek prey directly on small pelagic fish, so that changes in fisheries of snoek, for example, may affect the anchovy fishery.

Is it possible for the demersal trawl fishery to expand, and if so, what would be the likely ecosystem effects? Would anchovy and sardine catches increase if heavier fishing on horse mackerel were to be encouraged? Would it be possible to increase hake catches by increasing the fishing pressure on large fish to reduce "cannibalism"? These are some of the questions that arise when one considers expanding or developing South African fisheries. Whereas single-species assessments (Chapter 5, section 5.6.3) are useful when managing a stock in isolation or, at most, in relation to one or two other species, these questions can only be fully answered by taking a broader look at the stock as part of the whole ecosystem. It is important to consider the potential effects of harvesting on other groups and on other existing fisheries in the same system. These net effects incorporate both direct and indirect interactions between predators, prey, competitors and fisheries.

10.2 METHODS

In other parts of this dissertation, total catches of each group were modelled. In this chapter, catches are modelled using *Ecosim* on the basis of fishing gear type (Chapter 4, Table 4.2), so that the effects of fishing by the major fisheries can be distinguished. Further, conservative estimates of discards of small hakes are incorporated, as tested in Chapter 6 (section 6.2.5). Six fisheries are considered:

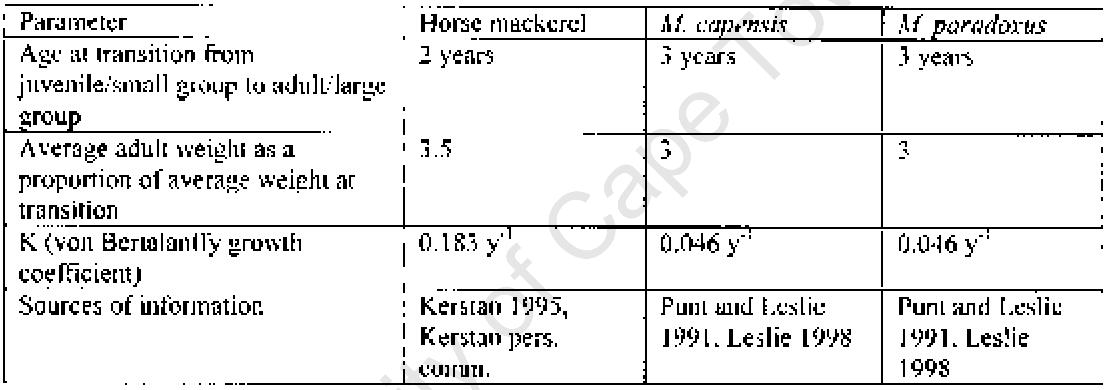
i) purse seine fishery,
ii) midwater trawl fishery (very small component of the total catch),
iii) demersal trawl fishery (includes inshore and offshore trawls on the south coast of South Africa, and demersal trawls on the west coast of South Africa),
iv) line fishery,
v) long line fishery and
vi) other (includes beach seine, gill net, handline, jig fishery for squid, recreational, deaths of seals by culling and from fishery-related causes).

The potential effects of altered fishing strategies on the southern Benguela ecosystem are simulated using *Ecosim*. It is assumed that the system is "wasp-waisted" (Chapter 9), i.e. that small pelagic fish control both their prey (top-down control) and their predators (bottom-up control). The model incorporates trophic ontogeny (Chapter 3, section 3.5), allowing adults and juveniles of three species to be linked in the southern Benguela models used here:

a) juvenile and adult horse mackerel *Trachurus trachurus capensis*
a) small and large shallow water hake *Merluccius capensis*
b) small and large deep water hake *M paradoxus.*

A delay-differential model is used to model the recruitment of juveniles/small individuals into the adult/large size pool (Walters *et al.* 1997), based on parameters tabulated (Table 10.1). Using this approach, it is possible to keep track of recruitment depending on changes in feeding conditions (Christensen and Walters 2000). Individuals in each group are subjected to total mortality that can change over time, depending on the sum of the amounts consumed by their predators, including fisheries. Natural mortality excluding predation ("baseline mortality") is calculated from the steady-state *Ecopath* balance in which P/B is input, and is assumed to remain constant in *Ecosim* simulations.

Table 10.1 Parameters used to model the growth of juvenile/small horse mackerel and hakes into adults.



Parameter	Horse mackerel	*M. capensis*	*M. paradoxus*
Age at transition from juvenile/small group to adult/large group	2 years	3 years	3 years
Average adult weight as a proportion of average weight at transition	3.5	3	3
K (von Bertalanffy growth coefficient)	0.183 y^{-1}	0.046 y^{-1}	0.046 y^{-1}
Sources of information	Kerstan 1995, Kerstan pers. comm.	Punt and Leslie 1991, Leslie 1998	Punt and Leslie 1991, Leslie 1998

The following questions are addressed in this chapter:

1) Could increased catches of anchovy be sustained during the 1980s scenario?
2) Could increased catches of sardine be sustained during the 1990s scenario?
3) Could more redeye be caught?
4) Could other fisheries expand if the purse seine fishery is closed?
5) Could a larger line fishery be supported?
6) Is there room for expansion of the demersal trawl fishery?
7) Could heavier fishing on large hakes reduce "cannibalism"?
8) Could heavier fishing on adult horse mackerel enhance stocks and catches of other small pelagics?

To answer these, the fishing mortality rates of various ecosystem components are altered, either simulating pressed or pulsed perturbations. Pressed perturbations occur when one or more species are perturbed continuously; there is sustained alteration of species densities until unperturbed species reach new equilibria (Bender *et al.* 1984). Pulsed perturbations are instantaneous changes of one or more species over a defined period, and recovery is then observed. In each fishing scenario modelled, a simulation period of 50 years is used so that the risk of missing long-term effects by only considering short time periods is avoided (Chapter 3, section 3.6). This is well within the 65-70 year period over which decadal changes in small pelagic fish have been reported for both the Benguela and Californian systems (Baumgartner 1992, 1996, M^{c}Laghlan 1995). Discrepancies between the biomass trends or absolute biomasses of fish ten years after implementation of altered fishing scenarios (i.e. in year 20) and at the end of the simulation (year 50) are shaded in Tables D.5-D.12 in Appendix D. Interspecific "cannibalism" of hakes is discussed in section 10.3.7 and corresponding hake in the diets of hakes given in Table 10.3.

10.3 POTENTIAL EFFECTS OF ALTERED FISHING

10.3.1 Could increased catches of anchovy be sustained during the 1980s scenario?

Rationale: Anchovy was the dominant small pelagic fish species in the southern Benguela ecosystem during the 1980s. Is it possible that larger catches of the species could have been supported under this average ecosystem scenario?

i) Pressed perturbation

Simulation: Fishing mortality of anchovy is increased by 10%, 25% and 50% from year ten to year 50.

Result:

Even an increase in anchovy fishing mortality of 10% causes a reduction in anchovy biomass and catches, so that at the end of the fifty year simulation period, the anchovy yield is more than 20% lower than in the 1980s (Fig. 10.1).

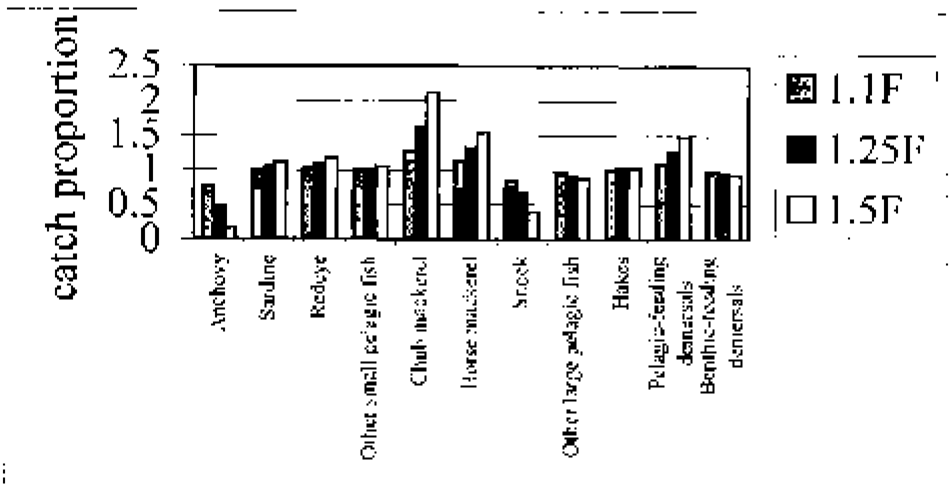


Fig. 10.1 Catches at the end of the fifty-year simulation period when the fishing mortality rate of anchovy is increased by three different factors from year 10 onwards, expressed as proportions of means estimated in the southern Benguela ecosystem for the 1980s.

Biomass and catches of most groups show signs of stabilizing by year 50 when the anchovy fishing mortality rate is increased by 25%. At the end of the simulation, anchovy biomass and yield are half the 1980s means, and snoek biomass and catches about 65% of previous levels (Fig. 10.1). Chub mackerel biomass and yield are still increasing by year 50, when they are a factor of 1.64 larger than the 1980s mean. Pelagic-feeding demersal fish (excluding hakes) and horse mackerel are sustained at biomasses 30% larger than in the 1980s. Overall, total catches are 30% larger when fishing on anchovy is increased by 25%.

Biomass and catches of many groups are still changing at the end of the simulation period when fishing mortality of anchovy is increased to 1.5 times the 1980s rate; the anchovy fishery collapses, with catches in year 50 only reaching 16% of the previous mean levels.

Future considerations:

If anchovy catches were to be increased, even by as little as 10%, likely consequences are a reduction in the anchovy fishery of more than 20%, and a 15% decrease in snoek catches. Simulations suggest that optimal anchovy catches were made in the 1980s.

ii) Pulsed perturbation

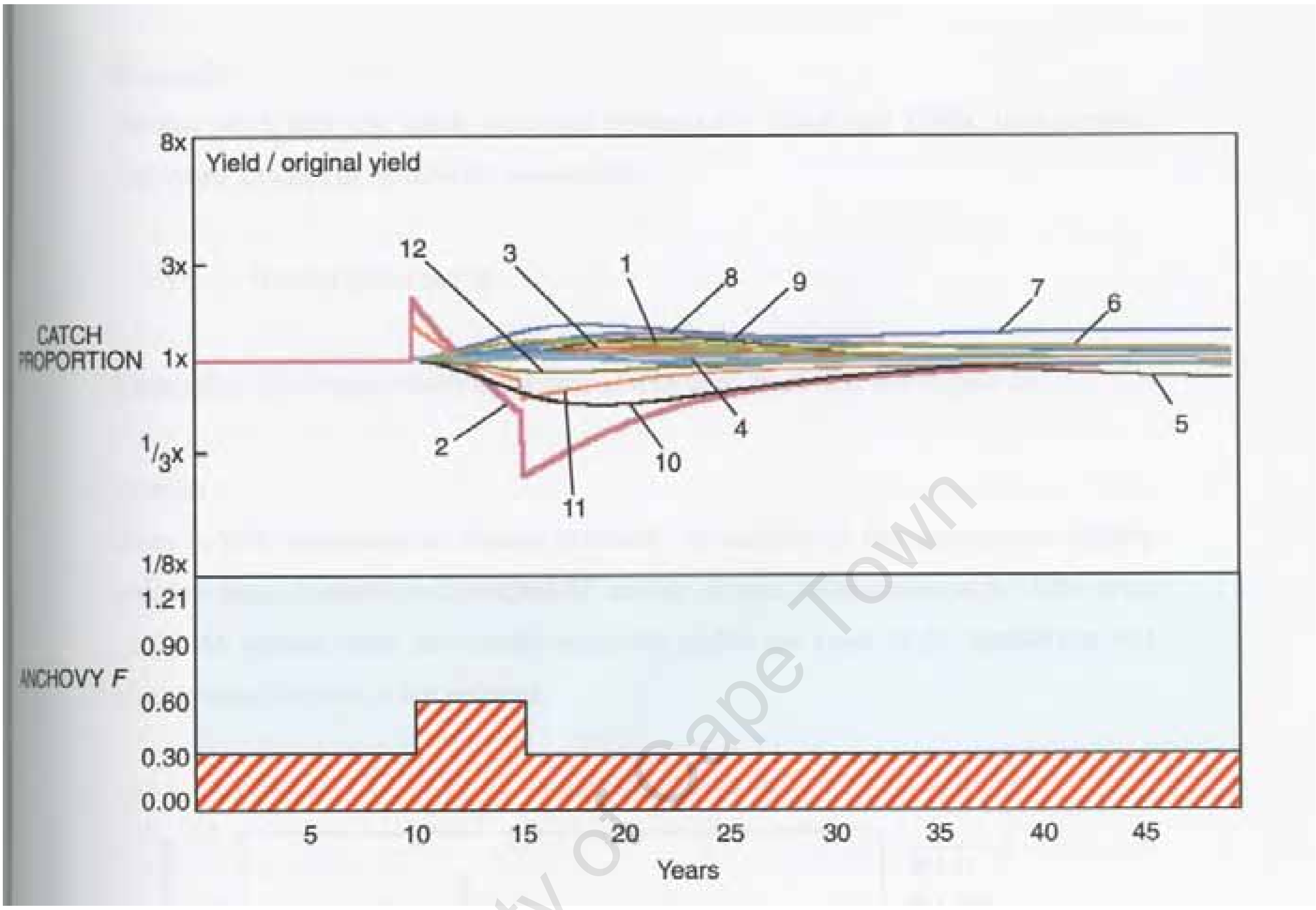
Simulation: Anchovy fishing mortality rate is doubled between year 10 and 15, whereafter it is returned to its original level.

Results:

Immediately after the five-year period of heavier fishing on anchovy, anchovy biomass and catches are reduced to a quarter of previous levels, and snoek catches have decreased by more than 10% (Fig. 10.2). Although by year 50, most groups return to biomass and catch levels similar to those in the 1980s, the system is still perturbed; chub mackerel biomass stabilizes at a biomass 1.44 times larger than that in the 1980s, and the abundance of other small pelagic fish is decreasing. In year 50, anchovy catches are still 7% lower than the means estimated for the 1980s. Horse mackerel and pelagic-feeding demersal fish biomass and catches are more than 10% larger than 1980s levels (Fig. 10.2).

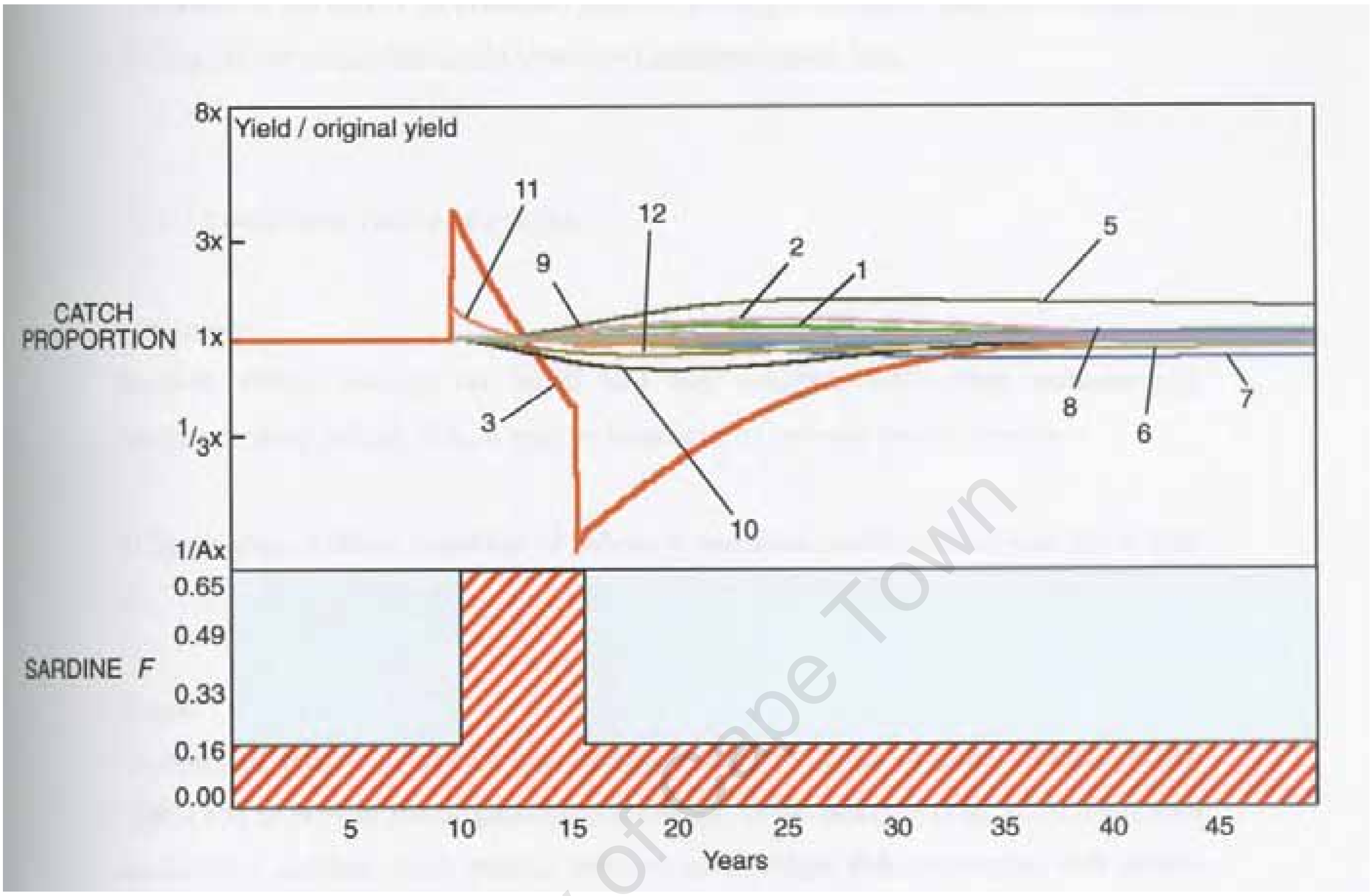
Future considerations:

Short-term impacts of fishing on anchovy may have long-term consequences for the ecosystem. If heavier fishing on anchovy for as short a period as five years were allowed, instead of boosting the anchovy fishery in the short term, it is likely that smaller catches would be made and the fishery would not completely recover in the long-term (by year 50).



1 = Redeye
2 = Anchovy
3 = Sardine
4 = Mesopelagics
5 = Other small pelagics
6 = Pelagic-feeding demersals
7 = Chub mackerel
8 = Juvenile horse mackerel
9 = Adult horse mackerel
10 = Snoek
11 = Total catch
12 = Other large pelagics

Fig.10.2 Catches of some groups in the southern Benguela ecosystem simulated over fifty years, when the fishing mortality rate of anchovy is doubled between year 10 and 15, whereafter it is restored to its original value. Catches are expressed as a proportion of those in the 1980s.



1 = Redeye
2 = Anchovy
3 = Sardine
5 = Other small pelagics
6 = Pelagic-feeding demersals
7 = Chub mackerel
8 = Juvenile horse mackerel
9 = Adult horse mackerel
10 = Snoek
11 = Total catch
12 = Other large pelagics

Fig 10.4 Catches of some groups in the southern Benguela ecosystem simulated over fifty years, when the fishing mortality rate of sardine is increased fourfold from year 10-15, whereafter it returns to its original level. Catches are expressed as proportions of those in the 1990s.

averaged, and it is possible that in the later part of the 1990s, sardine was more important in the diet of its predators than the averaged estimates used here. Therefore, fishing effects on sardine could have been underestimated here.

10.3.3 Could more redeye be caught?

Rationale:

Because redeye catches are small and they compete with other commercially important small pelagic fish, it may be beneficial to increase redeye catches.

a) Simulation: Fishing mortality of redeye is increased fourfold from year ten to year 50.

Result:

Biomass of redeye decreases but stabilizes at 41% of the original biomass in the 1980s and at 30% of the original biomass in the 1990s scenario (Fig. 10.5). Fish such as anchovy, sardine, small pelagic fish and mesopelagic fish, competing with redeye for zooplankton prey, increase in biomass (Fig. 10.5). Stocks of horse mackerel and pelagic-feeding demersal fish decline. Over the 50 years modelled, biomass (excluding detritus) of the system increases by 3% in the 1980s and by less than 1% in the 1990s. Total catches increase by 19% in the 1980s and by 10% in the 1990s, mainly because the system is able to support biomass and catch of anchovy 43% and 48% larger than the means for the 1980s and 1990s respectively. When redeye is heavily fished, horse mackerel biomass and catches are reduced to 76% and 81% of means during the 1980s and 1990s respectively. Redeye has a net negative mixed trophic impact on horse mackerel through competition for zooplankton food (Chapter 5, Fig. 5.7), thus it would be expected that the reduction in redeye biomass would favour an increase in horse mackerel because of reduced competition between horse mackerel and redeye. However, when redeye decline, anchovy and sardine increase and compete with horse mackerel for zooplankton prey. At the end of the 50-year simulation period using the 1980s model, the purse seine fishery catches 30% more fish, catches in the line fishery are 13% larger, and demersal trawl catches are reduced

10.3.2 Could increased catches of sardine be sustained in the 1990s scenario?

Rationale:

Sardine stock size and catch increased between the 1980s and 1990s. It is possible that larger catches of sardine are sustainable.

i) Pressed perturbation

Simulation: Fishing mortality of sardine is increased from year ten to year 50.

Results:

Even a 10% increment in fishing mortality of sardine in the purse seine fishery reduces mean biomass and catches of sardine in the 1990s scenario by 10% (Fig. 10.3). All groups reach new stable equilibria within ten years in the simulation, and total system biomass is not reduced.

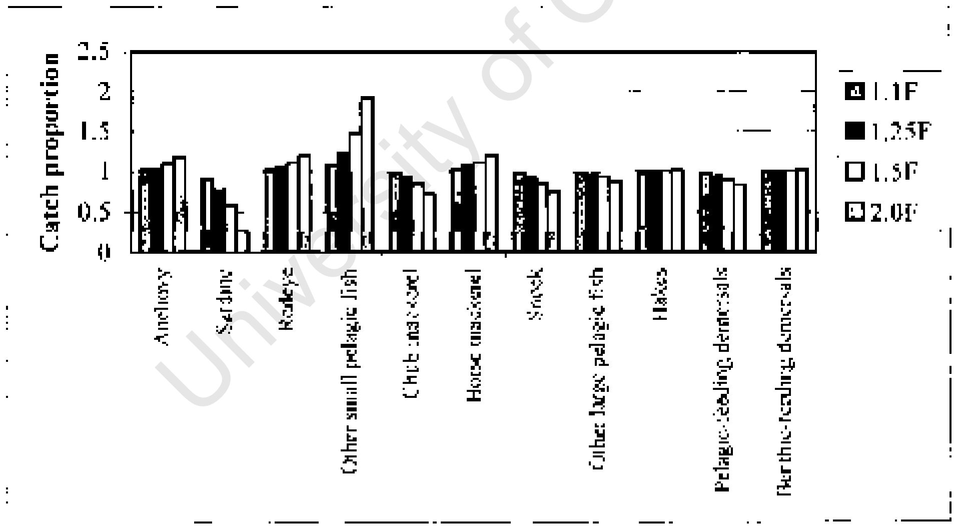


Fig. 10.3 Catches at the end of the fifty-year simulation period when the fishing mortality rate of sardine is increased by four different factors from year 10 onwards, expressed as proportions of means estimated in the southern Benguela ecosystem for the 1990s.

A fourfold increase in sardine fishing mortality (not shown) causes the sardine stock to crash, whereas a twofold increase reduces the sardine stock to less than a third of its original size by year 40, after which it stabilizes. A stable biomass at 60% of the original is reached by year 40 when sardine fishing mortality is increased by a factor of 1.5. Only in simulations that increase sardine fishing mortality by a factor of less than 1.25 is the total overall catch not reduced.

Future considerations:

If fishing pressure on sardine were to be increased, contrary to what one might expect, it is likely that catches of sardine, as well as total overall catches, would be reduced. However, should a 10% increase in catches of anchovy, redeye and horse mackerel economically outweigh a 40% reduction in sardine catches, the strategy of increasing fishing mortality of sardine by a factor of 1.5 could be considered favourably. In this case, it is likely that effects on biomass and catches of most groups would be small, and that groups would reach stable equilibria within 30 years of implementation of the new strategy. Careful weighting of management objectives would be required for such a decision to be made.

ii) Pulsed perturbation

Simulation: Sardine fishing mortality rate is quadrupled between year 10 and 15, whereafter it is returned to its original level.

Results: All groups have stabilized by year 35; stock sizes and catches are mostly at levels close to means in the 1990s (Fig. 10.4). At the end of the simulation period, only catches of other small pelagic fish (39% larger) and chub mackerel (17% smaller) differ by more than 5% from mean catches in the 1990s.

Future considerations: Should fishing on sardine be increased over a short 5-year period, it is possible that long-term detrimental effects on components of the southern Benguela ecosystem might be small. However, catches and biomasses in the 1990s scenario are by 3%. In the 1990s scenario, catches by the purse seine fishery increase by 17% and line fish catches increase by 13%.

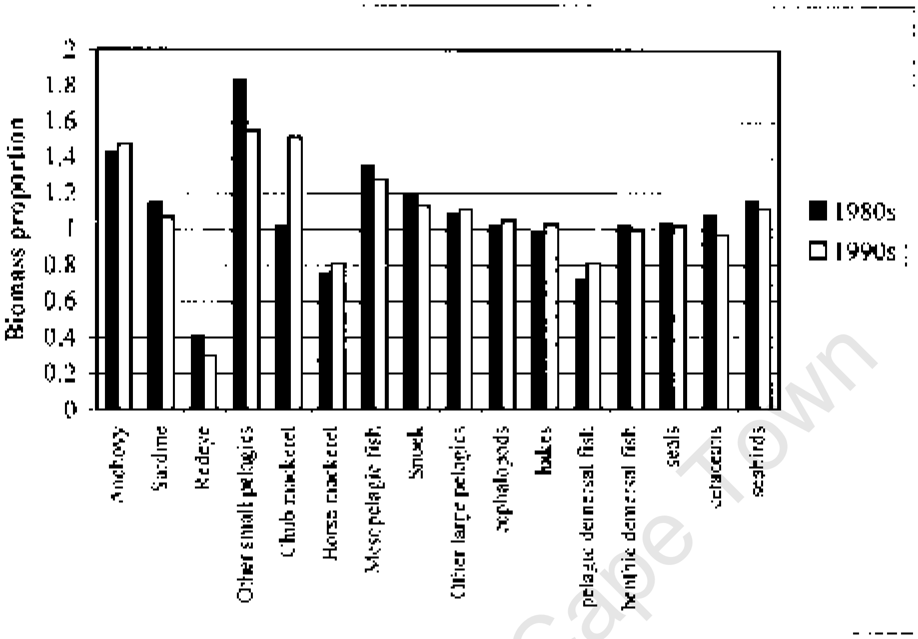


Fig 10.5 Biomasses at the end of the fifty-year simulation period when the fishing mortality rate of redeye was increased by a factor of four in each scenario from year 10 onwards, expressed as proportions of means estimated M the southern Benguela ecosystem for the 1980s and 1990s.

b) Additional simulation: Fishing mortality of redeye is increased eightfold from year ten to year 50.

Result: The redeye stock collapses, and by the end of the 50-year simulation period, most groups have not reached new stable equilibria.

c) Additional simulation: Fishing mortality of redeye is increased by 10% from year ten onwards.

Result: Total system biomass remains constant, and total catches are increased by 1%. However, redeye biomass is reduced to 98% of previous levels and larger catches are not sustained in the long-term (over 50 years).

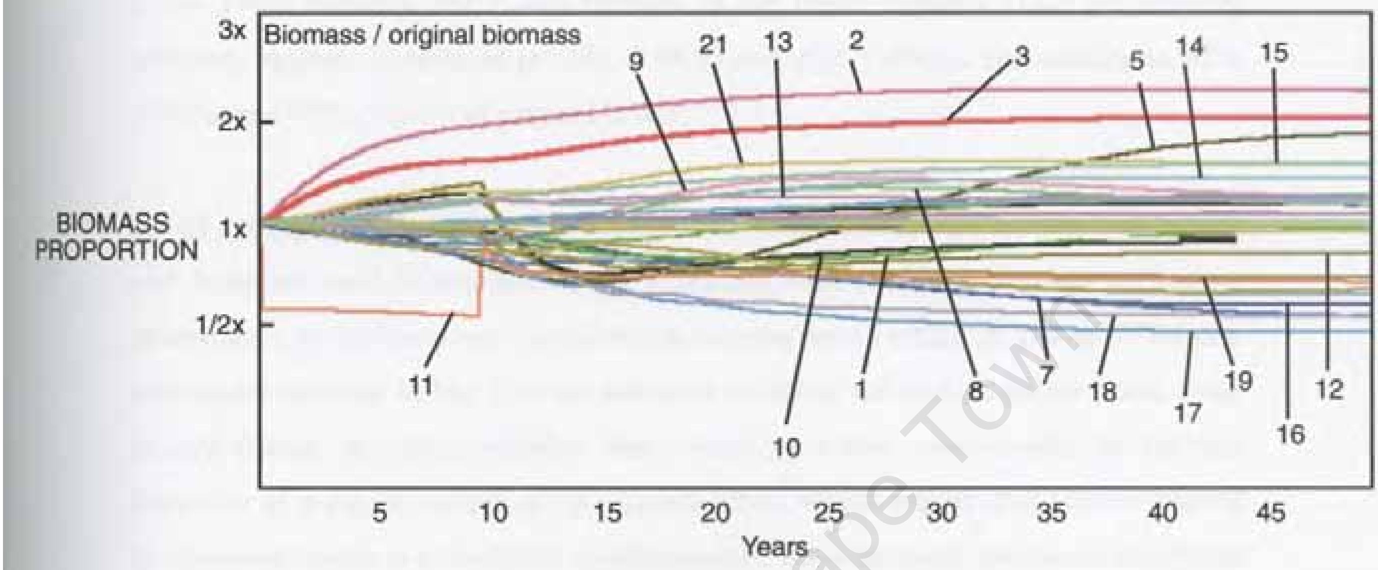
Future considerations: Although redeye catches are small in comparison to those of anchovy or hake, the ecotrophic efficiency of redeye exceeds 96% because redeye are an important prey of many other groups in the southern Benguela ecosystem (Chapter 4, Table 4.6). If fishing pressure on redeye were to be increased, one would expect a reduced average redeye biomass, which would result in reduced catches. In addition, catches of horse mackerel would be expected to decrease, but catches of other small pelagic fish (particularly anchovy) could potentially increase because of reduced competition for zooplankton food. However, this presupposes that food limitation controls pelagic fish biomass. Whether increased fishing on redeye is advantageous will depend on many factors, e.g. weighing up the socio-economic factors associated with a smaller horse mackerel fishery.

10.3.4 Could other fisheries expand if the purse seine fishery is closed?

Rationale: Abolishing the purse seine fishery targetting anchovy, sardine, redeye, chub mackerel, juvenile horse mackerel, other small pelagic fish and mesopelagic fish would increase the availability of these species to their predators, in particular large pelagic fish and demersal fish, which in turn could then support larger fisheries.

Simulation: The purse seine fishery is closed for the 50-year simulation period. Fishing mortality caused by the line fishery is increased fourfold from year 10-50. Fishing mortality in the demersal trawl fishery is increased twofold from year 10-50.

Results: In models of both decades, biomass and catches of all groups apart from chub mackerel reach new equilibrium levels by the end of the 50-year simulation period (Fig. 10.6). Chub mackerel continues to decline, reaching biomass levels 40% of original



1 = Redeye
2 = Anchovy
3 = Sardine
5= Other small pelagics

7 = Chub mackerel
8 = Juvenile horse mackerel
9 = Adult horse mackerel
10 = Snoek

11 = Total catch
12 = Other large pelagics
13 = Seals
14 = Apex chondrichthyans
15 = Seabirds

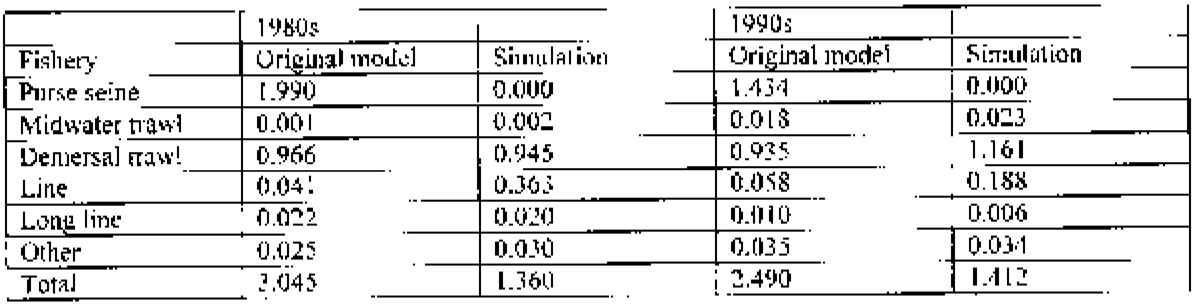
16 = Macrozooplankton
17 = Small *M.paradoxus*
18 = Large *M. paradoxus*
19 = Large *M.capensis*
21 = Cetaceans

Fig. 10.6 Biomass of some groups in the southern Benguela ecosystem simulated over fifty years, when the purse seine fishery is closed at the start of simulation, and the line and demersal trawl fisheries are increased fourfold and twofold respectively from year ten onwards. Biomasses are expressed as proportions of those in the 1990s.

biomass in the 1990s model and collapsing altogether in the 1980s model (Appendix D, Table D.1). When the purse seine fishery is closed and the line and demersal trawl fisheries expanded, total catches are greatly reduced to 45% (1980s) and 57% (1990s) (Table 10.2). Catches by the line fishery increase ninefold in the 1980s scenario and threefold in the 1990s scenario, and there is a 3% decrease in demersal trawl catches in the 1980s scenario and a 24% increase in the 1990s scenario. Hake are severely affected; biomass is reduced to 22% (1980s) and 43% (1990s), and catches to 47% (1980s) and 93% (1990s) of original levels.

<ins>Future considerations:</ins> If the purse seine fishery were to be closed and the line fishery and demersal trawl fishery were to be expanded, one would expect most ecosystem components to stablize at new equilibria in the long-term (within 50 years). Whether a substantial increase in line fish catches were to offset the closure of the purse seine fishery (snoek are more valuable than anchovy), either economically or through provision of a larger number of job opportunities, would require that heavier fishing by demersal trawls is considered simultaneously, because many species in the model may have been depressed by heavier fishing rather than limited by food. It is likely that increasing fishing pressure by demersal trawls would severely reduce the hake biomass and catches. Chub mackerel would need conservative management, although simulations suggest the stock might not be detrimentally affected in the 1990s scenario.

Table 10.2 Mean annual catches (t.km^{-2}.y^{-1}) taken in the major fisheries in the southern Benguela ecosystem during the 1980s and 1990s (original) when the purse seine fishery is closed from year 1-50, fishing mortality in the line fishery is increased fourfold and that by demersal trawls increases twofold from year 10-50, compared to modelled catches at the end of a 50-year simulation period (simulation).



	1980s		1990s	
Fishery	Original model	Simulation	Original model	Simulation
Purse seine	1.990	0.000	1.434	0.000
Midwater trawl	0.001	0.002	0.018	0.023
Demersal trawl	0.966	0.945	0.935	1.161
Line	0.041	0.363	0.058	0.188
Long line	0.022	0.020	0.010	0.006
Other	0.025	0.030	0.035	0.034
Total	3.045	1.360	2.490	1.412

10.3.5. Could a larger line fishery be supported?

Rationale:

Large pelagic fish such as snoek and tuna are commercially very valuable species. There would be economic benefits if larger catches of these groups were sustainable.

Simulation: Fishing pressure on snoek and other large pelagic fish is increased by doubling the fishing mortality of the line fishery from year 10 to 50.

Results: If catches in the line fishery are doubled for the duration of the 50-year simulation period, all groups reach new stable equilibria by year 20. Under these conditions, the line fishery supports 41% and 37% larger catches in the 1980s and 1990s respectively. The yield of snoek is 8% (1980s) and 4% (1990s) and other large pelagic fish 8% (1980s) and 5% (1990s) larger than in the original models (Appendix D, Table D.2). Purse seine, demersal trawl and total catches increase by 4-6% in the 1980s. In the 1990s, purse seine catches remain the same, total catches increase by 1% and demersal trawl catches by 4%. Snoek biomass decreases to 82% (1980s) and 75% (1990s) of original biomasses and other large pelagic fish decline to 55% (1980s and 1990s) of their original level.

Future considerations:

If fishing pressure on large pelagic fish were to be increased, one would expect biomasses and catches of most groups to reach stable equilibria after 20 years, that these biomasses would be close to original biomass levels for most groups apart from snoek and other large pelagic fish, and that catches would be larger. However, given the recent signs by the year 2000 that many large pelagic fish are over-exploited in the southern Benguela ecosystem (Griffiths 2000), this strategy would require extensive further testing. Further, because some large pelagic fish such as tuna are migratory and spend only part of their time within the boundaries of the southern Benguela ecosystem, implications of increased fishing pressure could be far-reaching and possibly different from those suggested in model simulations here, depending on fishing of these species in oceanic waters outside the area modelled.

10.3.6 Is there room for expansion of the demersal trawl fishery?

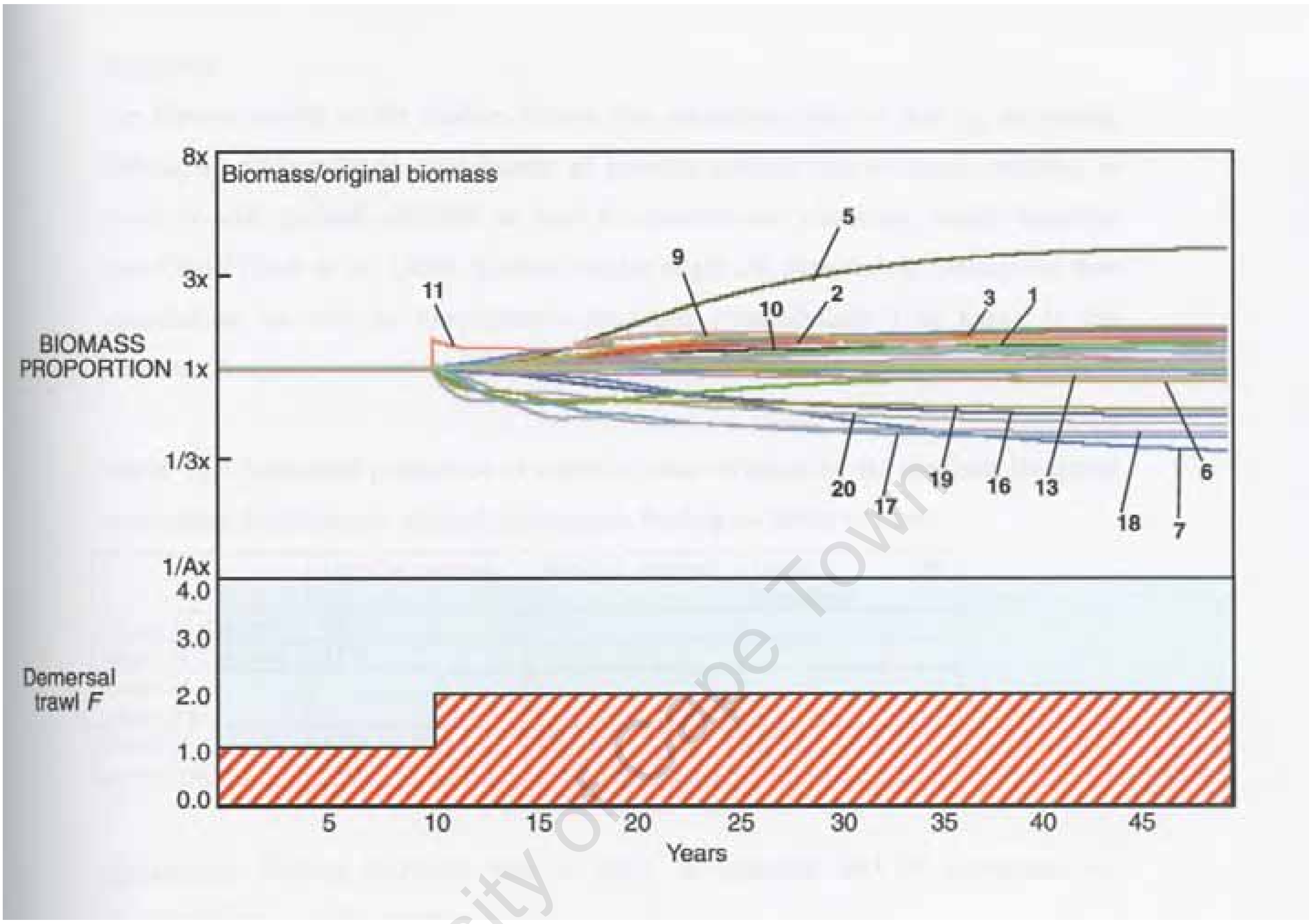
Rationale:

Demersal fish are a highly marketable and desirable catch. In particular, hake, sole and monkfish are commercially valuable. Therefore it would be beneficial to the fishing industry if larger catches of demersal fish could be supported.

Simulation: Fishing mortality in demersal trawls is doubled from year 10 onwards.

Results: After 25 years, all groups except chub mackerel and other small pelagic fish reach new stable equilibria (Fig. 10.7). At the end of the simulation period, chub mackerel abundance is still decreasing in simulations of both decades, although far more rapidly in the 1980s simulation. Hake biomass is severely reduced to 40% and 52% of the means estimated for the 1980s and 1990s respectively (Fig. 10.7; Appendix D, Table D.3). Other small pelagic fish biomass is increasing rapidly in the 1980s simulation. Catches by demersal trawls stabilize at 26% more than the 1980s mean and 36% more than the 1990s mean, and catches by purse seines increase by 40% (both models). Hake catches are reduced to 81% of the 1980s mean, the increase in demersal trawl catches being of other demersal fish. By comparison, in the 1990s, hake catches increase by 9% despite a halving of the hake biomass. Although longline catches only decline by 10% in the 1980s simulation, in the simulation of the 1990s, catches using long lines are reduced to 66% of their previous level. There is an increase of 35-36% in total catches in simulations of both decades (Appendix D, Table D.3).

Future considerations: If the demersal trawl fishery were to be expanded, one would expect a large decline of hake stocks. Small pelagic fish including commercially important anchovy and sardine are preyed upon by pelagic-feeding demersal fish including hakes. They could benefit from heavier fishing pressure on demersal fish and it is possible that in turn, they could support larger fisheries. However, advantages of these larger catches would need to be considered in the light of the likely reduction of hake catches.



1 = Redeye
2 = Anchovy
3 = Sardine
5= Other small pelagics

6 = Pelagic-feeding demersals
7 = Chub mackerel
9 = Adult horse mackerel
10 = Snoek

11 = Total catch
13 = Seals
15 = Seabirds
16 = Macrozooplankton

17 = Small *M.paradoxus*
18 = Large *M. paradoxus*
19 = Large *M.capensis*
20 = Small *M.capensis*

Fig. 10.7 Biomass of some groups in the southern Benguela ecosystem simulated over fifty years, when fishing mortality rate by the demersal trawl fishery is increased twofold from year ten onwards. Biomasses are expressed as proportions of those in the 1990s.

10.3.7 Could heavier fishing on large hakes reduce "cannibalism"?

<u>Rationale:</u>

An *Ecosim* model of the Eastern Bering Sea ecosystem showed that by increasing fishing on adult pollock, cannibalism of juvenile pollock was reduced, resulting in more juvenile pollock available as food for seabirds and mammals, which therefore benefited (Trites *et al.* 1999). Similar results might be expected in the case of true cannibalism as well as inter-generic predation ("cannibalism") of hakes in the southern Benguela ecosystem (Table 10.3).

Table 10.3 Estimated proportion of hakes in diets of hakes in the southern Benguela ecosystem. Predators are aligned in columns, feeding on hakes in rows.

	Large *M. capensis*	Small *M. capensis*	Large *M. paradoxus*
Large *M. capensis*	4%		
Small *M. capensis*	11%		
Large *M. paradoxus*			
Small *M. paradoxus*	15%	2%	15%

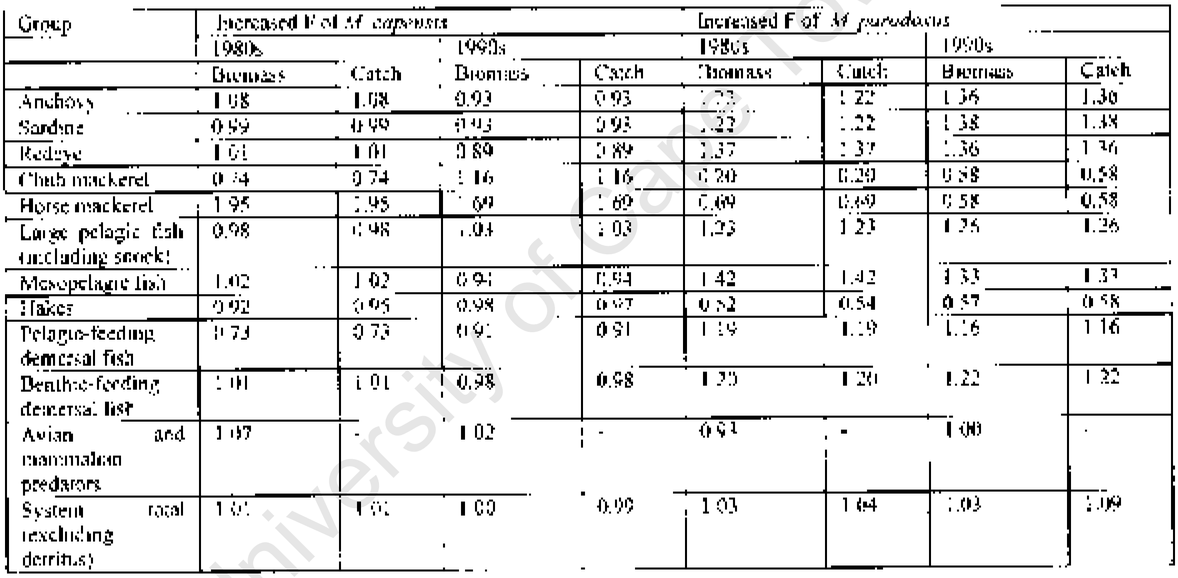
<u>Simulation:</u> Fishing mortality rates of large *M capensis* and *M paradoxus* are doubled from year 10 onwards.

<u>Results:</u>

Simulations show larger ecosystem changes when fishing mortality of *M paradoxus* is doubled than occur when there is a doubling of *M capensis* fishing mortality. This is because fishing mortality estimated for large *M capensis* is smaller ($0.28\ y^{-1}$ in 1980s, $0.23\ 37^{-1}$ in 1990s) than that for large *M paradoxus* ($0.39\ 3T^{-1}$ in 1980s, $0.33\ 3/^{1}$ in 1990s).

A doubling of the fishing mortality of *M capensis* does not have large effects on most components of the southern Benguela ecosystem over fifty years (Table 10.4). In simulations of the 1980s, most groups reach new equilibria during the simulation period, the exceptions being chub mackerel, which are still declining, and other small pelagic fish still on the increase. All groups reach new equilibria by year 50 in the 1990s model scenario. Large *M capensis* have large net negative mixed trophic impacts on horse mackerel (Chapter 5, Fig. 5.7), the stock size of which increases by 95% (1980s) and 69% (1990s) in this scenario. Juvenile *M capensis* do not increase as would be expected if cannibalism were viewed in isolation. Instead, biomass of juvenile *M capensis* decreases by 22% (1980s) and 10% (1990s), probably as a result of increased competition for zooplankton with horse mackerel and *M paradoxus*. In the 1980s, abundance of small *M paradoxus* is reduced by 2% whereas large *M paradoxus* biomass increases by 15%. Biomass of juvenile and large *M paradoxus* increase by 5% and 10% respectively in the 1990s.

Table 10.4 Biomasses and catches in year 50 when fishing mortality rates of large hakes are increased twofold from year 10-50, expressed as a proportion of original levels in models of the 1980s and 1990s.



Group	Increased F of *M capensis*				Increased F of *M paradoxus*			
	1980s		1990s		1980s		1990s	
	Biomass	Catch	Biomass	Catch	Biomass	Catch	Biomass	Catch
Anchovy	1.08	1.08	0.93	0.93	1.22	1.22	1.36	1.30
Sardine	0.99	0.99	0.93	0.93	1.22	1.22	1.38	1.38
Redeye	1.01	1.01	0.89	0.89	1.37	1.37	1.36	1.36
Chub mackerel	0.74	0.74	1.16	1.16	0.20	0.20	0.58	0.58
Horse mackerel	1.95	1.95	1.69	1.69	0.69	0.69	0.58	0.58
Large pelagic fish (including snoek)	0.98	0.98	1.04	1.03	1.23	1.23	1.26	1.26
Mesopelagic fish	1.02	1.02	0.94	0.94	1.42	1.42	1.33	1.33
Hakes	0.92	0.95	0.98	0.97	0.52	0.54	0.57	0.58
Pelagic-feeding demersal fish	0.73	0.73	0.91	0.91	1.19	1.19	1.16	1.16
Benthic-feeding demersal fish	1.01	1.01	0.98	0.98	1.20	1.20	1.22	1.22
Avian and mammalian predators	1.07	-	1.02	-	0.93	-	1.00	-
System total (excluding detritus)	1.01	1.01	1.00	0.99	1.03	1.04	1.03	1.09

In contrast, a doubling of fishing mortality of large *M paradoxus* has large effects on many groups (Table 10.4). At the end of simulation, biomass and catches of anchovy, sardine and redeye are 22-37% larger, biomass of other small pelagic fish is still increasing to more than triple the original level in the 1980s and to more than double in the 1990s, biomass and catches of snoek, other large pelagic fish, benthic-feeding demersal fish and seabirds increase by 12-20% in the 1980s and by 20-25% in the 1990s. Chub mackerel abundance declines by 80% and that of horse mackerel by 31% in the 1980s model. In simulations of the 1990s, biomasses of both chub mackerel and horse mackerel are reduced to 58%. Stock sizes of all four hake groups decrease; juvenile and adult *M paradoxus* stabilize at 37% (1990s: 45%) and 32% (1990s:

41%) of the original 1980s levels, juvenile *M capensis* is reduced by 30-31% and large *M capensis* by 13-14% in both decades. Heavier fishing on large *M paradoxus* allows their prey (small pelagic fish groups) to increase. These groups in turn compete with all hakes for zooplankton food, a likely explanation for the reduced abundance of *M capensis.* All groups reach new equilibra by year 50, with the exception of chub mackerel (both decades) and horse mackerel (1990s), which continue to decline slowly, and other small pelagic fish (1980s) which are slowly increasing.

Future considerations:

Simulations in which fishing mortality of large *M capensis* and *M paradoxus* in the southern Benguela ecosystem are increased contrast with those of the Bering Sea model. There are complex feedback mechanisms in the southern Benguela food web, so that a simple reduction in large hake stock sizes would not be expected to enhance abundance of small hakes by reducing "cannibalism".

10.3.8 Could heavier fishing on adult horse mackerel enhance stocks and catches of other small pelagics?

Rationale: Adult horse mackerel have negative mixed trophic impacts on anchovy, sardine and redeye (Chapter 5, Fig. 5.7). Therefore, heavier fishing on adult horse mackerel could be expected to enhance sizes of anchovy, sardine and redeye stocks and catches.

Simulation: Fishing mortality of adult horse mackerel is increased from year 10 — 50.

Results:

Unexpectedly, a fourfold increase in F of adult horse mackerel from year 10-50 in the 1980s model causes a 19% reduction in anchovy biomass and catches. As hypothesized, sardine and redeye biomasses increase by 12% and 34% respectively. However, in the 1990s model, anchovy, sardine and redeye stocks and biomasses are all reduced by 1-2% from original levels. At the end of the simulation period, biomasses of chub mackerel, pelagic-feeding demersal fish and macrozooplankton are still increasing and are respectively 147%, 72% and 22% larger than original 1980s levels, and 67%, 55% and 22% larger than original 1990s values (Appendix D, Table D.4). In simulations of the 1980s, anchovy stock size does not increase even when horse mackerel is overfished and crashes (i.e. when F of adult horse mackerel is increased eightfold from year 10-50). In 1990s simulations, an eightfold increase in adult horse mackerel F crashes the horse mackerel stock and allows anchovy, sardine and redeye biomasses to increase by 9%, 28% and 49% respectively.

Future considerations:

If fishing on the adult horse mackerel stock in the demersal trawl fishery were to be increased, one would not expect the stock sizes and catches of small pelagic fish to be enhanced. Therefore simple reduction of the competition between horse mackerel and small pelagic fish in the southern Benguela ecosystem by reduction of the horse mackerel stock size would not necessarily translate into larger stocks and catches of small pelagic fish.

10.3.9 Discrepancies between simulations in the medium- and long-term

In most cases, biomass trends of fish groups from year 0-20 are the same as those from year 20-50 (Appendix D, Tables D.5-D.12). However, in many cases, absolute biomasses in year 50 are larger (for groups becoming more abundant) or smaller (for groups undergoing a reduction) than in year 20 (see pale grey shading in Tables D.5-D.12). This suggests that considering the long-term effects (50 years) of altered fishing strategies provides useful information on the potential effects of altered fishing strategies on both decadal and long-term scales. Chub mackerel, pelagic-feeding demersal fish and other small pelagic fish are often still increasing or declining rapidly between year 20 and 50 (e.g. shaded cells in Tables D.9, D.11 and D.12).

Further, it appears that trends in the mid- and long-term correspond when species with high turnover rates are considered (e.g. anchovy, sardine) and/or when species directly affected by a modelled fishing scenario (e.g. hake) are considered. In contrast, longer-lived species (e.g. chub mackerel, snoek and horse mackerel), or species groups only indirectly affected by a simulated altered fishing scenario (e.g. pelagic-feeding demersals), can respond by showing fluctuations more than 10 years after the implementation of the new fishing strategy. In such cases, the direction of biomass change can still be reversed during the remaining 30 years of the simulation. For example, biomasses of groups such as chub mackerel, snoek, redeye and horse mackerel can increase/decrease between year 10 and 20-30, and then decline/increase again after this (see Fig. 10.4 and see dark grey shading in Tables D.6-D.12). These maxima or minima are short-lived. Therefore, when exploring impacts of fishing in the southern Benguela ecosystem independently from environmental fluctuations, it would be preferable to consider impacts in the long-term (full 50 year simulation period), by which time biomasses of most groups would have stabilized. However, it is possible that a strong environmental perturbation could amplify the consequent reverse biomass trends for some species 10 years after the implementation of an altered fishing strategy.

10.4 DISCUSSION AND CONCLUSIONS

Results of simulating the potential effects of altered fishing strategies will depend on the assumptions underlying the models used (see discussion on limitations of *Ecosim* Chapter 3, section 3.6). Here, fisheries and biological estimates have been averaged over ten years for the 1980s scenario, and over eight years for the 1990s scenario, and the ecosystem is considered to be in equilibrium. Therefore, in some cases, it is possible that modelled ecosystem effects of altered fishing may be dampened. Christensen (1995b) found that assuming equilibrium conditions could lead to overestimation of sustainable fishing rates.

Further, estimated diet compositions used as input for many modelled groups were derived from poor or scanty data, and in some cases depend on assumptions being made during balancing of the model (Chapter 4, Section 4.5). Although *Ecosim* accounts for changes in trophic interactions associated with changes in the diet composition of predators, switching of prey and satiation are not well represented (Walters *et al.* 1997). In particular, prey switching may be a confounding problem where predators of pelagic fish have fairly plastic diets and are able to switch prey species according to their abundance (Crawford *et al.* 1987).

In this chapter, "wasp-waist" flow control is assumed, with small pelagic fish controlling their prey (top-down) and predators (bottom-up). It is likely that results would be different if different "vulnerabilities" were selected to represent an alternative assumption regarding species interactions (as shown in Chapter 9).

Simulation of ecosystem effects of fishing is constrained by the aggregation of groups in the models used. For example, the demersal fish and other large pelagic fish boxes consist of many, non-interchangeable species. Subdivision of these two fish boxes into smaller categories in revised models would provide more detailed information on the possible effects of altered fishing on demersal and large pelagic fish.

This study considers ecosystem effects of fishing from a trophic perspective. Other considerations such as environmental effects are not incorporated into these models. Environmental perturbations may well affect how the ecosystem components respond to altered fishing scenarios. Therefore, although the simulations considered here are useful, it is important that adequate cognizance is taken of the underlying model assumptions and limitations when considering the possible impacts of altered fishing strategies suggested by these models.

Perturbations in biomass levels and catches are larger in simulations of altered fishing using the 1980s model than in simulations of the 1990s. This is because catches and fishing mortality rates are larger in the first decade, and because the ecosystem is more tightly constrained in terms of small pelagic predators and zooplankton (Chapter Four, section 4.6.2 and Chapter 6). In many cases, simulations of altered fishing strategies cause changes in abundance and catches that contrast with those hypothesized. This is because, as Christensen and Walters (2000) caution, interactions that are important in steady-state models (e.g. those highlighted by mixed trophic impact analyses) do not necessarily remain operative and important in dynamic simulations (also see Chapter 13, section 13.2). For example, simulated heavier fishing on horse mackerel, which compete with anchovy, sardine and redeye for zooplankton, does not increase the abundance and catches of all these groups.

Similarly, simulated heavier fishing on large hakes, feeding on small hakes, does not benefit the small hake groups because small pelagic fish are favoured by reduced predation by large hakes, resulting in more intense competition for zooplankton food between hakes and small pelagic fish.

Simulations in this study suggest that anchovy catches were optimal during the 1980s, and that larger sardine catches are unlikely to be sustainable in the 1990s scenario. This results from careful and conservative management of the South African pelagic fishery during the 1980s and 1990s (Cochrane *et al.* 1991b, Butterworth *et al.* 1992, De Oliveira *et al.* 1998a). By contrast, the line of thinking in managing the Namibian pelagic fishery in the 1970s differed; the fisheries targeted heavily on anchovy, with the view that reducing anchovy would benefit its competitor, viz. sardine (Butterworth 1983). The attempt to enhance sardine abundance failed, and both anchovy and sardine in the northern Benguela sub-system underwent major declines in the late 1970s.

The alternative fishing strategies considered in this study would have important implications for fisheries managers; increasing catches on one group or expanding one fisheries often requires that there is a corresponding reduction in catches of other groups or fisheries. Therefore, although the ecosystem may appear to stabilize (often at very different biomass equilibria from original levels), socio-economic factors need to be carefully considered and management objectives carefully defined before a new strategy can be considered as the preferred option. At first glance, heavier fishing of redeye could be favourably viewed as it causes increases in stock sizes and catches of competitors such as anchovy and sardine. However, if such a strategy were to be adopted, horse mackerel catches would be expected to decline. Further, because redeye are heavily utilised in the ecosystem as a food source for many predators, this fishing strategy could have severe effects on other groups in the ecosystem, particularly in the long-term. Similarly, closing the purse seine fishery may allow a substantially larger line fishery to be sustained. However, there would be a trade-off in adopting this strategy because there is likely to be a severe decline in hake stocks, currently supporting a valuable fishery.

CHAPTER ELEVEN

THE FUNCTIONAL ROLE OF SMALL PELAGIC FISH IN THE SOUTHERN BENGUELA ECOSYSTEM

ABSTRACT

Using models of the southern Benguela ecosystem, indices quantifying interactions between species and functional groups are developed to explore the definition of species interaction concepts in an upwelling system and to provide useful measures for the comparison of marine ecosystem structure and function. By definition, small pelagic fish are pivotal in a wasp-waist upwelling system. The index of interaction strength quantifies the effect that a change in biomass of one group has on abundance of other groups. Anchovy is the strongest interactor in the 1980s and sardine in the 1990s. The functional impact index quantifies the impacts of species on their own and other functional groups. Anchovy has large functional impacts on the small pelagic functional group, and redeye has large impacts on other zooplanktivorous fish. The trophic similarity index quantifies the trophic similarity between a species that is removed from an ecosystem and other species in that ecosystem. The strong similarities in trophic functioning of the southern Benguela ecosystem in the anchovy-dominated system of the 1980s, and the 1990s when there was a shift towards greater sardine abundance, are explained by the trophic similarity between anchovy and sardine. Anchovy and redeye have large trophic similarity indices, each compensating by increasing their abundance when the abundance of the other is reduced. Both species are able to compensate for reduced sardine biomass, but sardine, at small biomass levels in the models, is unable to compensate for a reduction in redeye abundance. Differences between the three indices and mixed trophic impact assessment are compared.

11.1 INTRODUCTION

Using a variety of examples from terrestrial and aquatic ecosystems, Collins and Benning (1996) illustrated the spatial and temporal variability in communities, concluding that ecosystem structure and function are strongly influenced by certain species in communities. A number of concepts have been used to describe these types of interactions. There has been slow progress beyond descriptive comparisons of these concepts across ecosystems, limiting the quantification of these terms to a narrow application specific to particular periods, environmental conditions and systems.

A characteristic of upwelling systems is the large abundance of small pelagic fish, occupying intermediate trophic levels and dominated by one or a few species (Cury *et al.* 2000). These fish play a pivotal role in upwelling ecosystems by exerting bottom-up control on their predators and top-down control on their prey, and for this reason have been termed "wasp-waist" populations (Cury *et al.* 2000, Chapter 9). Using models of trophic flows in the southern Benguela ecosystem, and focussing on the importance of small pelagic fish, the definition of species interaction concepts is explored. By simulating changes in biomasses within the small pelagic fish groups in the southern Benguela ecosystem, this study examines the application of interaction concepts in marine ecosystems and how the terms can be quantified to serve as useful measures for the comparison of marine ecosystems based on their structure and function (thereby addressing key question 1d).

11.1.1 Keystone species and quantifying interaction strength

Although there are varied meanings of the term "keystone species" (Mills *et al.* 1993), the most widely used definition is of a species "whose impact on its community or ecosystem is large, and disproportionately large relative to its abundance" (Power and Mills 1995, Power *et al.* 1996). Keystone species affect processes at the community or ecosystem level to a greater extent than would be expected based upon their relative abundance alone (Bond 1993). Tanner and Hughes (1994) used projection matrix models to look at patterns of succession in communities subjected to a major disturbance. They showed that some species that were rare at equilibrium had important roles to play in community dynamics.

One of the first examples of the keystone role of a species was presented by Paine (1966), who explored the effects of removal of predatory starfish from a rocky intertidal community, showing that a top predator can have major effects on a system. The keystone species concept applies to populations and not to whole species (Martinez 1996). This was illustrated by Menge *et al.* (1994), who showed that the seastar *Pisaster ochraceus* is not a keystone predator at all sites examined in Oregon, USA. Rather, they found that keystone status depends on environmental conditions such as wave action. The authors define a keystone predator as "only one of several predators in a community that alone determines most patterns of prey community structure, including distribution, abundance, composition, size and diversity". Navarrete and Menge (1996) manipulated intertidal communities (seastar and whelk populations) experimentally, showing that in keystone-dominated systems, species other than keystone species have minor or no effects on others in the community, and can be considered redundant.

A keystone species also has been defined by ecologists as one whose removal causes the collapse of more than half the other species in the system. Mills *et al.* (1993) warn against use of this criterion for classification of keystone species. The authors go so far as to recommend that ecologists abandon attempts to classify species as keystones. They conclude that scientists should concentrate on studying the strength of interactions between species and how these can assist in the development of management plans and policy decisions. Interactions are strong between keystone species and others in an ecosystem, whereas redundant species interact weakly (Martinez 1996).

In their quest for an operational, unambiguous definition of keystone species, Power *et al.* (1996) proposed a new measure called community importance (CI) to assess "the strength of the effect of a species on a community or ecosystem trait". This they defined as:

$$CI = \frac{d(trait)}{dp} \times \frac{1}{trait}$$

... Equation 11.1

where "p" is the proportional abundance of a group undergoing a change in biomass, and "trait" is a community or ecosystem trait such as abundance, productivity, species richness etc. of one or more functional groups or species.

The community importance index enables interactions between species to be assessed as a continuum. This has an advantage over the keystone species concept which requires that a species is either classified as a keystone or not, and ignores the degree of interaction strength between species. In marine ecosystems, trophic interactions are complex and linkages may be more numerous than in many terrestrial ecosystems where opportunistic feeding is probably less prevalent. The term keystone has been and still remains a flexible concept that needs to be quantified in an objective and repeatable fashion using indices that are able to characterize strengths of species interactions (Power *et al.* 1996).

The present study considers two indices that are meaningful for species classifications in marine ecosystems: the index of interaction strength (IS) quantifies the effect that a change in biomass of one group has on abundance of other groups in a system; the functional impact index (FI), based on the index of Power *et al.* (1996), quantifies the impacts of species on their own and other functional groups in the system. Limitations of these indices are examined in an attempt to clarify these concepts and their use in marine ecosystems. A third index is proposed below in section 11.6 on trophic similarity.

11.1.2 Ecosystem stability and the progression from redundancy to the trophic similarity concept

Lawton and Brown (1993) considered two extreme hypotheses about species interactions: the rivet hypothesis and the redundant species hypothesis. The rivet hypothesis (Ehrlich and Ehrlich 1981, Ehrlich 1993) assumes that as more species are eliminated from a system, there is a threshold at which further elimination of species will disrupt, destroy or negatively affect major ecosystem function (Collins and Benning 1996). The redundant species hypothesis considers species richness to be less important than maintenance of biomass of the various trophic levels (Lawton and Brown 1993). A most likely case of functional redundancy is when, after removal of a species, biomass is restored by density compensation among the remaining species in the same guild or functional group (Lawton and Brown 1993). If density compensation does not take place, then ecosystem function(s) (e.g. primary production) may be reduced when a species is deleted, and the species is not redundant. The reverse holds true for predator removal; if prey populations increase after the predator is removed, the predator is not redundant, whereas if prey populations decrease or remain stable, the predator is likely to be redundant (Lawton and Brown 1993).

Pimm (1991) defined ecosystem stability as a measure of whether or not a system returns to equilibrium after a disturbance. However, application of terrestrial perspectives to marine systems is often inappropriate because of the large differences in space and time scales upon which terrestrial and marine ecosystems respond to change (Steele 1991). Furthermore, in fisheries, equilibria are not easily defined; it is necessary to approach the problem in a different way, comparing the system to periods prior to altered fishing strategies, for example. Pimm (1979) introduced the term "species deletion stability" as the probability that after "experimental" deletion of a target species, the system retains all other species at local equilibria (Pimm 1979 and 1980). This implies that there is little species redundancy i.e. it is more consistent with the rivet hypothesis. Observations show that many real systems are not stable with regard to species deletion. Examples include the northern Benguela sub-system after the collapse of sardine in the 1970s (Crawford *et al.* 1989) and the Peruvian system before and after the collapse of anchovy (Jarre *et al.* 1991).

MacArthur (1955) proposed that stability is greater in communities with large numbers of species, because there are many links that buffer predators from fluctuations in prey resources. Conversely, it has been argued that increasing species diversity could reduce stability of populations, because negative feedback loops (leading to population explosions or extinctions) are more likely to occur when there are more interactions between species (May 1973). Lawton and Brown (1993) found little evidence (in studies, experiments or observations) to suggest that species richness buffers systems against fluctuations. On the biosphere scale, Lawton and Brown (1993) found unconvincing evidence to support the rivet hypothesis. On the ecosystem scale, they found that species richness does not determine major processes taking place in ecosystems. They conclude that food webs with different numbers of species may function in different ways, and propose that species redundancy may well occur. Walker (1992) advocates that ecological aspects critical to maintaining ecosystem resilience should be studied to prevent a decline in biodiversity. Here, resilience refers to the capacity of an ecosystem to maintain its rates of functions (such as primary production and energy exchange) when subjected to change (Walker 1992). As a start, conservation initiatives should focus on functional groups with little or no redundancy, as species in these groups will be most important to ecosystem function (Walker 1992). It has been suggested that the local species diversity of fauna is related to predator abundance and to the efficiency with which predators prevent a single predatory species from monopolising a limited resource (Paine 1966). The importance of species diversity is a research topic in its own right, and is not examined further in this study. Instead, an attempt is made to quantify and explore the usefulness of indices describing some of the ecological concepts mentioned.

Redundancy is a controversial topic (Collins and Benning 1996). "All species are decidedly not equal, and ... an understanding of redundancy will not be possible until we better understand how to define, identify and measure the impact of key species" (Lawton and Brown 1993, p. 267). The authors conclude that redundancy may be built into ecosystem processes and that, like the keystone function, species redundancy may depend on scale, process and site, although we do not yet fully understand the mechanisms involved. They propose that even keystone species in particular communities may be redundant in terms of ecosystem processes. Once a keystone predator species has been lost, previously redundant species can become important role players by partially compensating for reduced predation (Navarrete and Menge 1996). Schulze and Mooney (1993) propose that at times, some species may be similar in function, but that all species perform vital ecosystem functions, and that the relative importance of species depends on environmental conditions. This idea that all species contribute to ecosystem function is formulated in the uniqueness hypothesis of Martinez (1996), that a particular ecosystem function is eliminated when a species is eliminated. This is in contrast to the expendability of a species group, implicit in the term functional redundancy.

Therefore, the term redundancy may be a misnomer. Instead, ecologists favour the comparative measure of trophic similarity to that of redundancy (Jennings and Kaiser 1998, Collins and Benning 1996, Martinez 1996). Trophic similarity implies a continuum rather than a measure of "all or none" like redundancy, and is preferred when one considers that a species may be redundant in some characters but not necessarily in all. Trophic similarity in one character does not necessarily imply functional redundancy (i.e. that the species is expendable) because the species may play a crucial role in a different ecological process that is just as important (Collins and Benning 1996). To quantify trophic similarity, studies should incorporate measures of density, spatial pattern, physiological ecology and population dynamics, at spatial scales related to ecosystem function (Collins and Benning 1996).

11.1.3 Quantifying ecosystem effects of fishing in marine ecosystems

Developing ecosystem indices measuring properties related to production, diversity and variability has been recognized for its value in assessing the ecosystem effects of fishing (Murawski 2000). However, no single metric or group of metrics can be recommended without reservations (Rice 2000). The effects of fishing on ecosystems are most noticeable when an area is first fished. Once fished, the diversity, community structure and overall production of an ecosystem remain relatively stable for a wide range of fishing intensities, with pronounced effects only being observed once the level of fishing is so high that species have been lost (Jennings and Kaiser 1998). However, on time scales of decades and centuries, it is likely that local extirpation of species has consequences for ecosystem function; there may be significant differences in the roles played by previously functionally similar species (Jennings and Kaiser 1998).

In most cases, target fish species are not usually keystone species; changes in their abundance rarely have major or consistent impacts on their prey or competitors (Jennings and Kaiser 1998). Kitchell *et al.* (1999) made use of the *Ecosim* modelling approach (Walters *et al.* 1997) to explore whether keystone species existed among the apex predators (trophic level of 4 or higher) in the pelagic ecosystem of the central North Pacific. They achieved this by modelling a sudden ten times increase in fishing mortality of each apex predator over 30 years. They interpreted ecosystem change as a result of altered fishing mortality by classifying results into two categories: no substantial change (less than 50% increase or decrease) and substantial change (increase or decrease by more than 50%). They found that none of the apex predators considered clearly demonstrated keystone species characteristics, although adult yellowfin and adult skipjack tunas were found to play important roles in the food web (removal caused major perturbations). Fishers were the one clear keystone "species".

Removal of dominant species of small pelagic fish is likely to be a very different case. Pelagic fish are important prey for apex predators such as marine mammals, large pelagic fish and seabirds. Fishing on pelagic species can alter availability of small pelagics to their predators, and is likely to have more pronounced effects on predators such as marine mammals or birds, which are strongly dependent on abundances of prey species, than on other predatory fish, which have a more plastic diet (e.g. Crawford 1999, Cury *et al.* 2000).

How important are individual species to the functioning of the whole marine ecosystem under investigation? What effects would the removal of an exploited species have on others in the same ecosystem? To answer questions such as these, it is useful to define a set of indices quantifying the more useful of those ecological concepts discussed. Indices that quantify interactions and impacts along continuums and therefore allow comparisons between periods and systems, are more useful than "all or none" classifications such as the redundancy and keystone species concepts. It is important to recognize that ecosystem metrics derived from mass-balance models, such as those in this study, depend on the assumption that competition between species is more important than environmental forcing (Rice 2000). In this study, where the focus is on interactions between species, environmental forcing is not being explored.

Trophic models of the southern Benguela ecosystem are used to test the interaction strength and functional impact of species, and whether trophic similarity operates in the pelagic part of the ecosystem. The *"Ecopath with Ecosim"* approach (Christensen and Pauly 1992, Walters *et al.* 1997) is used to explore the ecosystem effects of removing small pelagic fish species by increasing fishing mortality. This chapter investigates whether trophically similar small pelagic fish species can assume the place of one that is removed from the southern Benguela ecosystem.

11.2 METHODS

Walker (1992) proposed a functional approach to analysing biodiversity as an alternative to a species-centred approach. He suggested four steps to achieve this:
1) separate species into guilds according to nontrivial functional attributes (i.e. those related to limiting or dominant ecosystem processes). Some degree of ecological redundancy exists in a guild for which this separation is not possible (Walker 1992),
2) assess the number of species in each guild,
3) examine interactions between species in a guild to assess whether density compensation occurs when one species is removed, i.e. to judge whether there is complete functional redundancy, and
4) assess the relative importance of functional groups, i.e. how a change in abundance of one functional group affects ecosystem processes such as predation, nutrient retention/uptake, biomass accumulation etc.

Models of trophic flows in the southern Benguela ecosystem are used to assess the functional role of species. For purposes of examining ecosystem indices, the earlier models of the southern Benguela ecosystem (Jarre-Teichmann *et al.* 1998, Shannon and Jarre-Teichmann 1999b) are used because they contain aggregated boxes for hakes and large pelagic fish, facilitating easy manipulation of these groups and giving results that are easily interpreted. How species interact in an ecosystem can influence the extent to which the other species respond to a perturbation. In Chapter 9, it was found that modelled responses of ecosystem components to disturbance are dampened when there is bottom-up control of predators by zooplankton (see also Shannon *et al.* 2000). Pimm (1980) deduced that donor-control (bottom-up control) does not operate in many real systems, and that stability does not always increase with increased complexity. By contrast, large effects propagate through an ecosystem when "wasp-waist" control is modelled, i.e. when there is bottom-up control of predators by small pelagic fish and top-down control of zooplankton by small pelagic fish (Curt' *et al.* 2000, Shannon *et al.* 2000, Chapter 9). Simulations based on "wasp-waist" control are used to test ecosystem indices. Using *Ecosim,* the effects of a collapse of small pelagic fish species are examined by increasing annual fishing mortality (F) on a species until the species is eliminated within ten years (F = $F_{critical}$). After the $F_{critical}$ is estimated (Table 11.1), the model is run for a further forty years with fishing at this level. In order to derive a comparative measure of possible keystone attributes, the same simulations are used to investigate behaviour of predatory hake and large pelagic fish predators.

Table 11.1 Annual fishing mortality (F) of selected groups and Fcritical causing the collapse of the group in question. "Factor" refers to the factor by which the original F in the steady-state southern Benguela model is increased to reach

	1980s			1990s		
Group tested	F (y^{-1})	Factor	$F_{critical}$ (y^{-1})	F (y^{-1})	Factor	$F_{critical}$ (y^{-1})
Anchovy	0.30	8	2.42	0.23	8	1.84
Sardine	0.32	4	1.28	0.16	8	1.28
Redeye	0.03	32	0.96	0.03	64	1.92
Hake	0.14	16	2.24	0.14	16	2.24
Large pelagic fish	0.22	16	3.52	0.22	16	4.48

11.3 SETTING THE SCENE

When sardine collapses, the net change in modelled system biomass is small, as is the change in the biomass of the small pelagic fish functional group, indicating that density compensation occurs with little overall effect on biomass of the model southern Benguela ecosystem in the 1980s and 1990s (Fig. 11.1). When an anchovy collapse is modelled, density compensation also occurs within the small pelagic fish functional group, but there is a larger overall change in total system biomass than in the case of a simulated sardine collapse. By contrast, elimination of redeye has large effects on the biomass of the small pelagic fish functional group. In the 1990s, when redeye biomass is large, the simulated effect is larger than in the 1980s. Similarly, the impact on the biomass of the system is also larger in simulations of the 1990s. Although simulated elimination of anchovy in the 1990s has less of an impact on the biomass of its functional group than in the 1980s, it has a larger impact on system biomass than the 1980s model in which anchovy are more abundant.

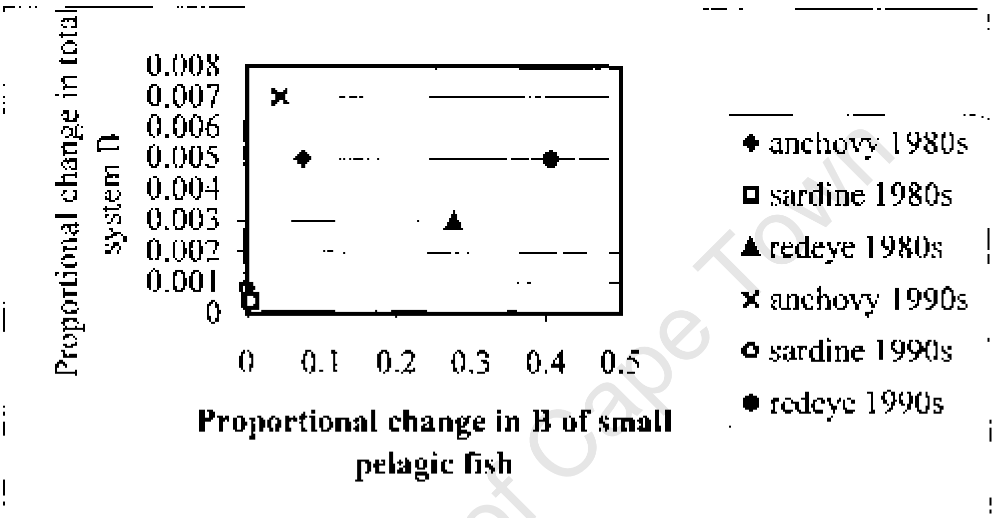


Fig. 11.1 The proportional change in total biomass (excluding detritus) of the southern Benguela ecosystem when stock collapses of each of anchovy, sardine and redeye are simulated, plotted against the proportional change in biomass of the small pelagic fish functional group (anchovy, sardine, redeye and other small pelagic fish).

A collapse in the sardine stock has very little impact on zooplankton, whereas the demise of redeye causes large changes in modelled zooplankton biomass (Fig. 11.2). In models of the southern Benguela ecosystem, predators of small pelagic fish are most affected by a collapse of redeye (Fig. 11.3). Assumptions made during construction of models upon which ecosystem indices are based should be considered when interpreting these indices. In this case, redeye biomass estimates are weak (Chapter 4). Redeye biomass at the upper limit of the estimated range was used in the construction of the models of the southern Benguela ecosystem to provide sufficient small pelagic fish to support predators in the modelled system.

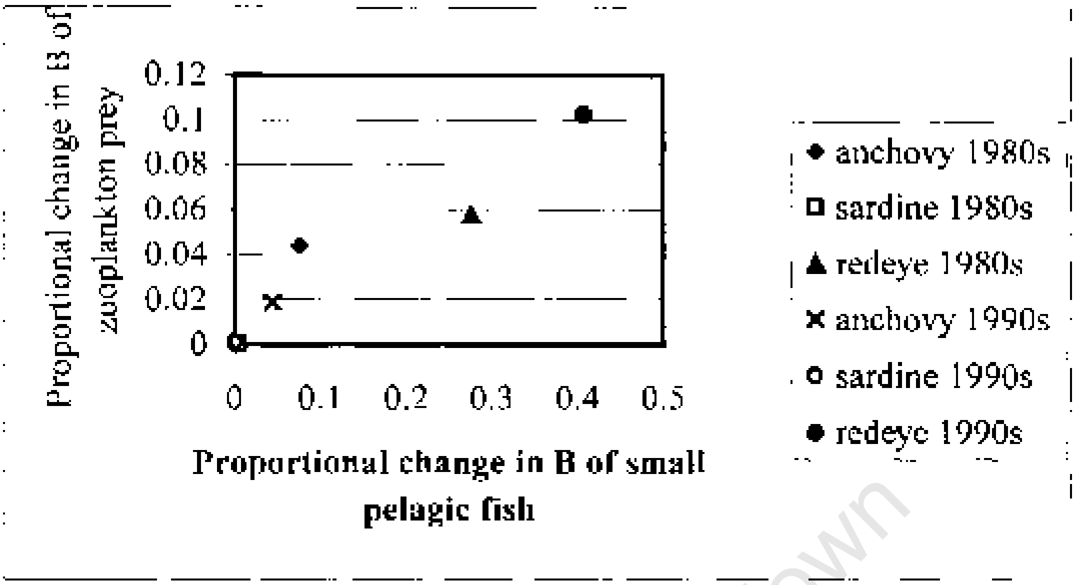


Fig. 11.2 The proportional change in biomass of meso- and macro-zooplankton (prey of small pelagic fish) in the southern Benguela ecosystem when stock collapses of each of anchovy, sardine and redeye are simulated, plotted against the proportional change in biomass of the small pelagic fish functional group (anchovy, sardine, redeye and other small pelagic fish).

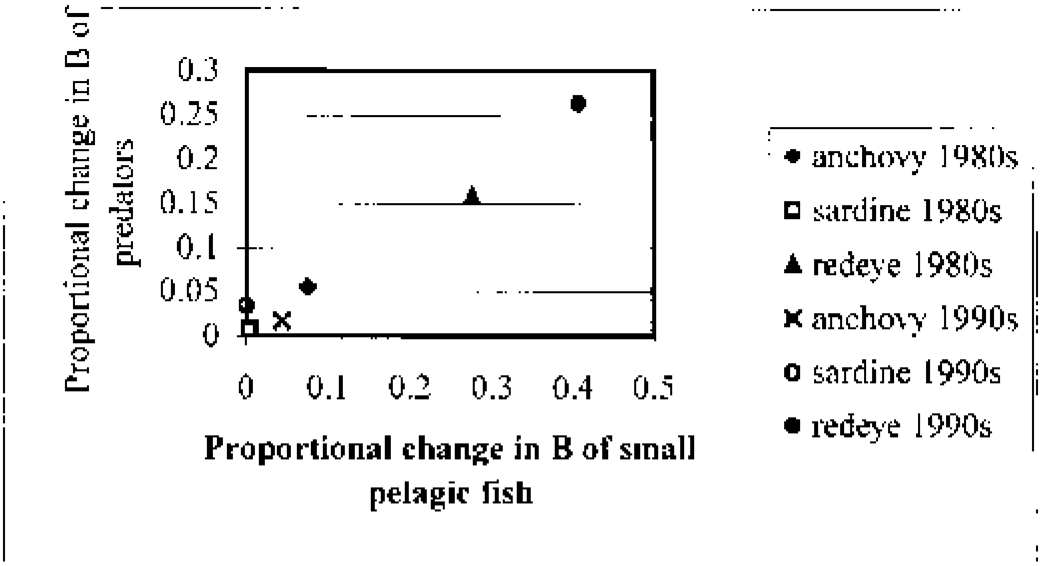


Fig. 11.3 The proportional change in biomass of three top predators (large pelagic fish, seabirds and seals) consuming small pelagic fish in the southern Benguela ecosystem when stock collapses of each of anchovy, sardine and redeye are simulated, plotted against the proportional change in biomass of the small pelagic fish functional group (anchovy, sardine, redeye and other small pelagic fish).

11.4 INDEX OF INTERACTION STRENGTH

In the present study, the original definitions of keystone species (Mills *et al.* 1993, Power *et al.* 1996) are rephrased to consider the strength of interactions. An index of interaction strength (IS) is developed here and it assumes that a change in biomass of a strong interactor causes large changes in the biomass of other groups. The relative change in the biomass of a species or functional group is expressed as a proportion of the sum of the relative changes of all groups in the system:

$$IS = 1 - \frac{\frac{\Delta B_i}{B_i}}{\sum_{i=1}^{n}\left|\frac{\Delta B_i}{B_i}\right|}$$

... Equation 11.2

where B is biomass in year 0, i is the group being tested for keystone attributes, j is a species or group in the ecosystem, AB is the change in biomass of a group (i.e. the difference between biomass at the end of the simulation in year 50 and that at the start in year 0) and n is the total number of groups in the model ecosystem. Values for the index lie between 1 and 0, with large values indicating that species (or group) i has a stronger impact on other groups than species with smaller values. IS is obtained from the model by changing biomass of one group at a time when the test group collapses through overfishing by year 10, and the system is simulated for a further 40 years.

11.4.1 Application of the index of interaction strength to the southern Benguela ecosystem

Hake is a strong interactor (i.e. hake has the largest IS index, Table 11.2) because a collapse in the hake stock causes large changes in the biomasses of ecosystem components in the models. The large effects of hake are related to its very large biomasses in both decades, and to the wide range of species on which hake feed. Of the three most abundant small pelagic fish species (anchovy, sardine and redeye), anchovy is the strongest interactor in simulations of the 1980s, whereas redeye has the largest interaction strength index in simulations of the 1990s. When a collapse of all three small pelagic fish stocks is simulated using the 1990s model, the interaction strength is comparable to that of a hake collapse. A collapse of large pelagic fish has a larger interaction strength index in the 1990s model, when fishing pressure is heavier than in the 1980s and when there are more cycles from the first trophic level to this group (Table 11.2).

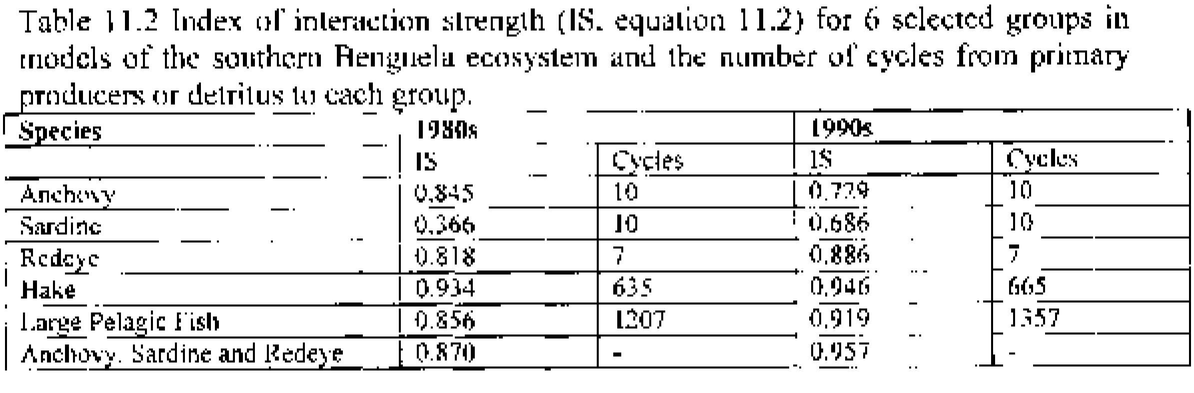


Table 11.2 Index of interaction strength (IS, equation 11.2) for 6 selected groups in models of the southern Benguela ecosystem and the number of cycles from primary producers or detritus to each group.

Species	**1980s**		**1990s**	
	IS	Cycles	IS	Cycles
Anchovy	0.845	10	0.729	10
Sardine	0.366	10	0.686	10
Redeye	0.818	7	0.886	7
Hake	0.934	635	0.946	665
Large Pelagic Fish	0.856	1207	0.919	1357
Anchovy, Sardine and Redeye	0.870	-	0.957	-

11.5 FUNCTIONAL IMPACT INDEX

Based on the "community importance" index of Power *et al.* (1996) discussed in section 11.1.1, the functional impacts of anchovy, sardine and redeye in the southern Benguela ecosystem during the 1980s are compared when fishing mortality of each of these groups is altered and the effects simulated using *Ecosim*. Three functional groups are considered:

i) *small pelagic fish* (anchovy, sardine, redeye and other small pelagic fish),

ii) *other zooplanktivorous fish* (chub mackerel, horse mackerel and mesopelagic fish) and

iii) *predators* of small pelagic fish (large pelagic fish, hake, birds, seals and cetaceans).

Fishing mortality (F) is modelled in increasing steps of factor two (2F, 4F, 8F, 16F, 32F), until each species is eliminated. In addition, simulations are considered in which fishing mortality of anchovy and sardine are three times the original fishing mortality rates (3F). These are required to give additional detail because the factors by which original Fs are increased to cause extinction of anchovy or sardine are smaller than the fishing factor required to eliminate redeye.

Three functional impact (F1) indices are compared; a value close to zero would indicate that the elimination of the target species has little impact on the combined biomass of the functional group in question.

1) $_{\text{Fipelagics}}$ is defined as the relative change in the biomass of small pelagic fish (anchovy, sardine, redeye and other small pelagic fish, excluding the species being tested) as a proportion of the relative biomass of the species being tested for its functional impacts. For example, if the fishing mortality of anchovy is being altered during simulations over 50 years,

$$FI_{pelagic} = \frac{[(B_{s,50} + B_{r,50} + B_{p,50}) - (B_{s,0} + B_{r,0} + B_{p,0})]}{(B_{s,0} + B_{r,0} + B_{p,0})} \times \frac{B_{T,0}}{|B_{s,50} - B_{s,0}|}$$

... Equation 11.3

where $B_{s,50}$ is the biomass of sardine *(s)* in year *50,13,0* is the biomass of redeye *(r)* in year 0, and so on. Similarly, p refers to other small pelagic fish and T to total of all groups (excluding detritus) within the system.

2)

zooplanktivorous fish (chub mackerel, horse mackerel and mesopelagic fish) as a proportion of the relative biomass of the species being tested. For example, when fishing on sardine is altered during simulation over 50 years:

$$FI_{zoo\ fish} = \frac{[(B_{cm,50} + B_{hm,50} + B_{m,50}) - (B_{cm,0} + B_{hm,0} + B_{m,0})]}{(B_{cm,0} + B_{hm,0} + B_{m,0})} \times \frac{B_{T,0}}{|B_{s,50} - B_{s,0}|}$$

... Equation 11.4

where $B_{cm,50}$ is the biomass of chub mackerel *(cm)* in year 50, $B_{hm,O}$ is the biomass of horse mackerel *(hm)* in year 0, and so on. Similarly, m refers to mesopelagic fish and T to total of all groups (excluding detritus) within the system.

3)

pelagic fish (large pelagic fish, hakes, seabirds, seals and cetaceans) as a proportion of the relative biomass of the species being tested for its functional impact. For example, when fishing on redeye is altered during simulations over 50 years:

$$FI_{predators} = \frac{[(B_{l,50} + B_{h,50} + B_{b,50} + B_{se,50} + B_{ce,50}) - (B_{l,0} + B_{h,0} + B_{b,0} + B_{se,0} + B_{ce,0})]}{(B_{l,0} + B_{h,0} + B_{b,0} + B_{se,0} + B_{ce,0})} \times \frac{B_{T,0}}{\left|B_{r,50} - B_{r,0}\right|}$$

... Equation 11.5

where $B_{1,50}$ is the biomass of large pelagic fish *(l)* in year 50, $B_{h,0}$ is the biomass of hake *(h)* in year 0, and so on. Similarly, *b* refers to marine birds, *se* to seals, *ce* to cetaceans and *T* to total of all groups (excluding detritus) within the system.

The functional impact indices used in the present study differ from the community importance index of Power *et al.* (1996) in the following respects:

i) changes in biomass are calculated as biomass at the end of simulation minus biomass at the start of simulation (Power *et al.* (1996) used biomass at start minus biomass at end)

ii) the second term is the inverse of the *absolute value* of the change in biomass of the group being tested, as a proportion of total system biomass at the start. (Power *et al.* (1996) did not use absolute values).

These differences make the functional impact index more straightforward to interpret: a negative index indicates that the group tested causes a reduction in the functional group considered, and vice versa.

11.5.1 Application of functional impact indices to the southern Benguela ecosystem

When fishing on one species is increased, the biomasses of the others within the same functional group increase, and vice versa. The modelled functional impact (FI) strengths of anchovy, sardine and redeye on small pelagic fish remain relatively constant for all modeled increased levels of fishing (Fig. 11.4). Reducing anchovy fishing mortality from 0.50F to 0.25F decreases the modelled impact of the species on others in its functional group, whereas the impacts of sardine and redeye are not substantially reduced at half or quarter of their original fishing mortalities. These results show that of the three pelagic fish, anchovy has the largest impacts on its own functional group (Table 11.3).

By comparison, redeye has the largest modelled impacts on other zooplanktivorous fish (Fig. 11.5). As in the previous instance, for all three species, maximum impacts are reached at modelled fishing mortalities less than those causing extinction of species. The impacts of sardine on zooplanktivorous fish are in the opposite direction to the impacts of anchovy and redeye. This is because other zooplanktivorous fish biomass in the model increases at reduced sardine fishing mortality, and when fishing on sardine increases, biomass of other zooplanktivorous fish decreases. Reduced fishing allows sardine abundance to increase, alleviating some of the predation pressure from other small pelagic fish species that were consumed in large quantities when sardine biomass was small, allowing other zooplanktivorous fish abundance to increase. When sardine fishing is increased, anchovy and redeye become more abundant, competing with other zooplanktivorous fish and causing a decrease in biomass of other zooplanktivorous fish. In contrast, when heavier fishing reduces anchovy and redeye abundances, competitive zooplanktivores become more abundant.

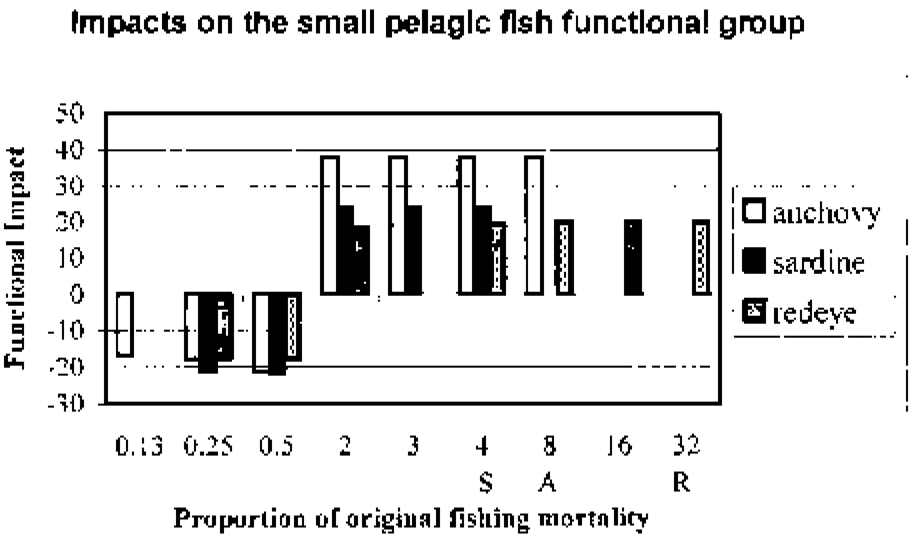


Fig. 11.4 The functional impact on small pelagic fish (FIpelagic) when altered annual fishing mortality rates of anchovy, sardine and redeye are simulated using the 1980s model of the southern Benguela ecosystem. S, A and R indicate Fcritical values for sardine, anchovy and redeye respectively.

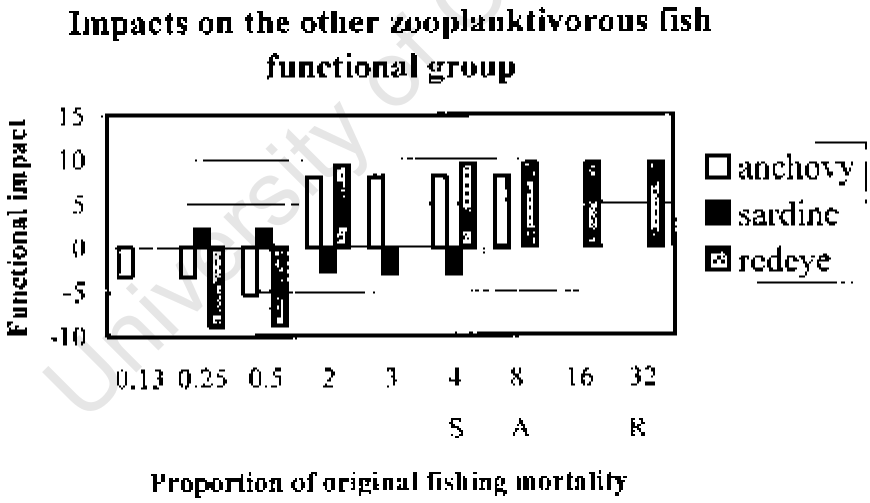


Fig. 11.5 The functional impact on zooplanktivorous fish (FIzoo fish) when altered annual fishing mortality rates of anchovy, sardine and redeye are simulated using the 1980s model of the southern Benguela ecosystem. S, A and R indicate Fcritical values for sardine, anchovy and redeye respectively.

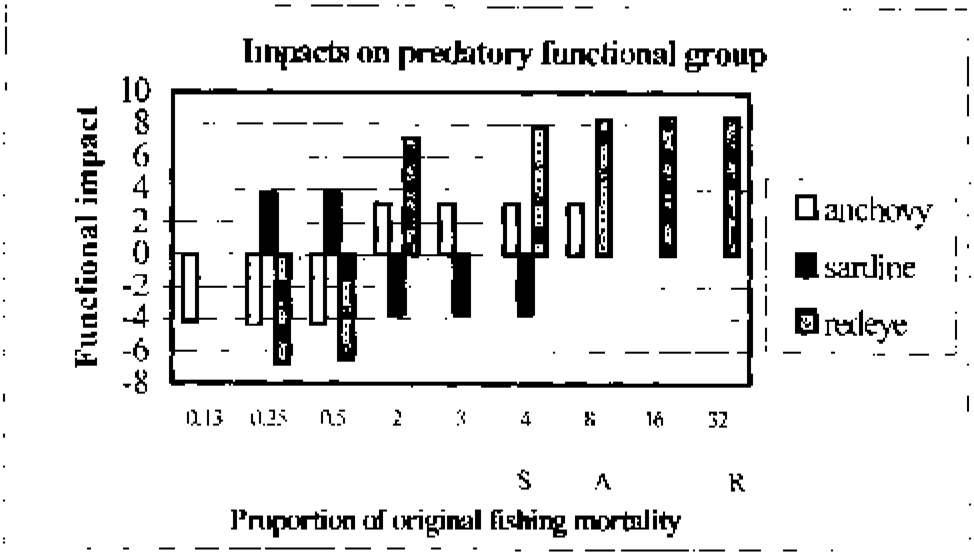


Fig. 11.6 The functional impact on predators of small pelagic fish ($FI_{predators}$) when altered annual fishing mortality rates of anchovy, sardine and redeye are simulated using the 1980s model of the southern Benguela ecosystem. S, A and R indicate

There are larger differences between the modelled impacts of anchovy, sardine and redeye within their own functional group than the other zooplanktivorous fish and predatory functional groups (Figs 11.4, 11.5 and 11.6. Note different vertical scales used in these three figures). Of the three pelagic species considered, redeye has the strongest impacts on other zooplanktivorous fish and predators of small pelagic fish. When modelled fishing pressure is increased, sardine has stronger impacts on predators than anchovy. Surprisingly, overall predator biomass increases when modelled fishing on anchovy and redeye increases (Fig. 11.6), as a result of increases in certain predators when other species of small pelagic fish become more abundant. For example, when heavy exploitation of anchovy is modelled, sardine, redeye, chub mackerel, horse mackerel and other small pelagic fish all become more abundant in response to reduced competition with anchovy for food, filling the niche previously occupied by anchovy, and in turn, supporting more hakes and cetaceans.

In the 1980s model, the demise of anchovy has stronger impacts (larger FI values) on all three functional groups than when the species are eliminated in simulations of the 1990s (Table 11.3). In the 1980s model, when biomasses of sardine and redeye are smaller, sardine and redeye have larger effects on other species within the small pelagic fish functional group than in the 1990s. This is probably related to the tighter constraints on the zooplankton-small pelagic fish part of the ecosystem in the 1980s than in the 1990s (Chapter 4, section 4.6.2). However, the impacts of overfishing of sardine and redeye on zooplanktivorous fish and predators are larger in 1990s simulations than in those of the 1980s.

Table 11.3 Functional Impact (FI, equations 11.3-11.5) indices derived from simulations of overfishing of anchovy, sardine and redeye, with impacts on small pelagic fish (FIpelagics), other zooplanktivorous fish (FIzoo fish) and predators of small fish (FIpredators)

Stock collapsed	$FI_{pelagics}$		$FI_{zoo\ fish}$		$FI_{predators}$	
	1980s	1990s	1980s	1990s	1980s	1990s
Anchovy	38.1	28.5	8.2	8.0	3.2	1.6
Sardine	24.1	23.6	-2.9	-5.5	-3.8	-5.1
Redeye	20.2	16.5	9.5	13.0	8.5	8.9

11.6 TROPHIC SIMILARITY INDEX

The trophic similarity (TS) index designed for use in this study quantifies the trophic similarity between a species that is removed from a system (e.g. collapsed through overfishing) and other species in the system. It quantifies the extent to which density compensation occurs following a collapse of, or increase in a target stock. The trophic similarity index is calculated for each group j belonging to the set of groups that show a change in biomass of the opposite sign to that of the target group i (e.g. if target group i collapses, m is a group undergoing an increase following the collapse of group i. Collapse is defined as elimination i.e. reduction of stock size to zero biomass):

$$TS = \left| \frac{\Delta B_j}{\sum \Delta B_m} \right| \qquad \text{... Equation 11.6}$$

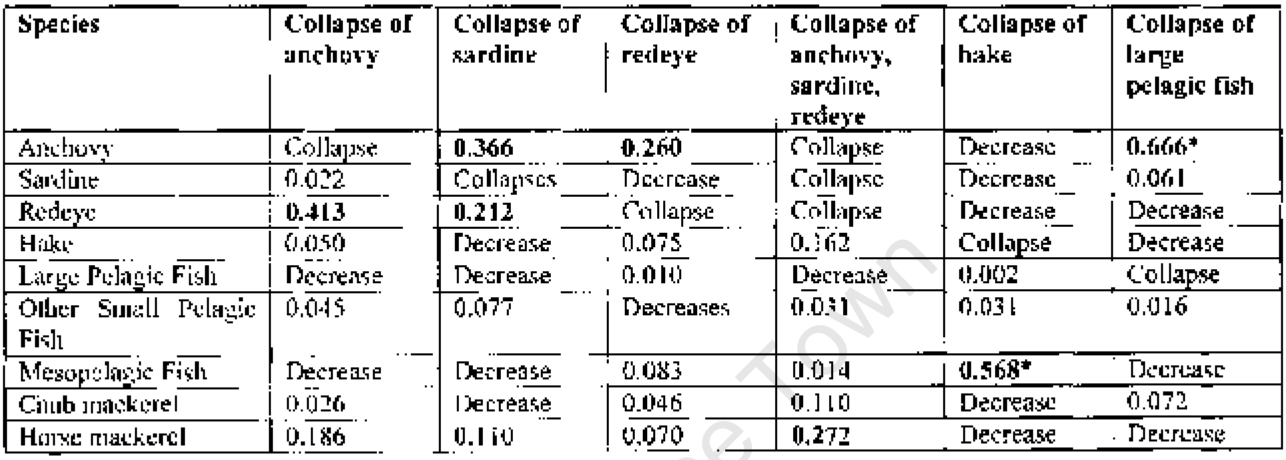
where B is biomass and AB is the change in biomass of a group between year 50 and year 0. The index ranges between 0 (no similarity) and 1 (total similarity).

11.6.1 Application of the trophic similarity index to the southern Benguela ecosystem

In both decades, most of the simulated density compensation resulting from the collapse of the anchovy stock is by redeye, and vice versa. This is reflected in the large trophic similarity indices of the two species when the other collapses (Tables 11.4 and 11.5). When anchovy collapses, the trophic similarity index of sardine in the 1990s is twice that in the 1980s simulations (Tables 11.4 and 11.5). This suggests that when sardine is more abundant in the 1990s, the stock is better able to take advantage of the collapse of anchovy than in the 1980s when sardine biomass is low. In the 1990s, the modelled increase in anchovy biomass is a smaller portion of the density compensation that occurs following the collapse of sardine than in the 1980s model in which anchovy is more abundant. Both modelled anchovy and redeye are able to proliferate when sardine is reduced, as reflected in their large trophic similarity indices when the collapse of sardine is simulated. A modelled collapse in the redeye stock is not beneficial to sardine in either decade; sardine abundance decreases when redeye collapses. This indicates that sardine abundance is not sufficient for the species to compete effectively with other groups (e.g. anchovy) for zooplankton prey made available when redeye collapses. It is likely that sardine is negatively impacted by predators switching to a diet of a larger proportion of sardine than before the elimination of redeye. Therefore, although redeye is shown to compensate for a reduction in model sardine biomass (i.e. redeye were trophically similar to sardine), sardine cannot be considered to be trophically similar to redeye. Because of the non-reciprocal nature of the trophic similarity index, it requires careful definition and use.

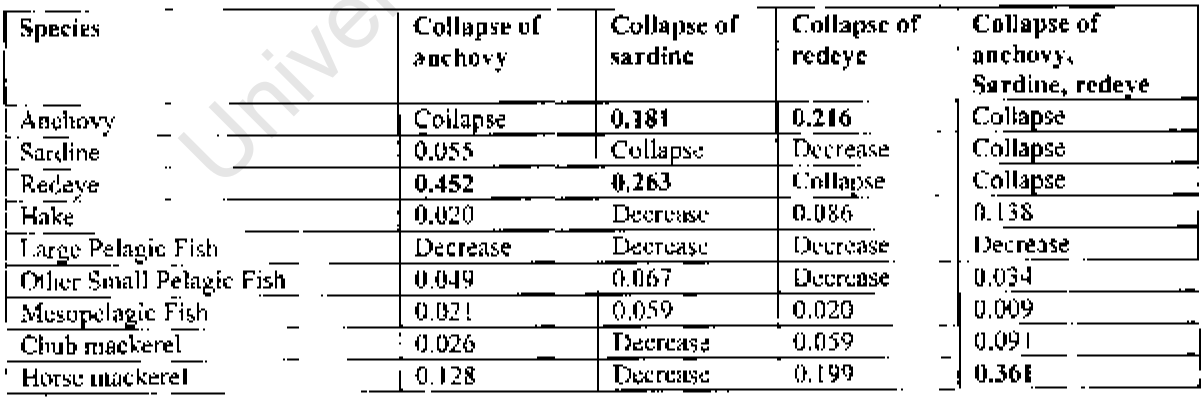
The strong trophic similarities between anchovy and redeye are in agreement with the large prey overlap indices for these two groups, calculated from steady-state *Ecopath* models (see Chapter 5, section 5.8).

Table 11.4 TS Index for 8 selected groups in models of the southern Benguela ecosystem during the 1980s, when collapses of 6 selected groups (columns) are simulated by overfishing. Strong trophic similarity indices (defined as larger than 0.2) are in bold type. "Decrease" indicates groups that decrease in biomass when a test group collapses i.e. they are not considered trophically similar to the test group. See section 11.7.1 for discussion of asterisks.



Species	Collapse of anchovy	Collapse of sardine	Collapse of redeye	Collapse of anchovy, sardine, redeye	Collapse of hake	Collapse of large pelagic fish
Anchovy	Collapse	**0.366**	**0.260**	Collapse	Decrease	**0.666***
Sardine	0.022	Collapses	Decrease	Collapse	Decrease	0.061
Redeye	**0.413**	**0.212**	Collapse	Collapse	Decrease	Decrease
Hake	0.050	Decrease	0.075	0.362	Collapse	Decrease
Large Pelagic Fish	Decrease	Decrease	0.010	Decrease	0.002	Collapse
Other Small Pelagic Fish	0.045	0.077	Decreases	0.031	0.031	0.016
Mesopelagic Fish	Decrease	Decrease	0.083	0.014	**0.568***	Decrease
Chub mackerel	0.026	Decrease	0.046	0.110	Decrease	0.072
Horse mackerel	0.186	0.110	0.070	**0.272**	Decrease	Decrease

Table 11.5 TS Index for 8 selected groups in simulations of the southern Benguela ecosystem during the 1990s, when collapses of anchovy, sardine and redeye are simulated by overfishing. Strong trophic similarity indices (defined as larger than 0.2) are in bold type. "Decrease" indicates groups that decrease in biomass when a test group collapses i.e. they are not considered trophically similar to the test group.



Species	Collapse of anchovy	Collapse of sardine	Collapse of redeye	Collapse of anchovy, Sardine, redeye
Anchovy	Collapse	**0.181**	**0.216**	Collapse
Sardine	0.055	Collapse	Decrease	Collapse
Redeye	**0.452**	**0.263**	Collapse	Collapse
Hake	0.020	Decrease	0.086	0.138
Large Pelagic Fish	Decrease	Decrease	Decrease	Decrease
Other Small Pelagic Fish	0.049	0.067	Decrease	0.034
Mesopelagic Fish	0.021	0.059	0.020	0.009
Chub mackerel	0.026	Decrease	0.059	0.091
Horse mackerel	0.128	Decrease	0.199	**0.361**

11.7 DISCUSSION

11.7.1 Index of Interaction strength

The index of interaction strength defined in this study is partly, although not entirely, related to abundance of the species or groups under investigation. In simulations of both decades, redeye biomass is larger than anchovy biomass, yet it is only the 1990s model that showed redeye to be a stronger interactor than anchovy. Stronger interactions are also related to the number of cycles from Trophic Level I to the groups in question (compare cycles to anchovy with those to large pelagic fish, for example, Table 11.2). However, hake is a stronger interactor than large pelagic fish despite fewer cycles from TL I to hake than to large pelagic fish, probably because biomass of hake is very large.

The index also incorporates the strength of trophic relationships, and may be used to compare, between species or functional groups, the sum of relative impacts of species or groups on all components within an ecosystem. However, the index was developed for use in theoretical scenarios where a change in the biomass of selected species or groups is simulated. When the index of interaction strength is used to compare effects of changes that occur between the 1980s and 1990s (i.e. when the index is applied to the two static *Ecopath* models of the 1980s and 1990s), groups like macro- and microbenthos, seabirds and cetaceans are the strongest interactors. This is because there are large relative changes in biomasses of these groups between the two decades, but it is not possible to separate the causes and effects of each of these changes from those related to changes within other groups such as pelagic fish. Therefore, the interaction strength index is only useful in cases where species collapses can be simulated while initially keeping the biomasses of other groups constant, so that any subsequent changes in the biomasses of these groups are known to be the result of the change in the selected group alone.

11.7.2 Functional impact indices

Three functional impact indices quantify the impact of changes in abundance of a species on various functional groups in the ecosystem. They help to quantify the underlying trophic relationships affecting the ecosystem and will serve as a basis for quantifying interactions between groups within an ecosystem, and eventually for inter-system comparisons.

Like the IS index, the FI index is not practical when comparing real ecosystems in different periods. A group undergoing a small change from one decade to the next may have a large FI when in fact it is actually the change in biomass of a different group that is responsible for the impact. Another limitation is that the FI index is not scaled between 0 and 1, and thus intersystem comparisons are difficult at this stage.

11.7.3 Trophic similarity index

There is some foresight required in selecting groups to consider for trophically similar characteristics. In Table 11.4, examples are marked with asterisks: when the large pelagic fish category collapses, anchovy biomass increases; when the hake group collapses, abundance of mesopelagic fish increases. These cases do not indicate trophic similarity. Instead, the increase in anchovy abundance is a direct consequence of lessened predation pressure (of large pelagics feeding on anchovy). The increase in mesopelagic fish biomass is a combination of reduced predation by hake, and reduced competition with hake for zooplankton prey. Therefore, it is necessary to consider trophic relationships between species when considering trophic similarity. This could be accomplished by refining subset m as "groups that undergo a change in biomass in the opposite direction to the target group, and which are not direct prey or predators of the target group i". Then the TS index would only be applicable to groups that are not interacting directly as prey or predators, but rather through competition for food. However, the index remains fuzzy when two species are related both through predation and the sharing of common prey resources (as in the case of hake and mesopelagic fish), and is most useful for comparing similarity between species within a carefully defined functional group.

An additional consideration is the aggregation of boxes in the model. In this case, phytoplankton, micro-, meso- and macro-zooplankton boxes have not been subdivided further to address likely differences in sizes of organisms consumed by small pelagic fish. Van der Lingen (1999) has found differences between the sizes of zooplankton consumed by anchovy and sardine in the southern Benguela ecosystem. Competition between anchovy, redeye and sardine for zooplankton prey may not be as important as suggested here if zooplankton size preferences of the three species were known and incorporated by modelling a larger number of planktonic boxes. The influence of meso-zooplankton size distribution on anchovy-sardine dynamics is explored in Chapter 12.

11.7.4 Comparison to indices of mixed trophic impact

To simultaneously assess both the direct effects of predation and the indirect effects of competition in trophic networks, mixed trophic impact assessment (Ulanowicz and Puccia 1990) is used (Chapter 3, section 3.4.1 and Chapter 5, section 5.7). Using this method, a matrix of relative, net impacts (scaled between —1 and +1) of each group on all other groups in the system is constructed so that important roles of certain groups, possibly overlooked otherwise, in the functioning of the system can be located. Mixed trophic impact analysis is a way of assessing how a change in the biomass of one group affects the biomasses of all other groups.

The three indices considered here are proposed to identify occurrences of density compensation in the case of trophic similarity of species and differ from mixed trophic impact assessment. The most important difference is that mixed trophic impact assessment assumes a constant diet matrix, whereas the indices developed here are based upon dynamic simulations, incorporating changes in diets according to the vulnerability and availability of prey groups. Responses (in time and magnitude) of model groups to a change in biomass of a group are dependent on their own turnover and consumption rates and those of predators and prey. Dynamic simulations take these into account whereas mixed trophic impact assessment is based on the static situation. Further, the three new indices consider net impacts in terms of changes in abundance only; these impacts are assessed as the total for all groups within the system (IS index) or as the total of a subset of species belonging to a defined functional or trophic group (FI and TS indices). By comparison, mixed trophic impacts are a matrix of net impacts of a species on every other group in the model.

Simulated changes in biomasses of most groups are in the directions expected from mixed trophic impact analysis. However, because of the static nature of the diet matrix used for mixed trophic impact analysis and the fact that relative response times of groups are not incorporated, some discrepancies result. For example, anchovy, sardine and redeye (Table 11.6) have mostly net negative impacts on other zooplanktivorous fish (chub mackerel, horse mackerel and mesopelagic fish), suggesting that an increase in their biomasses would negatively affect these groups (and presumably also that a reduction in the biomass of one of these groups would benefit other zooplanktivorous fish through reduced competition for prey). This is what occurs in simulations of anchovy and redeye, but not sardine; when sardine biomass is reduced through increased fishing on this group, chub mackerel and mesopelagic fish stocks decline in the 1980s, and chub mackerel and horse mackerel stocks decline in the 1990s, resulting in an overall reduction in the biomass of other zooplanktivorous fish in both decades. Similarly, predators on small pelagic fish decrease when sardine biomass decreases. However, in dynamic simulations reducing anchovy or redeye biomass, other zooplanktivorous fish biomass increases, corresponding to an increasingly large biomass of predators being supported.

Stocks of both anchovy and redeye are larger than sardine stocks in both decades, giving the former two species a competitive edge; mixed trophic impacts of anchovy and redeye on other zooplanktivorous fish are larger than those of sardine (Table 11.6). When sardine biomass is reduced in models of both decades, anchovy and redeye abundances increase and the net negative effects of increases in biomasses of these groups on chub mackerel outweigh the positive effect of a decrease in sardine biomass. In turn, chub mackerel has a larger positive and redeye a larger negative mixed trophic impact on horse mackerel in the 1990s than in the 1980s (Table 11.6); a decline in horse mackerel biomass in the 1990s is likely to be related to the increase in redeye biomass and reduced chub mackerel abundance. Reduced sardine biomass and increased anchovy and redeye biomasses all negatively affect mesopelagic fish in the 1980s, whereas in the 1990s, sardine have a negative mixed trophic impact on mesopelagic fish. (Table 11.6).

The above example emphasizes that the main difference between mixed trophic impact indices and the three proposed in this dissertation is the static versus dynamic nature of the models upon which they are based.

Table 11.6 Mixed trophic impacts (Ulanowicz and Puccia 1990) of selected groups in models of the southern Benguela ecosystem during the 1980s and 1990s. Impacting groups are tabulated in rows, the groups they impact are tabulated in columns.

	1980s			1990s		
Impacting/impacted group	Chub mackerel	Horse mackerel	Mesopelagic fish	Chub mackerel	Horse mackerel	Mesopelagic fish
Anchovy	-0.160	-0.231	-0.029	-0.084	-0.159	-0.019
Sardine	-0.011	-0.025	0.003	-0.026	-0.063	-0.002
Redeye	-0.159	-0.098	-0.071	-0.216	-0.156	-0.089
Chub mackerel	-0.007	0.001	-0.020	-0.010	0.009	-0.043
Horse mackerel	-0.028	-0.082	0.003	-0.026	-0.083	0.004
Other small pelagic fish	-0.005	-0.006	-0.001	-0.005	-0.006	0.001
Mesopelagic fish	-0.105	-0.250	-0.217	0.028	-0.232	-0.211

The IS index, which sums the impacts of one group on all others in the model should also be compared to mixed trophic impact indices (Table 11.7). Ranking of anchovy, sardine, redeye and hake according to size are the same for the two indices. However, when large pelagic fish are considered, rankings of the two indices do not correspond. This further highlights the differences between indices derived from dynamic simulation model outputs and the mixed trophic impact index based on static models where diet compositions are fixed and responses to changes in the biomass of a group are restricted.

Table 11.7 Ranking by size of the interaction index (IS) and the sum of the absolute values of mixed trophic impact indices (MTI) for anchovy, sardine, redeye and hake. Rankings in parentheses indicate those when the indices of large pelagic fish are included in the ranking. IS indices are based on dynamic and MTI indices on static models of the southern Benguela ecosystem.

	1980s		1990s	
	IS	MTI	IS	MTI
Anchovy	2 (3)	2	3 (4)	3
Sardine	4 (5)	4 (5)	4 (5)	4 (5)
Redeye	3 (4)	3	2 (3)	2
Hake	1	1	1	1
Large Pelagic fish	(2)	(4)	(2)	(4)

11.7.5 Ecosystem implications

In their review of redundancy in ecosystems, Lawton and Brown (1993) posed the question: do similar species, occupying similar trophic positions, have similar effects on community organization? In the case of anchovy, sardine and redeye in the southern Benguela ecosystem models, the answer is yes, to a varying degree depending on the species and its abundance during the periods examined. Anchovy and redeye compensate for one another by increasing their abundances when the other collapses, i.e. they show trophic similarity with one another. Redeye and anchovy are also found to be trophically similar to sardine as their abundances increase when sardine decreases. However, sardine abundance is low and it is unable to compensate for a collapse in the redeye stock, emphasizing the non-reversible nature of the trophic similarity index developed in this study.

Within the small pelagic fish functional group, the simulated collapse of the anchovy stock has the largest impact of all three species tested. Sardine has only small modelled impacts on its functional group, and on the functional groups containing its prey and predators. Overexploitation of redeye has the largest modelled impacts on the functional groups containing species competing with small pelagic fish for zooplankton prey and those preying on small pelagic fish. Therefore, a species like anchovy may have the strongest impacts within its functional group, but because there is efficient density compensation by other trophically similar species within its functional group, and given the ability of predators to switch to functionally-similar prey, it may have little overall effect on the functioning of the system. Although sardine feed at a lower trophic level than anchovy (Chapter 4) and are longer-lived, the two species in the southern Benguela ecosystem are similar in trophic function (they have the same predators and therefore it is likely that a change in their abundances would have similar impacts on their predators and competitors). This trophic similarity explains why there are only small differences in biomass and production of the small pelagic fish functional group between an anchovy-dominated (1980s) and sardine-dominated (1990s) regime. Therefore, changes in the relative abundances of anchovy and sardine have small effects on the trophic functioning of the southern Benguela system, whereas changes in redeye abundance may have larger impacts on the ecosystem.

11.7.6 Fishing-in-balance (FIB) index

At this stage it is worth making special mention of a new index proposed by Pauly *et al.* (2000a) that looks promising for assessing the ecosystem impacts of fishing (Christensen 2000). Pauly *et al.* (1998a, 2000a, 2000b) have shown that there has been a decline in the mean trophic level of fisheries worldwide, concluding that humans are "fishing down the marine food web". They have supported this finding by considering the fishing-in-balance (FIB) index to assess whether fisheries are ecologically balanced (Pauly *et al.* 2000). The FIB index compares catches, mean transfer efficiency and mean trophic level of the catch in a period to that in a reference year or period. Comparing fisheries in the southern Benguela ecosystem in the 1990s to those in the 1980s, a small positive FIB index is obtained (0.090), associated with the decrease in total catch and increase in mean trophic level of the catch between the 1980s and 1990s (see mean TL of catch, TE and catches in Chapter 5, sections 5.5 and 5.6).

11.8 CONCLUSIONS

All three types of indices developed in this study have their merits. The index of interaction strength is the simplest one. The index measures the relative impact of the demise of a test group on total system biomass. This renders the index comparable across systems, provided that species aggregations are comparable. For models of the southern Benguela ecosystem, the index shows that anchovy are the strongest interactors in the 1980s model and redeye in the 1990s model.

The strong similarities in trophic functioning of the southern Benguela ecosystem in the anchovy-dominated system of the 1980s, and the 1990s when there was a shift towards greater sardine abundance, are explained by the trophic similarity between anchovy and sardine. The trophic similarity index may help to explain differences in trophic functioning elsewhere, but would require careful selection of groups, and should not be used for inter-system comparisons. Aggregation of model boxes is likely to influence this and the other two indices. Model aggregation should be considered carefully where competition for zooplankton prey is shown to be important in determining the degree of trophic similarity between small pelagic fish species.

The index that provides the most information on the trophic functioning and interactions between species is the functional impact index. In this study, the functional impacts of small pelagic fish in the southern Benguela ecosystem are explored. Anchovy have the largest impacts on the small pelagic fish functional group, whereas redeye have the largest impacts on functional groups containing competitors (other zooplanktivorous fish) and predators of small pelagic fish. Although actual values of this index are system-specific, the functional impact index may provide information on the relative strengths of the functional impacts of selected species or groups in different systems. It is recommended that this index be the starting point for the further development of indices of ecosystem change and trophic functioning, so that potential outcomes of hypothetical management options can be compared across systems.

CHAPTER TWELVE

CHANGES IN THE SOUTHERN BENGUELA ECOSYSTEM FROM THE 1980S TO THE 1990S

ABSTRACT

Two approaches are taken in an attempt to simulate changes from the 1980s-1990s in the southern Benguela ecosystem. Firstly, using the 1980s model, four scenarios are considered in which fishing mortality rates of sardine and horse mackerel are changed to those estimated in the 1990s model, and anchovy biomass is reduced. Results show that it is unlikely that observed changes in pelagic fisheries between the 1980s and 1990s played a large role in driving the changes in abundance of anchovy and sardine. Secondly, changes in the susceptibility of phyto-and zooplankton prey to feeding by anchovy and sardine are simulated for the two decades. Results show that shifts between anchovy and sardine regimes in the southern Benguela ecosystem may be caused by changes in the availability of mesozooplankton prey to anchovy and sardine, mediated through changes in environmental conditions.

12.1 INTRODUCTION

The occurrence of alternating periods of pelagic fish dominance (regime shifts) was discussed in Chapter 2 and it was noted that the mechanisms responsible for these sudden changes in ecosystem state are poorly understood (Lluch-Belda *et al.* 1989, 1992a, 1992b). The two factors most likely to account for many of the changes in dominance states of upwelling ecosystems are changes in fishing pressure and environmental changes (Larkin 1996).

By manipulating fishing rates in a model of the Gulf of Thailand ecosystem for 1980, Christensen (1998) was able to back-simulate changes in the ecosystem to obtain an ecosystem state close to that before intensive fishing began in the area (1963). This work provides an example of a system in which changes are likely to have been driven by changes in fishing behaviour. On the other hand, Trites *et al.* (1999) found that in the eastern Bering Sea, fishing and trophic interactions alone did not account for the ecosystem changes that have been observed: there was an increase of 400% in the abundance of pollock between the 1950s and the 1980s. Their models suggest that environmental changes must have played a large part in changing the eastern Bering Sea ecosystem. In their review, Jennings and Kaiser (1998) conclude that collapses of pelagic fish stocks and subsequent replacement of dominant species are primarily environmentally linked, with fisheries usually serving to hasten and intensify the collapse rather than driving the regime shift.

In the southern Benguela ecosystem, there is alternation between anchovy-dominated and sardine-dominated states (Chapter 2, section 2.3). Moloney and Wickens (1985) modelled sardine-anchovy alternation in the southern Benguela ecosystem from the 1950s to the 1980s, showing that overfishing can cause replacement of one fish population by its competitor. Similarly, modelling by Korrubel (1992) showed that harvesting can play an important role in species replacement. On the other hand, van der Lingen and Hutchings (in prep.) concluded that anchovy-sardine regime shifts are associated with structural changes in the ecosystem, caused by environmental conditions favouring one species over the other. Shannon *et al.* (1992) showed that there was a warm period during the 1980s and that environmental changes can sometimes impact many species simultaneously. This chapter addresses key question le, exploring whether there is a trophic mechanism capable of sustaining regimes over extended periods or precipitating a switch between dominant pelagic fish species in the southern Benguela ecosystem. In this chapter, models of the southern Benguela ecosystem during the anchovy-dominated 1980s on the one hand and on the other, the 1990s, when sardine abundance increased, are examined with respect to i) observed changes in fishing (see discussion in Chapter 2, section 2.2.3) and ii) changes in planktonic food availability to anchovy and sardine mediated through changes in environmental conditions (see discussion in Chapter 2, sections 2.2.4 and 2.3.3).

Therefore, this dissertation partly addresses one of the future tasks for marine scientists mentioned by Magnusson (1999), namely that biological interactions are identified (Chapters 4, 5 and 6), their importance quantitatively assessed (e.g. by means of ecosystem indices in Chapter 11) relative to the influence of the physical environment (this chapter).

12.2 METHODS

Separate *Ecopath* models of the southern Benguela ecosystem in the 1980s and 1990s are used to explore the role of fishing and environmental factors in driving the regime shift in pelagic fish dominance In all simulations, wasp-waist flow control was assumed i.e. there is bottom-up control of predators and top-down control of zooplankton by small pelagic fish (see Chapter 9). This describes the dominant role of small pelagic fish in upwelling systems, showing that they play an important role in ecosystem structure and function (Cury *et al.* 2000). It has been found that effects of altered fishing are more pronounced when wasp-waist control is assumed than when mixed control is modelled, or when bottom-up control of small pelagic fish by zooplankton is assumed to occur (Chapter 9, Cury *et al.* 2000, Shannon *et al.* 2000). Therefore, by assuming wasp-waist control in the current model simulations, the effects of fishing and environmental forcing are unlikely to be hidden by a flattening of perturbations, as might occur if mixed control or bottom-up control were assumed.

12.2.1 First approach — could changes in fishing pressure have caused the 1980s-1990s "regime shift"?

Data

In both decades, the pelagic fishery was carefully and conservatively managed (Cochrane *et al.* 1991b, Butterworth *et al.* 1992, De Oliveira *et al.* 1998a, also see Chapter 5, section 5.6.3) so that it is unlikely that changes in fishing strategies would have caused the ecosystem changes observed. Nevertheless, the possible effects of fishing on the abundance of major species should be examined before conclusions are drawn. Fishing mortality rates (F's) of anchovy, sardine and horse mackerel in the 1990s, estimated from catches, stock sizes and natural predation estimates in the model, differ from those in the 1980s (Table 12.1). Biomasses of sardine and horse mackerel are larger and F's of these groups are smaller in the 1990s than the 1980s. By comparison, anchovy biomass and F are smaller in the 1990s than in the 1980s.

Table 12.1 Mean annual modelled fishing mortality rates (F) and biomasses (B) of some small pelagic fish in the southern Benguela ecosystem, from *Ecopath* models of the 1980s and 1990s (Chapter 4).

	1980-1989		1990-1997	
	B (t.km^{-2})	F (y^{-1})	B (t.km^{-2})	F (y^{-1})
Anchovy	5.216	0.30	3.573	0.23
Sardine	0.586	0.31	2.091	0.16
Juvenile horse mackerel	0.200	0.11	0.484	0.07
Adult horse mackerel	1.618	0.09	1.937	0.06

Simulations

Using the 1980s model, four scenarios of altered fishing test whether changes in fishing mortality rates of small pelagic fish could have caused the 1980s-1990s regime shift. Years 1-10 mimic the ecosystem in the 1980s.

i) From year 10-20, fishing mortality rates of sardine, juvenile and adult horse mackerel are reduced to reflect those in the 1990s (Table 12.1). Thereafter, Fs return to 1980s values for the remainder of the 50-year simulation period.

ii) From year 10-20, fishing mortality rates of sardine, juvenile and adult horse mackerel are reduced to reflect those in the 1990s. In addition, anchovy biomass is reduced to the 1990s level (69% of the 1980s B) by increasing anchovy F by a factor of 1.3 from year 10-20. Thereafter, all Fs return to 1980s values for the remainder of the 50-year simulation period.

iii) From year 10-20, anchovy biomass is reduced to the 1990s level (69% of the 1980s B) by increasing anchovy F by a factor of 1.3, but Fs of sardine and horse mackerel are not altered. From year 21-50, Fs are returned to original 1980s values.

iv) From year 10-20, fishing mortality rates of sardine, juvenile and adult horse mackerel are reduced to reflect those in the 1990s. In addition, anchovy biomass is heavily reduced (to 14% of the 1980s B) by increasing anchovy F by a factor of 2.0 from year 10-20. From year 21-50, Fs are returned to original 1980s values.

12.2.2 Second approach — could environmental changes have caused the 1980s-1990s "regime shift"?

Data

In the 1990s, abundance of anchovy, the dominant pelagic fish species of the 1980s, is reduced and biomasses of sardine, redeye, mesopelagic fish and horse mackerel all increase. Predator and prey niche overlaps of anchovy, sardine, redeye and juvenile horse mackerel are larger in the 1990s than in the 1980s (Chapter 5, section 5.8, Table 5.4), suggesting a period during which the pelagic niche previously occupied by anchovy is filled by a suite of species of small pelagic fish. This has been discussed by Crawford (1987); it is frequently the case that generalised feeding allows more than one species to be able to take advantage of the energy made available by the collapse of a single stock. Whether a species becomes the dominant replacing species will depend on the extent of fishing on the species both during and after the collapse of the stock being replaced (Crawford 1987). It cannot be expected that reduction of a stock through fishing will result in another single species being fully able to take its ecological place because it is unlikely that the different geographic distribution and behaviour of the replacing species are as well adapted to utilize the part of the resource vacated by the collapsed stock (Jones and Henderson 1987).

Verheye *et al.* (1998) found that there were substantial shifts in the species composition and size structure of the crustacean zooplankton community on the west coast of South Africa between 1951 and 1996. They propose that these changes are caused by the changes in relative predation pressure of anchovy and sardine, and that the long-term increase in zooplankton abundance over the period may relate to the intensification of coastal upwelling in the region, increasing phytoplankton production and causing a shift in the phytoplankton size-spectrum.

Simulations

Simulations are explored in which forcing functions are applied to the prey of anchovy and sardine, in an attempt to simulate the observed biomass changes between the 1980s and the 1990s. In this model, a forcing function is a factor changing the amount of a prey group that is consumed by a predator, so that susceptibility of a prey group to a predator can be altered to reflect what may occur under certain environmental conditions. The reasoning behind these simulations of the southern Benguela ecosystem is that in periods of intermittent mixing i.e. cool periods with frequent upwelling events, a large phytoplankton biomass is supported, dominated by large, chain-forming diatoms (Fig. 12.1). Zooplankton are consequently larger in size (dominated by large copepods such as *Calanus* and *Calanoides)* and the environment is therefore favourable to the biting feeding behaviour of anchovy (van der Lingen 1999). In warm periods the water column is stable, upwelling events are weak and less frequent and phytoplankton is dominated by small cells. Small copepods dominate the zooplankton, favouring filter-feeding sardine (van der Lingen 1999).

The following scenarios are investigated:

i) Using the 1980s model, a negative forcing function equivalent to 45% of the maximum is applied to the trophic links between anchovy and its phyto-and zooplankton prey, and a positive forcing function equivalent to 40% of the maximum is applied to sardine and its phyto-and zooplankton trophic links. This reduces and increases the susceptibility of plankton prey to anchovy and sardine respectively.

ii) Similarly, using the 1990s model, a positive forcing function equivalent to 14% of the maximum is applied to the trophic links between anchovy and its phyto-and zooplankton prey, and a negative forcing function equivalent to 38% of the maximum is applied to sardine and its phyto- and zooplankton prey, lowering susceptibility of prey to sardine.

iii) Using the 1980s model, a positive forcing function equivalent to 40% of the maximum is applied to trophic links between sardine and its phyto-and zooplankton prey and anchovy is unaffected.

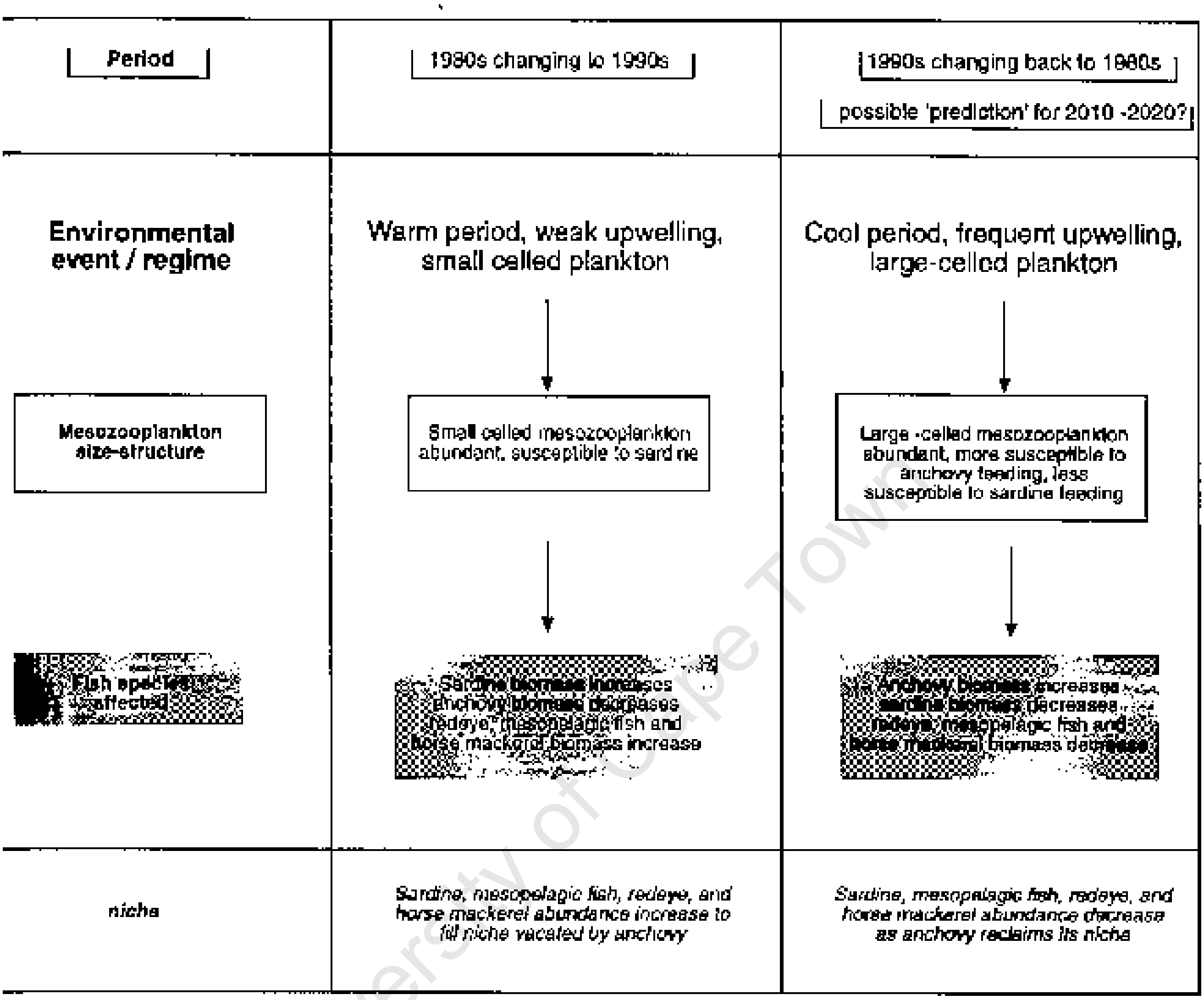
iv) Using the 1990s model, a positive forcing function equivalent to 14% of the maximum is applied to trophic links between anchovy and its phyto- and zooplankton prey and sardine is unaffected.

v) Using the 1980s model, a negative forcing function equivalent to 45% of the maximum is applied to the macro- and mesozooplankton-anchovy trophic links, and a positive forcing function equivalent to 40% of the maximum is applied to the macro- and mesozooplankton-sardine links.

vi) Using the 1990s model, a positive forcing function equivalent to 14% of the maximum is applied to the macro- and mesozooplankton-anchovy trophic links, and a negative forcing function equivalent to 38% of the maximum is applied to the macro- and mesozooplankton-sardine links.

vii) Using the 1980s model, a negative forcing function equivalent to 45% of the maximum is applied to the mesozooplankton-anchovy trophic link only, and a positive forcing function equivalent to 40% of the maximum is applied to the mesozooplankton-sardine link only.

viii) Using the 1990s model, a positive forcing function equivalent to 14% of the maximum is applied to the mesozooplankton-anchovy trophic link, and a negative forcing function equivalent to 38% of the maximum is applied to the mesozooplankton-sardine link.



lg. 12.1 Diagrammatic representation of the hypothesized mechanism driving alternating periods of anchovy and sardine dominance in the southern Benguela ecosystem. Row headers appear in the first column. The first row indicates the periods being modelled: 1) changing from the 1980s to the 1990s ecosystem state and 2) reverting from the 1990s ecosystem state to that of the 1990s (possibly also a prediction of the ecosystem changes which may occur over the next decade or two).

12.3 RESULTS AND DISCUSSION

12.3.1 First approach — could changes in fishing pressure have caused the 1980s-1990s "regime shift"?

Using the southern Benguela model of the 1980s, fishing mortality rates of sardine, juvenile horse mackerel and adult horse mackerel are altered over a ten-year simulation period to reflect those estimated for the 1990s (Table 12.1). Resulting biomasses of many groups do not change by the same factors as observed in the system (Scenario 1, Table 12.2). Modelled changes in biomasses of the major groups are more realistic when anchovy biomass is reduced and Fs of sardine and horse mackerel are altered simultaneously to reflect the 1990s situation (scenario 2, Table 12.2). Reduced anchovy biomass is accomplished by increasing model F for anchovy by a factor of 1.3, in contrast to the real situation in which anchovy F declined as biomass declined in the 1990s. Simulated changes are nearly as large when only anchovy biomass is reduced and F's of sardine and horse mackerel are unaltered (scenario 3, Table 12.2). An additional scenario in which heavy fishing on anchovy reduces anchovy biomass below the level estimated in the 1990s shows that changes in the major groups considered may occur when anchovy declines, irrespective of changes in fishing intensities on sardine and horse mackerel (scenario 4, Table 12.2).

These results suggest that fishing alone was not responsible for the observed fluctuations between anchovy and sardine from the 1980s to the 1990s, and that observed changes may be more strongly linked to a decline in anchovy abundance that was independent of the fishery.

Table 12.2 Biomass ratios of 1990s:1980s, in original models (Chapters 4 and 5) and for simulated models of the 1990s compared to the original 1980s model. Results from simulated models of the 1990s are for year 15 when different F combinations and reduced anchovy biomass are modelled (scenarios 1, 2, 3 and 4). Where altered, Fs are those in the 1990s.

	Original models	Altered F's of sardine, juvenile and adult horse mackerel *Scenario 1*	Altered F's of sardine, juvenile and adult horse mackerel, and anchovy biomass reduced by increasing F by a factor of 1.2 *Scenario 2*	Anchovy biomass reduced by increasing F by a factor of 1.3. F's of other groups unaltered *Scenario 3*	Anchovy biomass greatly reduced by increasing F by a factor of 2.0, altered F's of sardine, juvenile and adult horse mackerel *Scenario 4*
Micro-, meso- and macrozooplankton	1.09	0.99	1.02	1.02	1.04
Anchovy	0.69	1.02	0.69	0.69	0.31
Sardine	3.6	1.82	1.85	1.06	1.88
Redeye	1.12	0.97	1.02	1.04	1.08
Juvenile horse mackerel	2.42	1.13	1.21	1.06	1.29
Adult horse mackerel	1.20	1.15	1.2	1.05	1.26
Mesopelagic fish	1.19	0.99	1.03	1.04	1.08
Hakes	1.24	0.99	1.01	1.01	1.03

12.3.2 Second approach — could the environment have caused the 1980s-1990s "regime shift"?

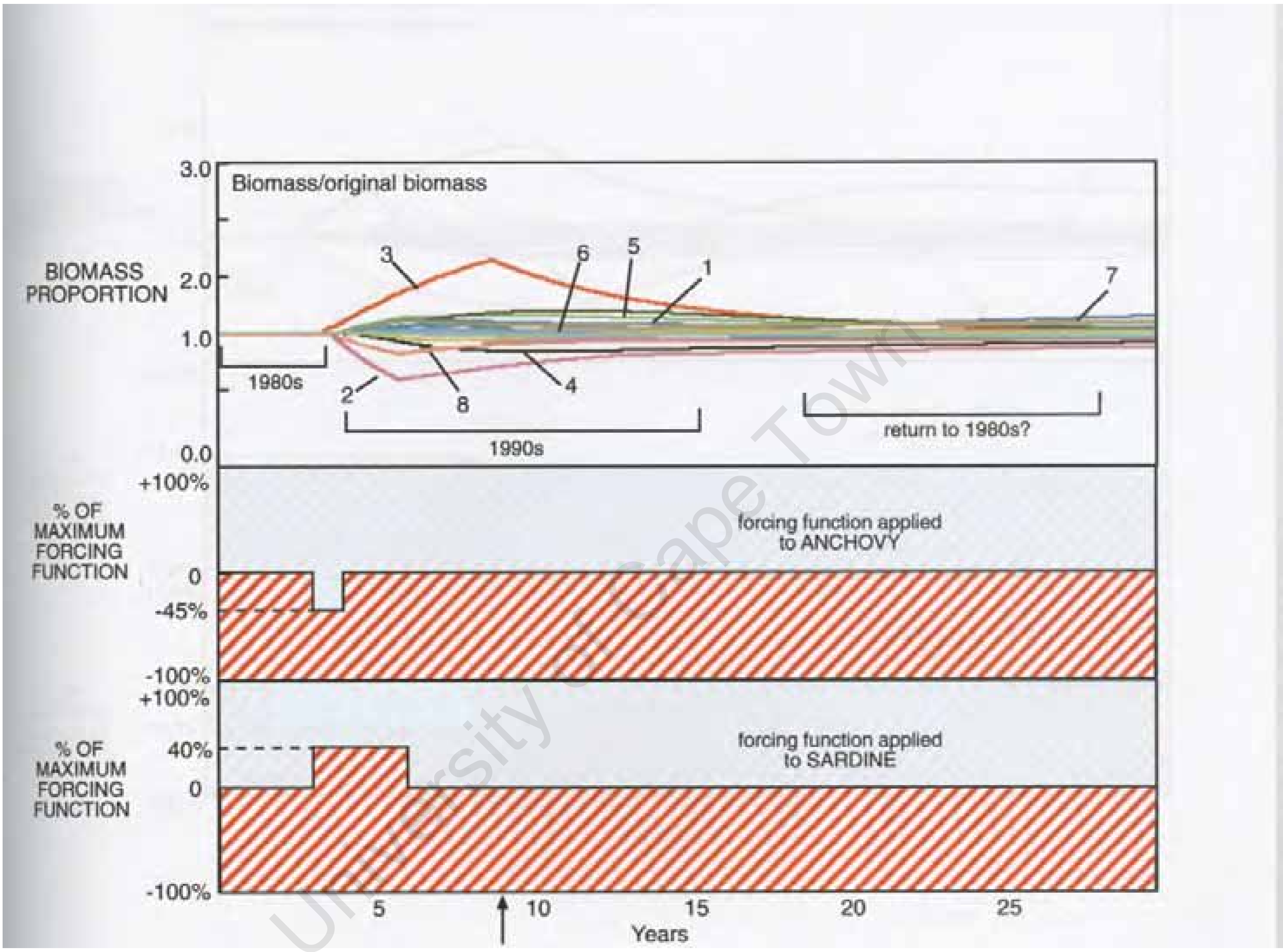
Using the 1980s model, a negative forcing function equivalent to 45% of the maximum is applied to anchovy-plankton trophic links and a positive forcing function equivalent to 40% of the maximum is applied to sardine-plankton trophic links (middle and lower panels of Fig. 12.2 on p. 256). Similarly, using the 1990s model, forcing functions favouring anchovy (14% of maximum effect) and lowering susceptibility of prey to sardine (38% of maximum effect) are used (middle and lower panels of Fig. 12.3 on p. 257). In both cases, a model ecosystem describing the "opposite" regime is obtained, with changes in biomasses of many groups in the same direction and of a similar order of magnitude to changes estimated from the 1980s to the 1990s in original models (Appendix E, Fig. E.1).

Subsequent tests show that ecosystem changes similar to those observed can also be simulated using forcing functions applied only to sardine feeding in the 1980s model, and only to anchovy feeding in the 1990s model (Appendix E, Fig. E.2). However, in these scenarios, simulated biomass changes are mainly in the observed directions but magnitudes do not match observed biomasses. Results of simulations in which both anchovy and sardine feeding are affected are closer to original estimates of the ecosystem during the two periods (Appendix E, Figs. E.1, E.3 and E.4).

Van der Lingen (1999) suggests that the major factor favouring anchovy or sardine in the southern Benguela ecosystem is not phytoplankton biomass, but rather the size-structure and species composition of zooplankton. For this reason, zooplankton susceptibility to anchovy and sardine is further explored. Sardines derive most of their ingested carbon from small calanoid copepods less than 1 200 pm, crustacean eggs and nauplii and anchovy eggs (van der Lingen 1999). These groups fall into the lower size range of the mesozooplankton group in this dissertation. By comparison, anchovy feed predominantly by biting behaviour (van der Lingen 1999), making use of prey larger than 700 pm (James and Findlay 1989), i.e. in the upper range of modelled mesozooplankton (200-2000 pm) and within the macrozooplankton size range (2-20mm) assumed in this study (Appendix A, Table A.1). Because size structure within the mesozooplankton group is not incorporated in the ecosystem models here, complementary modes of feeding by the two fish on mesozooplankton of different sizes is simulated by changing the susceptibility of anchovy and sardine to mesozooplankton.

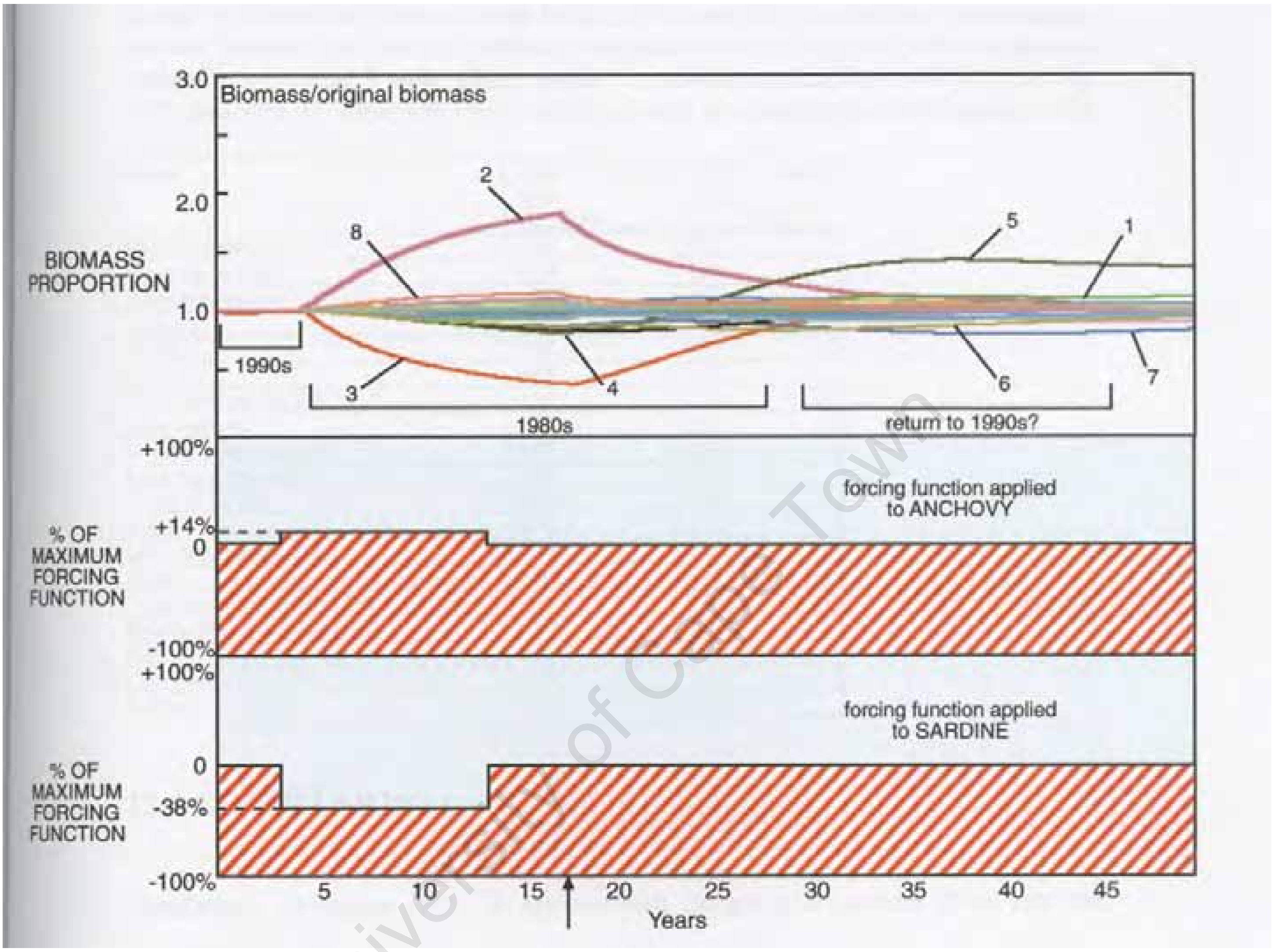
Tests in which trophic paths from meso- and macrozooplankton to anchovy and sardine are manipulated have similar effects to those in which only mesozooplankton links to anchovy and sardine are affected (Appendix E, Figs. E.3 and E.4). These show that the susceptibility of mesozooplankton to anchovy and sardine in the 1980s and 1990s is the key to simulating regime changes in the southern Benguela ecosystem. Using the 1980s model, a negative forcing function is applied to the mesozooplankton-anchovy relationship, and a positive forcing function to the mesozooplankton-sardine link (Fig. 12.2). Similarly, using the 1990s model, mesozooplankton are considered to be less susceptible to sardine and more susceptible to anchovy (Fig 12.3). The modelled changes in biomasses are in the observed directions and mostly of similar magnitudes to those in the two original models (Appendix E, Fig. E.4). Two exceptions are simulated changes in the biomasses of sardine and juvenile horse mackerel, which are smaller than the interdecadal changes observed. When the forcing functions are removed during the simulation of the 1990s situation using the 1980s model, the modelled system returns to a state similar to that of the 1980s (Fig. 12.2, Table 12.3). However, in the simulation of the 1980s using the 1990s model, some groups (anchovy, other small pelagic fish, chub mackerel and pelagic-feeding demersal fish) do not return to states similar to original 1990s levels (Fig. 12.3, Table 12.3).

The duration of an environmental perturbation, causing changes in the susceptibility of mesozooplankton to anchovy and sardine, should be further investigated in collaboration with environmental scientists. For modelling purposes here, short periods (2-5 years) over which forcing functions apply are modelled in the 1980s to reduce susceptibility of mesozooplankton to sardine (45% of maximum negative effect) and increase susceptibility of mesozooplankton to anchovy (40% of maximum positive effect) (Fig. 12.2, middle and lower panels). Weaker forcing functions (14% of maximum positive effect for anchovy and 38% of the maximum negative effect for sardine) are applied for longer periods (10 years) when the 1990s model is tested (Fig. 12.3, middle and lower panels). The forcing functions applied in these simulations were explorative and their magnitudes and durations were selected so that simulated changes were similar to those observed between the 1980s and 1990s. There is a need for development of a rigorous method to quantify environmental perturbations changing susceptibility of mesozooplankton to anchovy and sardine in terms of forcing function strength and duration.



1 = Red eye
2 = Anchovy
3 = Sardine
4 = Snoek
5 = Other small pelagics
6 = Pelagic - feeding demersals
7 = Chub mackerel
8 = Total catch

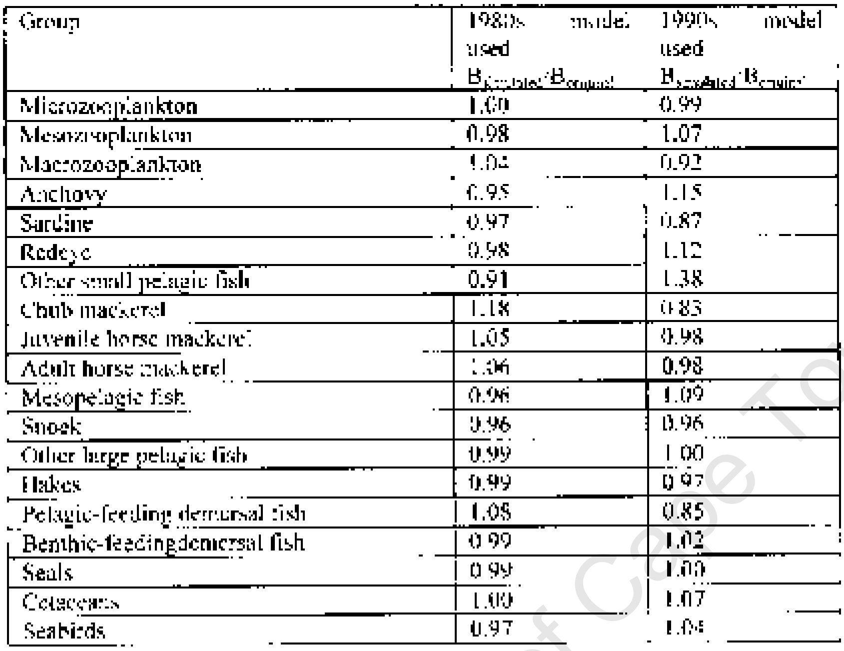
Fig. 12.2 Plot of simulated biomass as a proportion of original biomass in the 1980s, when a forcing function is applied so that mesozooplankton are less susceptible to anchovy feeding from year 3-4 and more susceptible to sardine feeding from year 3-6, causing changes in the system over a ten-year period (year 5-15). The 1980s model is used to simulate the 1990s situation. The middle panel depicts the forcing function applied over time to the



1 = Red eye
2 = Anchovy
3 = Sardine
4 = Snoek
5 = Other small pelagics
6 = Pelagic - feeding demersals
7 = Chub mackerel
8 = Total catch

Fig. 12.3 Plot of simulated biomass as a proportion of original biomass in the 1990s, when a forcing function is applied so that mesozooplankton are less susceptible to sardine feeding and more susceptible to anchovy feeding from year 3-13, causing changes in the system over a twenty-year period (year 5-25). The 1990s model is used to simulate the 1980s situation. The middle panel depicts the forcing function applied over time to the mesozooplankton-anchovy link and the bottom panel depicts the forcing function applied over time to the mesozooplankton-sardine link.

Table 12.3 Biomass (B) ratios of groups in original: simulated models during the 1980s and 1990s when forcing functions (altering the susceptibility of mesozooplankton to anchovy and sardine) are applied and then removed, so that the system is allowed to recover. Refer to Figs. 12.2 and 12.3 for graphic representation (arrows indicate year used to estimate biomasses of the 1980s and 1990s regimes in simulations i.e. year 9 when 1980s model is used to simulate the 1990s state in Fig. 12.2, and year 17 when the 1990s model is used to simulate the 1980s state in Fig. 12.3).



Group	1980s model used $B_{simulated}/B_{original}$	1990s model used $B_{simulated}/B_{original}$
Microzooplankton	1.00	0.99
Mesozooplankton	0.98	1.07
Macrozooplankton	1.04	0.92
Anchovy	0.95	1.15
Sardine	0.97	0.87
Redeye	0.98	1.12
Other small pelagic fish	0.91	1.38
Chub mackerel	1.18	0.83
Juvenile horse mackerel	1.05	0.98
Adult horse mackerel	1.06	0.98
Mesopelagic fish	0.96	1.09
Snoek	0.96	0.96
Other large pelagic fish	0.99	1.00
Hakes	0.99	0.97
Pelagic-feeding demersal fish	1.08	0.85
Benthic-feeding demersal fish	0.99	1.02
Seals	0.99	1.00
Cetaceans	1.00	1.07
Seabirds	0.97	1.04

12.4 CONCLUSIONS

Simulations of regime shifts in the southern Benguela ecosystem show that the observed changes in pelagic fisheries between the 1980s and 1990s are unlikely to have played a large role in driving the changes in abundance of anchovy and sardine. Rather, model shifts between anchovy (1980s) and sardine (1990s) "regimes" in the southern Benguela ecosystem may be caused by changes in the availability of mesozooplankton to anchovy and sardine (Fig. 12.1). These changes are in opposite directions for anchovy and sardine, and are assumed to be mediated through changes in environmental conditions. This supports the hypothesis of van der Lingen (1999), that alternating periods of anchovy and sardine dominance are related to complementary feeding strategies of the two species, enabling zooplanktivorous anchovy to take advantage of periods during which large copepods dominate the zooplankton, and sardine, a plankton generalist, to maintain its populations under a range of zooplankton community structures.

CHAPTER THIRTEEN

A NEW APPROACH TO FISHERIES MANAGEMENT

ABSTRACT

A new way of approaching fisheries management in the southern Benguela is proposed according to a "4-step plan". Firstly, using steady-state ecosystem models, important interactions can be highlighted in mixed trophic impact assessments. Secondly, using a dynamic simulation approach, indices quantifying interaction strength and functional impacts can provide information on the size of impacts on various ecosystem components when a species or group is overfished. Thirdly, dynamic simulations can suggest some possible short- and long-term ecosystem effects of altered fishing on a group. Fourthly, the net ecosystem effects of all revised fishing strategies need to be considered together. For this to be accomplished, the overall objective for fisheries management in the region, the objectives for each fishery, and the non-consumptive objectives for the region need to be clearly stated because all will play major roles in the advice provided in an ecosystem context.

13.1 INTRODUCTION

We need to begin putting into place practical methods of managing fisheries as ecosystems. This was Larkin's hope for future ecosystem modellers and has been mentioned as a shortcoming of the *Ecopath* modelling approach (Larkin 1996). In answering the question "can we manage our multispecies fisheries", Murawski (1991) concluded that the dynamics of species and fisheries interactions are poorly known and that in the future, fisheries management will need to depend on research focussed on the mechanisms underlying these interactions.

The aim of this dissertation is to compare the trophic functioning of the Benguela ecosystem during alternating periods of abundance of anchovy and sardine, with a view to advising on multispecies management of marine resources in the region. In Chapters 4-12, trophic flows and interactions between species in Benguela ecosystems are modelled and compared. Further, some of the possible ecosystem implications of altered fishing strategies are examined. However, at this stage, there are no clear guidelines as to how the information derived from the various model simulations can be used towards ecosystem management. In this chapter, addressing key question 3d, a framework is proposed for accomplishing this (Fig. 13.1).

Although, in the past, fisheries management in the southern Benguela ecosystem has considered two or three "focus" species simultaneously (see section 13.2, Step 4), a true ecosystem approach to fisheries management has not been implemented. It is necessary to consider the impacts of fisheries on all ecosystem components, as well as the ways in which the various fisheries interact with one another. For this to be accomplished, a new approach to ecosystem management should be explored, so that potential fishing strategies can be examined simultaneously.

13.2 4-STEP PLAN TO MANAGE FISHERIES IN AN ECOSYSTEM CONTEXT

Step 1

In the *Ecopath* approach to ecosystem modelling, mixed trophic impact assessments (Chapter 3, section 3.4.1, Chapter 5, section 5.7, Chapter 11, section 11.7.4) measure the relative impacts of a change in biomass of one group on others in the ecosystem. By constructing mass-balanced *Ecopath* models of the ecosystem in question and examining the mixed trophic impacts from balanced models, step 1 establishes which groups have negligible impacts on others in the ecosystem, and which groups are likely to have large effects. Because mixed trophic impacts are estimated for a mass-balanced ecosystem in steady state, they may not necessarily reflect the actual net impacts of changing the biomass of a group when biomasses and diets fluctuate in the dynamic situation (Chapter 10, section 10.4). For example, in steady-state models of the southern Benguela ecosystem, horse mackerel compete with anchovy, sardine and

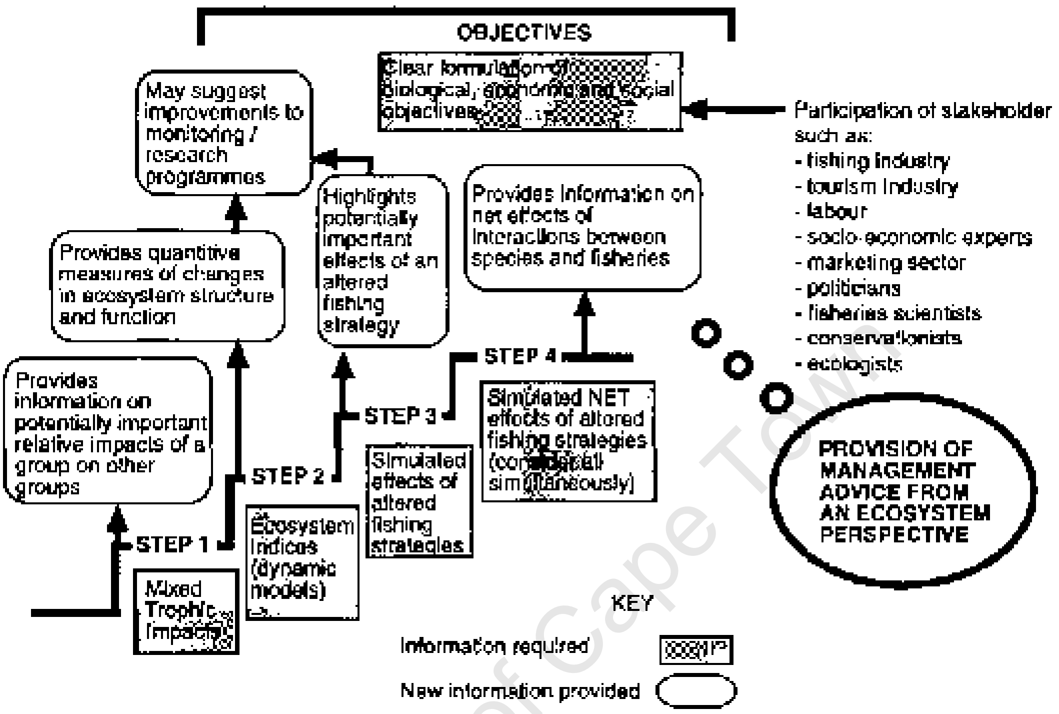


Fig. 13.1 Diagrammatic representation of proposed 4-step framework to manage fisheries in an ecosystem context.

redeye for zooplankton prey, and have negative net mixed trophic impacts on these groups (Chapter 5, Fig. 5.7). Contrary to what may be hypothesized from these results, when horse mackerel is heavily fished and its stock size is reduced, anchovy, sardine and redeye biomasses do not always increase in response to reduced competition with horse mackerel (Chapter 10, section 10.3.8). However, in many cases mixed trophic impacts and dynamic simulations agree. For example, anchovy negatively impact horse mackerel (Chapter 5, Fig. 5.7). When heavy fishing on anchovy is simulated, abundance of horse mackerel increases (Chapter 10, section 10.3.1). Therefore, step 1, to identify the mixed trophic impacts, is important because it highlights potentially important effects to be considered when exploring the ecosystem effects of altered fishing behaviour using a dynamic approach (steps 2-4).

Step 2

More than two decades ago, May *et al.* (1979) forecasted the increasing need for fisheries managers to take species interactions into account. Rose *et al.* (1996) attributed the fact that there has been little improvement of multispecies models over the years to the lack of knowledge about the underlying biological interactions being modelled. Indices quantifying species interactions could assist in advancing multispecies models and improving fisheries management.

The results of dynamic simulation models such as *Ecosim* can provide quantitative indices of interactions in ecosystems. These indices are estimated for situations when diets and biomasses of all ecosystem components fluctuate over time in response to altered fishing and altered abundances of affected groups (Chapter 11). Therefore they represent the results of dynamic as opposed to static analyses, and further advance ecosystem understanding. The indices used in this study are derived from theoretical simulations of intense overfishing on one group, causing its stock to collapse. By considering the effects of altered fishing on certain species, it is possible to derive indices that could be applied in a generic fashion across different ecosystems. For example, in this study, the index of interaction strength (Chapter 11, section 11.4) measures the relative impact of a reduction in one group on others in the ecosystem. This index could be used to determine which groups could have the strongest effects on others in the ecosystem, thus affecting ecosystem structure. In the southern

Benguela ecosystem, anchovy had the largest interaction strength in the 1980s whereas redeye was the strongest interactor in the 1990s. The functional impact indices measure the relative impacts of one functional group on its own and other functional groups, and these indices can indicate sensitivities in the functioning of the ecosystem to altered exploitation of species. In the 1980s, anchovy in the southern Benguela had large impacts on functional groups such as small pelagics, their zooplanktivorous competitors and their predators (Chapter 11, section 11.5.1). Ecosystem indices such as this may be useful to fisheries management as they suggest for which species potential fishing strategies may have impacts that are wide ranging, affecting other ecosystem components. Some of these ecosystem components may themselves be commercially important, whereas others may indirectly affect species of commercial value.

Step 3

Altered fishing scenarios do not necessarily involve overexploitation. However, the persistence of any changes in the ecosystem and the resilience of the ecosystem to perturbations caused by fishing should be investigated. Undesirable short- and long-term effects can be identified using *Ecosim*, and scientists and managers should be alerted to these possible situations. One of the advantages of ecosystem models compared to single-species approaches is that they can assist in directing research by identifying data gaps and information critically required (Christensen and Walters 2000). It might be necessary to recommend changes to sampling programmes in order to monitor changes in ecosystem structure and functioning. For example, in the southern Benguela ecosystem, redeye and mesopelagic fish are not heavily exploited and therefore their stocks are not regularly assessed or monitored. However, both groups have large ecotrophic efficiencies because they are important prey for many forage fish that are commercially important. Their heavier exploitation is likely to have consequences for species currently supporting large fisheries (e.g. Chapter 10, section 10.3.3). Foresight would suggest that a programme to monitor such stocks and their interactions with others should be initiated.

Step 4

The ecosystem effects of an altered fishing strategy should be considered in the context of all the fisheries in a system, so that the net effect can be quantified. At present in the southern Benguela ecosystem, fisheries management is based mostly on single species assessments. In some instances, a few species are managed together. For example, sardine is managed as a directed fishery on adult sardine and as a bycatch of juveniles and adults in directed fisheries on anchovy and redeye (De Oliveira *et al.* 1998a). In other cases, the ecosystem effects of fishing have been taken into account by considering the effects of an exploited species on non-exploited species, including species of conservation concern. The interactions between seals and hakes off the west coast of South Africa were modelled to examine the possible effects of seal culling on catches of hakes in demersal trawls (Punt and Butterworth 1995). A model linking anchovy and Cape Cormorants *Phalacrocorax capensis* suggested that the purse seine fishery for anchovy may have reduced the bird population off South Africa (Crawford *et al.* 1992). Increased competition between fishers, seals and seabirds for pelagic fish may have reduced the reproductive success or juvenile survival rate of African Penguins *Spheniscus demersus* (Crawford 1998). The African Penguin is a species "vulnerable" to extinction and of considerable importance to South Africa's ecotourism industry (Crawford *et al.* in prep.).

The above examples, although using multispecies considerations, are not ecosystem management approaches in the strict sense. They do not make provision for the full impact of fisheries on all ecosystem components, neither do they quantify the net effects of the various fisheries on one another. A new approach to ecosystem management is required, whereby all fishing strategies under consideration are tested simultaneously, and their net potential long-term effects are taken into account.

Caveat: clearly defined objectives

To carry out steps 3 and 4 effectively, the underlying fisheries management objectives need to be known and clearly formulated (Fig. 13.1). One example from the southern Benguela ecosystem would be how to weight the objective of maximizing catches of anchovy and sardine against conservation and ecotourism objectives for African Penguins. Another would be the relative weighting of objectives maximizing linefish and purse seine catches: in an extreme example, closure of the purse seine fishery might allow expansion of the line fishery (Chapter 10, section 10.3.4).

Additional caveat: spatial aspects

Changes in the spatial distributions of fish are often associated with changes in abundances of these species, affecting their availability to predators, particularly those with limited breeding ranges (see Chapter 2, section 2.3.2). For example, the population of African Penguins on the South African south coast declined sharply as a result of shifts in anchovy and sardine distributions and abundances between the 1980s and 1990s, reducing availability of pelagic fish to penguins in this area (Crawford 1998). Therefore, simply putting into place management approaches that ensure sufficient biomass of small pelagic fish to sustain mammalian or avian populations in an ecosystem as a whole may well be inappropriate if availability of these prey species to their predators is not also taken into account. It may be necessary to consider spatial restrictions on fishing in important feeding areas of mammals and birds, as has been implemented in the management of the Bering Sea ecosystem (Livingstone and Tjelmeland 2000). Although spatial aspects have not been dealt with in this dissertation, in the future, useful insights are likely to be obtained by means of spatial modelling approaches such as *Ecospace* (Walters *et al.* 2000), a new tool that has been incorporated into the *Ecosim* package to investigate the spatial aspects of ecosystem management. The use of GIS and purpose built spatial models is also on the increase.

13.3 DISCUSSION

13.3.1 Balancing management objectives

Incorporating ecosystem considerations into fisheries management is often problematic because management objectives are often only broadly stated (Sainsbury *et al.* 2000). Fisheries management advice should be based on a trade-off between the net benefits of social and economic implications in an ecologically sustainable set of fisheries strategies (Caddy 1999, Larkin 1996, Jennings and Kaiser 1998, Pauly 1998). Moreover, it is suggested that to maximize economic benefits, fisheries management in the future should aim towards rebuilding ecosystems to achieve species compositions and abundance levels comparable to those in the ecosystems before heavy exploitation by humans (Pitcher and Pauly 1998, Pitcher 2000). However, it is recognized that fishing inevitably reduces pristine biomass but it may be important to attempt to maintain ecosystem structure as unchanged as possible.

An important reason for the failure of fisheries management worldwide is the conflict between sustainability of fisheries and economic and social priorities (Cochrane 2000). An example of such conflict from the southern Benguela sub-system is the pelagic fishery, in which the overriding factors influencing management decisions in the past were the short-term benefits of maintaining employment and income (Cochrane *et al.* 1998). An additional consideration is the large difference between the values of anchovy and sardine. Sardine is a more valuable fish because it is directly consumed by humans, whereas anchovy is reduced to oil and meal (Shelton 1992). Commenting on the South African pelagic fishery, Barnes (1999) notes that socio-economic benefits and industrial and biological factors all need to be taken into account, but that the management procedure should be underpinned by sound scientific research and modelling.

A formal method for optimising the three objectives of sustainability, social and economic benefits is currently being incorporated into the dynamic *Ecosim* model (Christensen *et al.* 2000). An objective function is defined by weighting the social, economic and ecological objectives for fisheries in an ecosystem model, and is used as the criterion for searching for "optimal" fishing patterns over time. Using a non-linear optimisation procedure (the Davidson-Fletcher-Powell method, Press *et al.* 1992), relative fishing rates are changed in an attempt to iteratively improve the objective function. Preliminary explorative simulations (Pitcher in prep.) suggest that this approach shows much promise. The new tool will be extremely helpful to fisheries managers by highlighting potential conflicts and trade-offs between different fishing strategies favoured for different sets of objectives.

Successful fisheries management procedures need constant monitoring and revision (Cochrane 2000). This has been the case in implementing the Convention on the Conservation of Antarctic Marine Living Resources (CCAMLR). The CCAMLR management approach is based on the Precautionary Principle, and involves assessment of catch controls on single species, prediction of the effects of fishing and monitoring of the ecosystem (Constable *et al.* 2000). Constable *et al.* (2000) highlight two important lessons learnt from CCAMLR: (i) it is necessary to implement management measures even in the absence of extensive data sets and (ii) it is possible to reach scientific consensus despite uncertainties in parameter estimates and predictions of ecosystem responses. The latter is also emphasized by Cochrane (1999) and de la Mare (1998), who caution against the current belief that quantification of uncertainties and improved implementation through ever-increasing consultation are solutions to fisheries management problems. Attempting to estimate all uncertainties is impossible and may lead to further uncertainties (de la Mare 1998). Instead, de la Mare (1998) proposes that the objectives of fisheries management should be carefully formulated, and that an ecosystem should be considered as a whole.

13.3.2 Using ecosystem models for management

This chapter shows how results from ecosystem models of the southern Benguela ecosystem may be used as input to a first attempt at a practical framework through which ecosystem considerations can be incorporated into fisheries management. In the past, the main criticisms of an ecosystem management approach have been:

i) the lack of knowledge about ecosystem functioning,

ii) past failures of predicting even simple processes using single-species models, hence the concern about advancing to more complex multispecies models,

iii) the lack of suitable tools for exploring the benefits and implications of alternative management strategies, and

iv) the lack of clearly stated management objectives (Pauly 1998).

Using the example of Marine Protected Areas (MPAs) and the goal of maintaining biodiversity, Pauly (1998) countered each of these criticisms. Similarly, results from the models used in this dissertation can also assist in addressing the four concerns:

i) The trophic functioning of ecosystems can be quantified using indices (Chapter 11)

ii) Steps 1 and 3 of the proposed plan for fisheries management from an ecosystem perspective highlight the fisheries-ecosystem interactions that are potentially the most important considerations for managers

iii) In step 4, the net benefits and trade-offs of alternative fishing strategies are explored by considering all fisheries in an ecosystem simultaneously

iv) Steps 3 and 4 depend on the careful formulation of clear fisheries management objectives.

As with all models, and especially in the case of complex models in which many ecosystem components are modelled, uncertainty about the many parameter estimates should be recognized when considering formulation of fisheries management advice (Cochrane 2000).

13.3.3 Future development of a management procedure for ecosystems

The proposed 4-step framework (Fig. 13.1) could be extended further to put into place a formal management procedure (MP) for ecosystems. An MP is a set of rules, pre-agreed upon by scientists, industry and managers, for using fishery data to set annual total allowable catches (Butterworth *et al.* 1997, De Oliveira *et al.* 1998b). Selection of a suitable MP is based on Monte Carlo simulations to assess the trade-offs in the medium term, between catches or profits, risks (e.g. of collapse of a stock) and interannual variability in catches (Butterworth *et al.* 1997). Once an MP is adopted for a resource, it should be allowed to run its course for 3-5 years before being extensively reviewed and modified (Butterworth *et al.* 1998, Cochrane *et al.* 1998). This differs from conventional fishery management procedures requiring review and incorporation of updated data on an annual basis. In South Africa, MPs are in place for three fisheries: the demersal trawl fishery for hakes, the purse seine fishery targeting anchovy and sardine and the rock lobster fishery (De Oliveira *et al.* 1998b, Cochrane *et al.* 1998). It is suggested that the 4-step management plan proposed in this chapter is used as part of a Strategic Management Procedure (SMP) in which the whole southern Benguela ecosystem is considered, i.e. all fisheries, as well as resources that are important for non-consumptive exploitation, are simultaneously considered and managed. Once an ecosystem SMP is agreed upon, it should be allowed to function for 5-10 years before being reviewed and modified according to updated ecosystem models and revised management objectives.

13.4 CONCLUSION

Cochrane (2000) proposes that if eight principles were followed, fisheries management worldwide would be improved. Of relevance here is his fourth principle stating that it is not possible to optimise or maximize catches of all fisheries simultaneously; responsible fisheries management requires that unambiguous objectives are agreed upon and that all users participate and co-operate (Cochrane 2000).

It is not too soon to implement practical ecosystem management measures in the southern Benguela ecosystem. Information from models described in this dissertation can be used to follow the proposed 4-step plan given carefully defined objectives, and in this way can contribute towards a first attempt at incorporating ecosystem considerations into fisheries management. Other studies in which different modelling approaches are taken, or in which ecosystem data are collected and analysed, will feed into the process at some or all of the steps, so that the advice provided is continuously improved and updated. For example, other measured or model-derived indices could provide helpful input at step 2. Garcia and Staples (2000) discuss the value of sustainability indicators based on measured parameters or calculated from models, and which track changes or levels of resources, socio-economic aspects, environmental conditions, technological limitations or developments, management policies, fishing rights and enforcement measures.

It is imperative that objectives are carefully defined for each fishery and for each non-consumptively exploited group when undertaking step three. Further, it is essential that overall objectives for the fisheries and non-consumptive exploitation of the southern Benguela ecosystem are negotiated before undertaking step 4. It is recommended that all stakeholders should be involved in formulating and refining these management objectives (Fig 13.1). This would involve public participation through an integrated approach, as suggested by Penhorn (1999) for the South African demersal fishery, and inputs to high-level policy-making. A formal procedure by which these inputs should be considered and by which consensus would be reached in setting these management objectives should be established, aimed ultimately at advising the final decision-making body. Once there is agreement on the objectives, it is a matter of following the steps of the proposed management plan to provide fisheries management advice that accounts for ecosystem considerations based on sound objectives. This gives us hope that it will be possible to provide advice on fisheries management strategies from a true ecosystem perspective, and that this may not be as far into the distant future as has been predicted by many.

CHAPTER 14

SUMMARY AND CONCLUSIONS

In many upwelling areas, periods of anchovy and sardine abundance alternate. These "regime shifts" make the management of fisheries a tricky and complex task. It has been estimated that 60% of the world's major fisheries resources are either fully exploited ("mature") or overexploited and showing signs of declining catches (F.A.O. 1997b). Present fisheries management techniques appear to be failing. If fisheries management is to be improved, new approaches should be adopted. These should include approaches that take into account the possible net effects of potential fishing strategies on the whole ecosystem by considering ecosystem structure and function in addition to those considering the biology and dynamics of the stocks concerned. In this study, the trophic functioning of the Benguela ecosystem is explored during alternating periods of abundance of anchovy and sardine, with a view to advising on multispecies aspects of management of marine resources in the region.

Classic ecological approaches consider food chains based on trophic flows between discrete trophic levels (Lindeman 1942). These allocate species to distinct trophic levels and positions in a food chain or food web. More recently, it has been recognized that it is useful to assign species or groups to non-integer trophic levels, accommodating feeding by a species across a range of trophic levels. This is the basis of network analysis and the *Ecopath* modelling approach (e.g. Wulff *et al.* 1989, Pauly *et al.* 2000a). Using the steady-state *Ecopath* modelling approach, mass-balanced models are constructed of the trophic flows in the southern Benguela sub-system for 1980-1989 and 1990-1997 (Chapters 4 and 5) and in the northern Benguela sub-system for the 1980s (Chapter 7).

14.1 Trophic flows in the southern Benguela sub-system

In the southern Benguela sub-system, anchovy were the dominant pelagic fish in the 1980s whereas sardine abundance increased in the 1990s. There was a 10% increase in model zooplankton biomass between the 1980s and the 1990s (Chapter 4). This agrees with observed trends in zooplankton abundance off the west coast of South Africa (Verheye *et al.* 1998). It is likely that surveys underestimate the biomass of demersal fish in the southern Benguela region because many of the species occur over untrawlable grounds and are missed during surveys (Badenhorst and Smale 1991). The biomass of hakes in mass-balanced models of the southern Benguela sub-system is 34% and 22% larger than survey estimates for the 1980s and 1990s respectively (Chapter 4). The additional biomass was in the small hake classes, indicating that juvenile mortality is likely to be underestimated in production models, as might be expected (R.W. Leslie, MCM, pers. comm.).

Model biomass and mean annual production of small pelagic fish are larger and total catches are smaller in the 1990s than in the 1980s. Mean transfer efficiency for trophic levels II-VIII is estimated to be 12% in the southern Benguela sub-system (Chapter 5), greater than the mean of about 5% estimated for other upwelling systems (Jarre-Teichmann and Christensen 1998a). Primary production required (PPR) to sustain catches in the southern Benguela ecosystem was estimated to have been 4.39% of the total primary production in the 1980s and 4.47% in the 1990s. These estimates are more similar to those for open ocean and coastal regions (Pauly and Christensen 1995) than the mean of 9.5% estimated by Jarre-Teichmann and Christensen (1998a) for seven other upwelling systems.

14.2 Indices quantifying species interactions

Using dynamic simulation models of the southern Benguela sub-system, indices are developed to quantify theoretical concepts of species interactions in ecosystems (Chapter 11). Indices of interaction strength, functional impact and trophic similarity are developed and explored. These indices are a useful starting point for the further development of indices of ecosystem change and trophic functioning, so that potential outcomes of hypothetical management options can be quantitatively assessed.

The index of interaction strength measures the relative impact of a collapse of one stock on the biomass of all other groups in the model ecosystem. For models of the southern Benguela sub-system, the index shows that hake are strong interactors and that, of the small pelagic fish groups, anchovy were the strongest interactors in the 1980s and redeye in the 1990s. The index is comparable across systems, provided that the aggregation of species into groups is comparable. The trophic similarity index quantifies the extent to which density compensation occurs amongst trophically-similar species following a collapse of, or increase in a target stock. Trophic similarity indices for anchovy and sardine explain the strong similarities in trophic functioning of the southern Benguela ecosystem in the anchovy-dominated system of the 1980s, and the 1990s when there was a shift towards greater sardine abundance. The functional impact index shows that in the southern Benguela ecosystem, anchovy have the largest trophic impacts on the small pelagic fish functional group, whereas redeye have the largest impacts on functional groups containing competitors (other zooplanktivorous fish) and predators of small pelagic fish.

14.3 Comparing the trophic functioning of the southern Benguela sub-system during two different decades

Comparing steady-state model outputs such as biomass per trophic level, transfer efficiencies, mixed trophic impacts and whole system properties suggests that trophic functioning of the southern Benguela ecosystem was similar in the 1980s and 1990s (Chapter 5). Further, the trophic similarity index for anchovy and sardine, derived from dynamic model simulations, also underlines the strong similarities in trophic functioning of the southern Benguela ecosystem in the 1980s and 1990s (Chapter 11). However, considering ecosystem-level attributes of an extension of E.P. Odum's ecosystem development theory (Odum 1969) suggests that the southern Benguela sub-system was more mature in the 1990s than in the 1980s (Chapter 5); total primary production/total respiration, net system production, total primary production/total biomass, residence time and relative ascendancy were all smaller in the 1990s model, and flows to/from detritus, connectance and total respiration/total biomass were larger in the 1990s than in the 1980s. Because catches were lower and model zooplankton and small pelagic fish biomasses were larger in the 1990s, the ecosystem was less tightly constrained by predators (including fishers) and food availability than in the 1980s. Sensitivity analyses (Chapter 6) further underline the fact that the southern

Benguela sub-system is tightly constrained; exploring variability about mean parameter estimates used in the models shows that there are limited combinations of parameter values within the best estimated ranges that give balanced models for the southern Benguela sub-system. Further, total mean biomasses in alternative models are similar to those in original models based on best estimates of input parameters.

Alternating periods of abundance of sardine and anchovy in many upwelling regions have been well documented, yet the mechanisms responsible for initiating, sustaining and terminating sudden increases in population sizes on a decadal time-scale are still poorly understood (Lluch-Belda *et al.* 1989, Lluch-Belda *et al. 1992a*, Lluch-Belda *et al.* 1992b, Schwartzlose *et al.* 1999). Two ways in which "regime shifts" may operate in the southern Benguela sub-system are considered: fishing and prey availability (Chapter 12). Dynamic simulations suggest that it is unlikely that observed changes in pelagic fish catches between the 1980s and 1990s played a large role in driving the changes in abundance of anchovy and sardine in the southern Benguela sub-system. It is hypothesized that changed environmental conditions may have influenced the size composition of planktonic food of anchovy and sardine, thus changing their relative abundance, with some signs of a "regime shift' from anchovy to sardine dominance. In particular, it is suggested that the mechanism operates via the trophic link between mesozooplankton and anchovy and sardine. Sardine filter-feed efficiently on smaller planktonic organisms, whereas anchovy do better in "biting" mode on larger mesozooplankton (van der Lingen and Hutchings in prep.).

14.4 Modelling effects of altered fishing strategies in the southern Benguela ecosystem

Dynamic simulation models are used to explore the possible effects of alternative fishing strategies in the Benguela sub-system (Chapters 9 and 10). Potential effects of altered fishing are larger in 1980s simulations than in those of the 1990s because the model ecosystem is more tightly constrained in the 1980s. Simulations of the potential effects of altered fishing strategies depend on assumptions upon which the models are based, particularly the period for which input data are averaged. When considering alternative fishing strategies, results often contradict those hypothesized, highlighting the importance of taking into account direct and indirect ecosystem interactions and the way in which they change over time. For example, it was hypothesized that heavier fishing on large hakes would be favourable for small hakes because the heavy "cannibalism" of small hakes would be reduced. However, these simulations show that in the southern Benguela sub-system, biomasses of small hakes are reduced by 10-45% when heavier fishing on adult hakes is modelled over 50 years.

Anchovy catches appear to have been optimal during the 1980s because even a modelled increase in anchovy catches of as little as 10% causes a decline of more than 20% in modelled anchovy catches over 50 years, and a 15% decrease in modelled snoek catches. Larger sardine catches are unlikely to have been sustainable during the 1990s because simulations show that catches of sardine and total catches are reduced when fishing pressure on sardine is increased. Simulations suggest that if the demersal trawl fishery were to be expanded, decreases of more than 40% in hake stocks would be expected, although catches of other species in demersal trawls would increase and it may be possible to expand the purse seine fishery. The modelled decline in hake stocks under this management option is in agreement with production models that suggest that hakes off South Africa are close to their optimal level of exploitation (Punt 1994).

Trade-offs between fisheries would be required if larger catches in some fisheries are to be sustained. To assess the benefits of alternative fisheries management strategies, socio-economic benefits and constraints would need careful consideration in relation to the likely ecosystem effects, and clearly defined management objectives would be required.

14.5 Assumptions of top-down versus bottom-up control of trophic flows in ecosystems

Upwelling systems are considered to be "wasp-waist" systems because there are few small pelagic fish species but they are abundant, preyed on by many species of large pelagic fish, seabirds and mammals, and prey on many species of zooplankton, hence the narrow waist in terms of biodiversity of the trophic guild (Rice 1995, Bakun

1996). Variation in population size of small pelagic fish may have major effects on both the predators and prey of this group (Rice 1995), so that control is neither top-down nor bottom-up, but rather from the "waist", up and down (Bakun 1996). This concept is explored in the light of ecosystem effects of fishing when different types of flow control are assumed (Chapter 9).

Large differences are found between the effects of altered fishing simulated under different scenarios of top-down and bottom-up control. Bottom-up control of zooplanktivorous fish by their zooplankton prey dampens effects of altered fishing. Wasp-waist control (top-down control of zooplankton by their predators and bottom-up control of predators by small pelagic fish) causes vigorous effects to propagate through the ecosystem. In some cases, fishing strategies that appear to be sustainable if bottom-up flow control is assumed cause fisheries collapses if wasp-waist control is assumed. For example, when bottom-up flow control is assumed and heavier fishing on small pelagic fish is modelled, anchovy catches are sustainable at about double those in the 1980s. However, the anchovy fishery collapses when control is mixed or wasp-waisted. It is likely that of the three flow control types modelled, the wasp-waist scenario represents best the flow of matter between components of the southern Benguela ecosystem.

14.6 Comparing trophic models of the southern and northern Benguela sub-systems

During the 1980s, estimates of total biomass (excluding detritus) and annual catches were smaller in the southern Benguela sub-system (297 $t.km^{-2}$ and 3 $t.km^{-2}.y^{-1}$ respectively) than in the northern Benguela sub-system (360 $t.km^{-2}$ and 7 $t.km^{-2}.y^{-1}$ respectively). All other major trophic flows were larger in the southern Benguela sub-system (Chapter 8). The proportion of primary production transferred from trophic level I to II is close to 42% in the southern Benguela sub-system and more than twice this (88%) in the northern Benguela sub-system, indicating that the Namibian ecosystem relies more heavily on phytoplankton and emphasizing the greater importance of herbivory in the north than in the south. However, the transfer efficiency at trophic level III is 12.3% in the north compared to almost double this (22.1%) in the south. Top predators are important components in the southern

Benguela sub-system, requiring twice the primary production of the north to support modelled consumption by top predators. Mesopelagic fish, redeye (in the southern Benguela sub-system) and pelagic goby (in the northern Benguela sub-system) are of little commercial value but are important prey species in the Benguela ecosystem. Therefore caution should be exercised when considering heavier exploitation of these groups, as there may be ripple effects at the ecosystem level.

Because there are structural and functional differences between the northern and southern Benguela sub-systems, hypothetical fishing strategies have very different effects in the two sub-systems, related to the complex and different responses to indirect and direct competition. For example, because hake and horse mackerel interact more strongly in the southern Benguela sub-system, heavier fishing on hake has a larger negative impact on modelled horse mackerel biomass in the south than in the northern Benguela ecosystem. Similarly, heavier exploitation of small pelagic fish has larger negative effects on large pelagic fish in the southern Benguela sub-system than in the north.

14.7 What has this study achieved?

This study is the first to use both steady-state and dynamic ecosystem models to quantify trophic flows in the Benguela upwelling system. It is the first time that a comparison is made between the trophic structure and functioning of the two Benguela sub-systems: the northern and southern sub-systems. Further, it is the first time that the trophic functioning of the southern Benguela sub-system has been compared across different decades or regimes. To date, ecosystem considerations have not been formally incorporated into fisheries management in the Benguela region. A new framework for approaching fisheries management is proposed in the form of a 4-step plan (Chapter 13): (1) mixed trophic impact assessment using steady-state ecosystem models shows which interactions may be important in an ecosystem, (2) indices of ecosystem interactions provide quantitative estimates of the possible ecosystem impacts of heavy fishing, (3) dynamic simulations suggest some possible short- and long-term ecosystem effects of altered fishing strategies, (4) the net ecosystem effects of all revised fishing strategies need to be considered simultaneously. Both steady-state and dynamic ecosystem models are sources of information with great potential to be incorporated into an ecosystem-based fisheries management approach such as this. Additional information that should feed into the proposed ecosystem management approach would be derived from alternative modelling or field studies. For example, it would be useful to develop models that consider potential ecosystem effects other than those related to trophic interactions. One aspect would be advice based on modelling the impacts of disturbance on seabirds through ecotourism (Shannon *et al.* in prep.). There is much scope for incorporating advice from many such studies into the proposed management plan at one or more of the four steps.

Multispecies approaches to fisheries management should not assume the place of single-species approaches. Instead, they should be viewed as complementary, so that each approach is valued as one in a "toolbox" of models used to manage a particular renewable resource (Starfield *et al.* 1988, Crawford *et al.* 1989, Whipple *et al.* 2000). Multispecies models can build on and improve the results of single-species models and also provide input to single species models. It has been shown that multispecies approaches yield very different long-term management advice from traditional single species models (Magnusson 1995, Stokes 1992), but that in the short term the advice is sometimes similar (Christensen 1996b). Murawski (1991) notes that conflict between management strategies for single species results from the absence of any formal process whereby the feasibility of simultaneously attaining the goals of various single-species approaches is evaluated. This is where a multispecies or ecosystem approach is applicable and useful. However, for an ecosystem approach to fisheries management to function, the overall objective for fisheries management in the region, the objectives for each fishery, and the non-consumptive objectives for the region need to be clearly stated because all will play major roles in the advice provided in an ecosystem context.

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APPENDIX A

INPUT DATA FOR MODELS OF THE SOUTHERN BENGUELA ECOSYSTEM DURING THE 1980S AND 1990S

Tables A.1-A.9 contain input data and their sources for each group used in the *Ecopath* models of the southern Benguela ecosystem. Where the value used differs from the original source value, the revised value is given and comments included. Biomass (B) is wet mass (t) unless specified (as in some of the plankton groups, where there is some discrepancy converting from carbon). P is annual production ($t.y^{-1}$), Q is annual consumption ($t.y^{-1}$) and U is the percentage of Q that is not assimilated. P, Q and U are wet mass terms.

Table A.1 PLANKTON: Input data for southern Benguela *Ecopath* models.

Parameter	Original Value	Source	Value used	Comments
PHYTOPLANKTON				
B	$1.2X10^6$ t C	Brown *et al.* 1991; used conversion factor of 14.25 for C:wet mass		
P/B	$133.3\ y^{-1}$		$154.4\ y^{-1}$	Primary production in Brown *et al.* (1991) increased by 18% to account for particulate dissolved organic C (1989 workshop).
Sediment-ation	$368.4\ t.km^{-2}.y^{-1}$	Pitcher *et al.* 1991		Sedimentation estimated to be 3.7% of daily production (Pitcher *et al.* 1991).
MICROZOOPLANKTON (2-200μm equivalent spherical diameter: nanoflagellates, ciliates, zooplankton larvae)				
B	$5.525\ t.km^{-2}$	Jarre-Teichmann *et al.* 1998, from Brown *et al.* (1991) and Painting *et al.* (1992); used conversion factor of 14.25 for C:wet mass	Estimated	Using *Ecopath*, estimated B required in 80s and 90s.
P/B	$482y^{-1}$			
P/Q	20%	Calculated from U and respiration/Q in Painting *et al.* 1992	25%	Jarre-Teichmann *et al.* 1998
U	20%	Stoecker 1984		
MESOZOOPLANKTON (200-2 000μm; copepods, in particular *Calanoides carinatus* and *Calanus agulhensis*)				
B	187 600 t C	Hutchings *et al.* 1991	Estimated	Using *Ecopath*, estimated B required during each decade.
P/B	$20\ y^{-1}$		$40\ y^{-1}$	P/Bs estimated from Verheye *et al.* (1992) were larger, between $30\ y^{-1}$ and $91\ y^{-1}$.
P/Q	30%	Omori and Ikeda 1984		
U	35%	Verheye *et al.* 1992; Probyn *et al.* 1990, Probyn 1992; H. Verheye, MCM, pers. comm.		11%-50% of food consumed by South African copepods is egested as faecal pellets. As in Jarre-Teichmann *et al.* (1998), U was estimated to be 35%.
MACROZOOPLANKTON 2-20 mm; mainly euphausiids (on which most of the macrozooplankton estimates are based), but also includes groups such as amphipods and fish larvae				
B	63 600 t C	Hutchings *et al.* 1991	Estimated	Using *Ecopath*, estimated B required during each decade.
P/B	$13\ y^{-1}$			
P/Q	41%			
U	35%	Jarre-Teichmann *et al.* 1998	20%	Assimilation efficiency of euphausiids is closer to 80% H. Verheye, MCM, pers. comm.
GELATINOUS ZOOPLANKTON Cnidaria, Ctenphora, tunicates, chaetognaths				
B	$55X10^6$ t	A.J. Boyd, MCM, pers. comm.	10^6 t	Biomass more likely in the range of 10-50% of combined meso- and macro-zooplankton biomass (L. Hutchings, MCM, pers. comm.).
P/B	$0.584\ y^{-1}$	Jarre-Teichmann *et al.* 1998		
P/Q	35%	H. Verheye, MCM, pers. comm.		This is from gross efficiency of chaetognaths and siphonophores.
U	20%	Purcell 1983		This is from assimilation efficiency of siphonophores.

Table A.2. SMALL PELAGIC FISH: Input data for southern Benguela *Ecopath* models.

Parameter	Original Value	Source	Value used	Comments
CAPE ANCHOVY (*ENGRAULIS CAPENSIS*)				
B	1 106 000 t	Armstrong *et al.* 1991	1 147 500 t 786 143 t	1984-1989 acoustic estimate, Barange 1997. 1990-1996 acoustic estimate, Barange 1997.
P/B	1.2 y^{-1}	Hewitson and Cruickshank 1993		Data for northern Benguela, agrees with South African estimate (J. De Oliveira, MCM, pers. comm.)
Q/B	12.3 y^{-1}	Armstrong *et al.* 1991		
SARDINE (*SARDINOPS SAGAX*)				
B	146 000 t	Armstrong *et al.* 1991	129 000 t 460 000 t	1984-1989 acoustic estimate, Barange 1997. 1990-1996 acoustic estimate, Barange 1997.
P/B	1.1 y^{-1}	Hewitson and Cruickshank 1993, Northern Benguela	1.2 y^{-1}	From P/B=Z=F+M, P/B of South African sardine estimated to be 1.2 y^{-1} (1980s) and 1.0 y^{-1} (1990s). However, to account for larger increase in B in 1990s (Barange 1997), P/B was assumed equivalent in both decades, i.e. 1.2 y^{-1}.
P/Q	9.7%	Armstrong *et al.* 1991		Q/B lies within the range estimated from van der Lingen's (1998) daily rations for sardine.
REDEYE (ROUND HERRING; *ETRUMEUS WHITEHEADI*)				
B 1980s	1 222 000 t	Roel and Armstrong 1991		Minimum estimate from acoustic surveys (1986, 1987,1989). Likely that redeye B was larger, particularly in 1990s (L. Hutchings and C. van der Lingen, MCM, pers. comm.). Therefore allowed *Ecopath* to estimate B required in 1990s.
B 1990s			Estimated	
P/B	1.2 y^{-1}			Assumed similar to P/Bs of anchovy and sardine.
P/Q	10%			Assumed similar to other clupeoids (Jarre-Teichmann *et al.* 1998).
OTHER SMALL PELAGIC FISH SAURY (*SCOMBERESOX SAURUS*), FLYING FISH (Exocoetidae), PELAGIC GOBY (*SUFFLOGOBIUS BIBARBATUS*)				
B	80 000 t	1989 Workshop		B assumed constant in 1980s and 1990s.
P/B	0.9 y^{-1}		1.0 y^{-1}	Assumed closer to P/B of anchovy, sardine and redeye.
P/Q	10%			Assumed similar to other clupeoids (Jarre-Teichmann *et al.* 1998).

Table A.3. HORSE AND CHUB MACKEREL: Input data for southern Benguela *Ecopath* models.

Parameter	Original Value	Source	Value used	Comments
SMALL (<20 cm) HORSE MACKEREL (*TRACHURUS TRACHURUS CAPENSIS*)				
B 1980s B 1990s	44 000 t 106 560 t	See explanation section 3.2.3.		
P/B	1.2 y^{-1}			Assumed similar to P/Bs of anchovy and sardine.
Q/B	12 y^{-1}			Assumed similar to Q/Bs of anchovy and sardine.
U	35%			Juveniles are zooplanktivorous.
LARGE (>20 cm) HORSE MACKEREL (*TRACHURUS TRACHURUS CAPENSIS*)				
B 1980s B 1990s	356 000 t 426 240 t	1980s: B on south coast (1975-1983) estimated from Kinloch *et al.*'s (1986) VPA analysis and Kerstan and Leslie's (1994) length-mass relation. 1990s: Based on Barange *et al.* (1998).		B on west coast is five times smaller than on south coast (Barange *et al.* 1998).
P/B	0.52 y^{-1}	Jarre-Teichmann *et al.* 1998	1.0 y^{-1}	Calculated from larger Q/B with P/Q at 10%.
Q/B	5.1 y^{-1}		10 y^{-1}	Q/B larger from daily rations in Pillar and Barange (1998).
U	30%			Large horse mackerel eat zooplankton and fish.
CHUB MACKEREL (*SCOMBER JAPONICUS*)				
B 1980s B 1990s	62 500 t 100 000 t	Crawford 1989, Crawford *et al.* 1983, Jarre-Teichmann *et al.* 1998		B in 1990s estimated to be that prior to heavy exploitation in the 1970s, i.e. that in Crawford 1989.
P/B 1980s P/B 1990s	0.6 y^{-1} 0.5 y^{-1}	Assuming fish were smaller in 1980s after collapse of stock P/B assumed similar to other predatory fish (snoek)	0.9 y^{-1} 0.8 y^{-1}	P/B=0.89 y^{-1} used off North West Africa (Jarre, DFU, pers. comm. based on F= 0.49 and M=0.4y^{-1}). If P/Q=10%, Q/B likely exceeds 5-6 y^{-1} considering daily ration (Hatanaka *et al.* 1957, in Livingston and Goiney 1984).
P/Q	10%	Assumed		
U 1980s U 1990s	25% 20%			Heavy exploitation left more small, zooplanktivorous fish in 1980s, whereas by 1990s fish were larger (piscivorous).

Table A.4 OTHER LARGE PELAGIC FISH: Input data for southern Benguela *Ecopath* models.

Parameter	Original Value	Source	Value used	Comments
SNOEK (*THYRSITES ATUN*)				
B 1980s	52 700 t	Penney *et al.* 1991a	52 700 t	Similar estimate for 20% exploitation rate (L. Hutchings, MCM, pers. comm.). Larger catches in 1990s, reflect increased B? *Ecopath* estimated B required in 1990s.
B 1990s	?		Estimated	
P/B	0.5 y^{-1}			P/B=Z=F+M, where M assumed same as chub mackerel (O. Centurier-Harris, formerly MCM, unpublished data) and barracuda (Opitz 1991). F calculated from catches.
P/Q	10%			Assumption.
U	20%			Following Winberg 1956, snoek assumed to be efficient predators.
OTHER LARGE PELAGIC FISH				
B	28 775 t	Penney *et al.* 1991a		No indication of change in B in 1990s, B constancy assumed.
Group P/B	0.48 y^{-1}			Combined P/B calculated by weighting according to relative Bs. Geelbek P/B estimated from Z=F+M using Griffiths (1995) and Griffiths and Hecht (1995). Tuna P/B estimated from M using Pauly (1980) and Laurs and Wetherall (1981) and F using Penney *et al.* 1991a.
Kob	0.36 y^{-1}	Penney *et al.* 1991a		
Yellowtail	0.53 y^{-1}	Penney *et al.* 1991a		
Geelbek	0.88 y^{-1}			
Tuna	0.47 y^{-1}			
P/Q	5.6 y^{-1}			Considered P/Q=5% for tuna, 10% for others. Tuna P/Q corresponds to Q/B within Palomares and Pauly's (1998) estimated range.
U	20%			Large pelagic fish assumed efficient predators.

Table A.5 CEPHALOPODS AND MESOPELAGIC FISH: Input data for southern Benguela *Ecopath* models.

Parameter	Original Value	Source	Value Used	Comments
		CEPHALOPODS		
B	40 000 t	1989 Workshop	300 000 t	Maximum B index for chokka squid is 100 000t (Lipinski 1992). B of cephalopods assumed to be three times B of chokka alone.
P/B	1.5 y^{-1}	Jarre-Teichmann *et al.* 1998	3.5 y^{-1}	Larger P/B required to obtain P of 1 million t estimated by Bergh *et al.* (1985). Their P is an order of magnitude larger than if P/B=1.5 y^{-1}
P/Q	10%		35%	At lower limit of range estimated by O'Dor *et al.* (1980, in Livingston and Goiney 1984).
U	20%			
		MESOPELAGIC FISH (LANTERNFISH *LAMPANYCTODES HECTORIS* AND LIGHTFISH *MAUROLICUS MUELLERI*)		
B	1 – 2.4 x10^6 t	Armstrong and Prosch 1991, Armstrong *et al.* 1991	Estimated	*Ecopath* used to estimate actual B required in each decade (fell within indicated range)
P/B	1.2 y^{-1}	Hewitson and Cruickshank 1993		
P/Q	10%			Assumed similar to P/Q of anchovy
U	35%			Assumed same as U of other zooplanktivorous fish

Table A.6. HAKE: input data for southern Benguela *Ecopath* models.

Parameter	Original Value	Source	Value used	Comments
SMALL *MERLUCCIUS CAPENSIS*				
B 1980s	65 457 t	See explanation in section 3.2.4.	Estimated	*Ecopath* used to estimate B required in both decades
B 1990s	73 752 t		Estimated	
P/B	1.2 y^{-1}	Jarre-Teichmann *et al.* 1998, similar to small pelagic fish	2.0 y^{-1}	Bergh *et al.* (1985) estimated hake P/B= 4.8y^{-1} given rapid turnover of small hake. P/B increased for *Ecopath* model.
P/Q	15%	Jarre-Teichmann *et al.* 1998		
U	35%			Assumed similar to other zooplanktivorous fish
LARGE *M. CAPENSIS*				
B 1980s	181 036 t	See explanation in section 3.2.4.		
B 1990s	247 909 t			
P/B	0.6 y^{-1}	Jarre-Teichmann *et al.* 1998	0.8 y^{-1}	P/B and P/Q adjusted so that Q/B=4.4 y^{-1}, estimated from daily ration of large *M. capensis* in Punt and Leslie 1995
P/Q	25%		18%	
U	20%			Assumed similar to other predatory fish
SMALL *M. PARADOXUS*				
B 1980s	226 866 t	See explanation in section 3.2.4.	Estimated	*Ecopath* used to estimate B required in both decades
B 1990s	290 249 t		Estimated	
P/B	1.2 y^{-1}	Jarre-Teichmann *et al.* 1998, similar to small pelagic fish	2.0 y^{-1}	Bergh *et al.* (1985) estimated hake P/B= 4.8y^{-1} given rapid turnover of small hake. P/B increased for *Ecopath* model.
P/Q	15%	Jarre-Teichmann *et al.* 1998		
U	35%			Assumed similar to other zooplanktivorous fish
LARGE *M. PARADOXUS*				
B 1980s	150 553 t	See explanation in section 3.2.4.		
B 1990s	234 646 t			
P/B	0.6 y^{-1}	Jarre-Teichmann *et al.* 1998	0.8 y^{-1}	P/B and P/Q adjusted so that Q/B=4.7 y^{-1}, estimated from daily ration of large *M. paradoxus* in Punt and Leslie 1995
P/Q	25%		17%	
U	20%			Assumed similar to other predatory fish

Table A.7. OTHER DEMERSAL FISH AND CHONDRICHTHYANS: input data for southern Benguela *Ecopath* models.

Parameter	Original Value	Source	Value used	Comments
		PELAGIC- AND BENTHIC-FEEDING DEMERSAL FISH (P/B, P/Q and U are assumed to be the same for both groups)		
B	230 000t for all demersals	Japp *et al.* 1994, 1989 workshop	Estimated	Using *Ecopath*, B of each group estimated each decade.
P/B	1.0 y^{-1}	Jarre-Teichmann *et al.* 1998		P/B estimated for Q/B=5 y^{-1}, in middle of range estimated by Palomares and Pauly (1988) for flatfish, and double that for more sedentary kingklip (MacPherson 1983).
P/Q	20%			Assumed similar to large hake; within range estimated for flatfish (Livingstone and Goiney 1984).
U	20%			Assumed similar to large hake.
		PELAGIC-FEEDING CHONDRICHTHYANS		
B	128 000 t			Chondrichthyan B estimated to be 330 000 t (Jarre-Teichmann et al. 1998). Pelagic-feeders estimated to comprise 40% of B excluding apex predators.
P/B	0.5 y^{-1}			Assumed similar to other large pelagic fish.
Q/B	4.5 y^{-1}			Similar to Q/B for dogfish (Livingstone and Goiney 1984) and sandbar shark (Stillwell and Kohler 1993).
U	20%			Assumed similar to other predatory fish and carnivores.
		BENTHIC-FEEDING CHONDRICHTHYANS		
B	192 000 t			Estimated to comprise 60% of B excluding apex predators.
P/B	1.0 y^{-1}			Assumed similar to P/B of demersal fish.
P/Q	10%			Assumption.
U	20%			Assumed similar to other predatory fish and carnivores.
		APEX PREDATORY CHONDRICHTHYANS		
B	10 000 t			Assumed to comprise 3% of total chondrichthyan B.
P/B	0.5 y^{-1}			From Z of great white sharks off South Africa (Cliff *et al.* 1996).
P/Q	10%			Assumption.
U	20%			Assumed similar to other predatory fish and carnivores.

Table A.8. MARINE MAMMALS AND BIRDS: input data for southern Benguela *Ecopath* models.

Parameter	Original Value	Source	Value used	Comments
SEALS (*ARCTOCEPHALUS PUSILLUS PUSILLUS*)				
B	29 180 t	1989 Workshop		Counts of pups from 1971 to mid-1990s do not show overall increase in seals off South Africa, therefore B assumed constant.
P/B	0.946 y^{-1}			
Q/B	19.3 y^{-1}			Estimated from Balmelli and Wickens' (1994) Q estimate, Butterworth *et al.*'s (1988) mean weight and Wickens *et al.*'s (1992b) abundance estimate.
U	20%			Furness (1984) for carnivorous mammals.
CETACEANS				
B 1980s	16 200 t	B of Bryde's whales estimated from Best and Rickett (1984).		B of other trophically important cetaceans probably doesn't exceed B of Bryde's whales.
B 1990s	18 000 t			Assuming 1% annual increase.
P/B	0.6 y^{-1}	1989 Workshop		
Q/B	7.5–10 y^{-1}	Jarre-Teichmann *et al.* 1998	10 y^{-1}	From daily rations of bottlenose and humpback dolphins (Smale *et al.* 1994) and Bryde's whales (Best and Rickett 1984). Within Tamura and Ohsumi 's (2000) range for cetaceans in the Southern Hemisphere.
U	21%	Gaskin 1982		
SEABIRDS				
B 1980s B 1990s	3 257 t 2 616 t	Crawford *et al.* 1991		1990s B estimated from unpublished data, MCM; Crawford *et al.* 1991, 1995, 1999.
P/B	0.123 y^{-1}			
Q/B	118 y^{-1}			
U	26%			

Table A.9. BENTHOS: input data for southern Benguela *Ecopath* models.

Parameter	Original Value	Source	Value used	Comments
		BENTHIC PRODUCERS		
B	?		Estimated	Using *Ecopath*, required B estimated for each decade; EE assumed 50% because benthic producers often consumed as decaying matter, modelled as detritus.
P/B	15.0 y^{-1}	Jarre-Teichmann *et al.* 1998		
		MEIOBENTHOS		
B	?		Estimated	Using *Ecopath*, required B estimated for each decade.
P/B	4.0 y^{-1}	Jarre-Teichmann *et al.* 1998		
P/Q	12%			
U	20%		10%	Assimilation efficiency of benthic consumers is high (H. Verheye MCM, pers. comm.)
		MACROBENTHOS		
B	?		Estimated	Using *Ecopath*, required B estimated for each decade.
P/B	1.2 y^{-1}	Jarre-Teichmann *et al.* 1998		
P/Q	12%			
U	20%		10%	Assimilation efficiency of benthic consumers is high (H. Verheye MCM, pers. comm.)

APPENDIX B

DISTRIBUTIONS OF BIOMASS FOR WHICH SOUTHERN BENGUELA MODELS ARE BALANCED

Using *Ecoranger*, distributions of biomass estimates are generated for which models of the southern Benguela ecosystem during the 1980s and 1990s are balanced. Pertinent distributions discussed in Chapter 6 are plotted (Figs B1-B12). "Acceptable" models are those for which the combination of parameter values satisfies the following criteria: ecotrophic efficiencies (EEs) for all groups do not exceed 1.0, values for output model parameters are within user-defined ranges (Chapter 6, Table 6.2) and P/Q ratios do not exceed 60%. In each case, the frequency of the 54 "acceptable" models for the 1980s, and 129 "acceptable" models of the 1990s, falling into each decile of the biomass range is shown. Actual ranges are not depicted because they differ between decades and would prevent simple inter-decadal comparisons of the distributions.

Figures compare the distribution of biomass estimates of selected groups in balanced models of the southern Benguela ecosystem during the 1980s and 1990s.

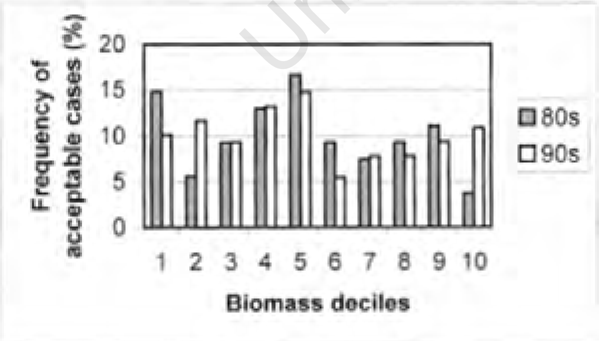

Fig. B1 Phytoplankton

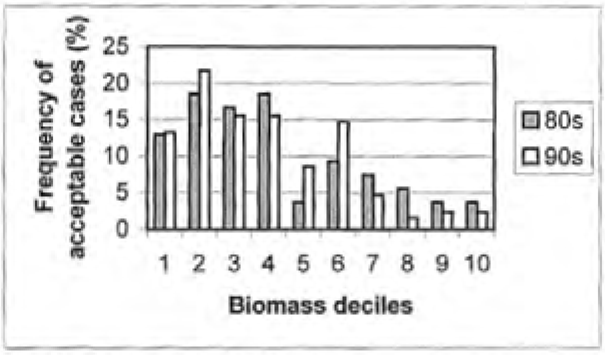

Fig. B2 Microzooplankton

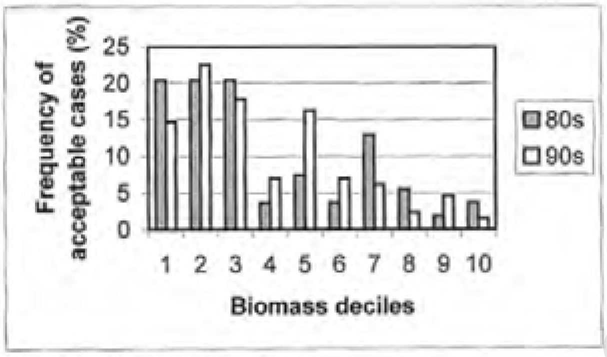

Fig. B3 Mesozooplankton

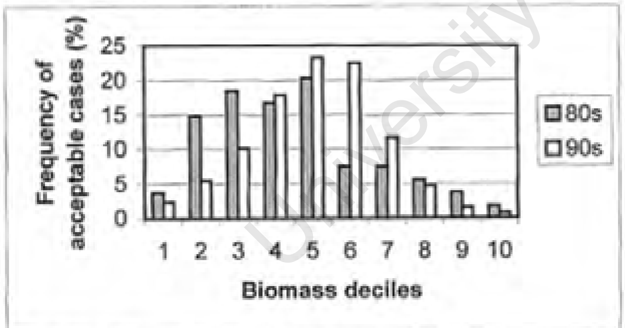

Fig. B4 Macrozooplankton

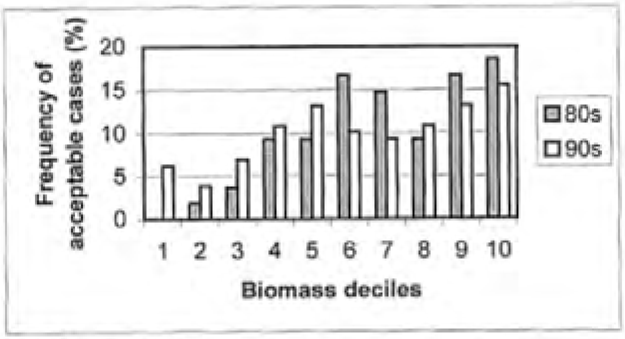

Fig. B5 Anchovy

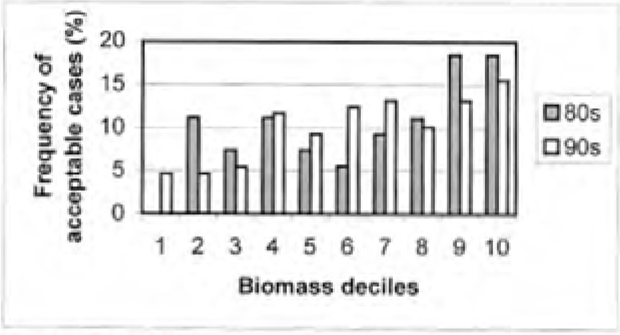

Fig. B6 Sardine

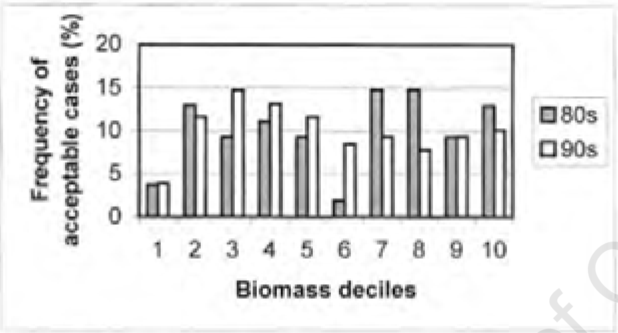

Fig. B7 Redeye

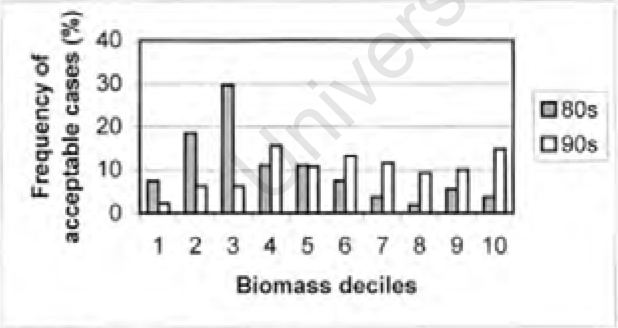

Fig. B8 Mesopelagic fish

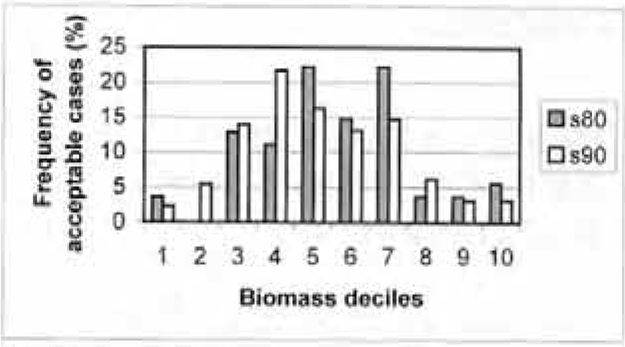

Fig. B9 Small *Merluccius capensis*

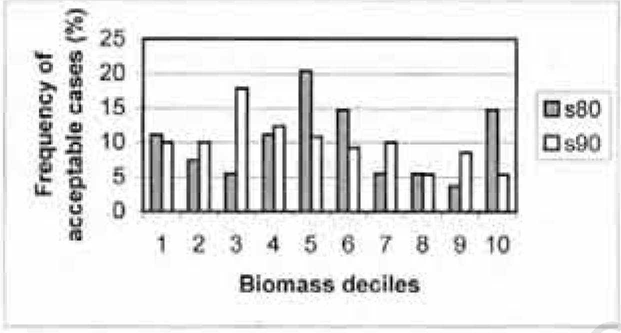

Fig. B10 Large *M. capensis*

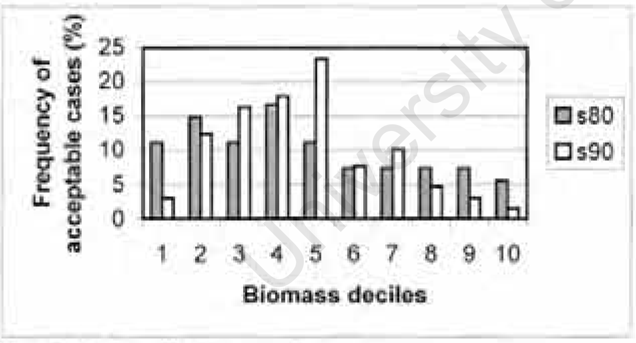

Fig. B11 Small *M. paradoxus*

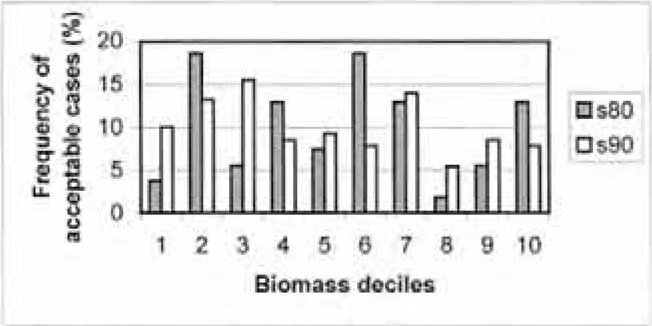

Fig. B12 Large *M. paradoxus*

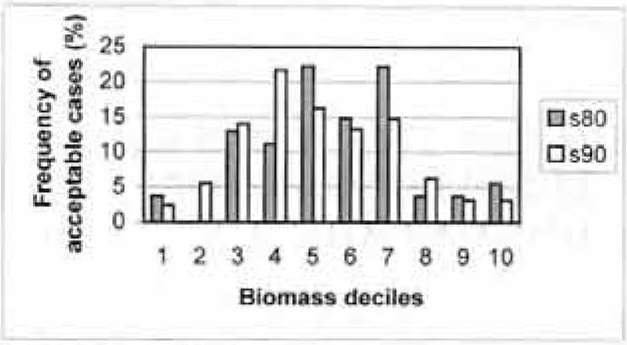

Fig. B9 Small *Merluccius capensis*

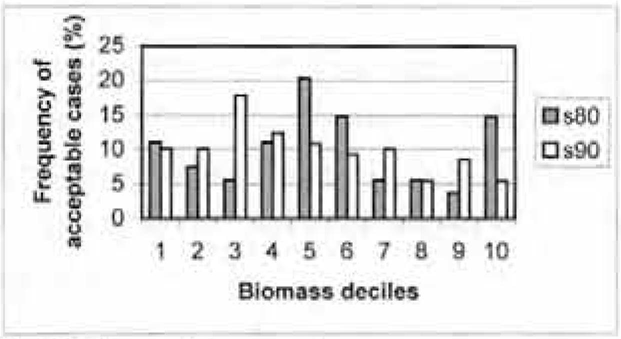

Fig. B10 Large *M. capensis*

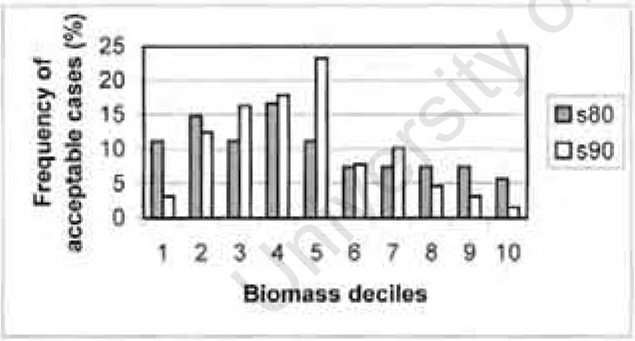

Fig. B11 Small *M. paradoxus*

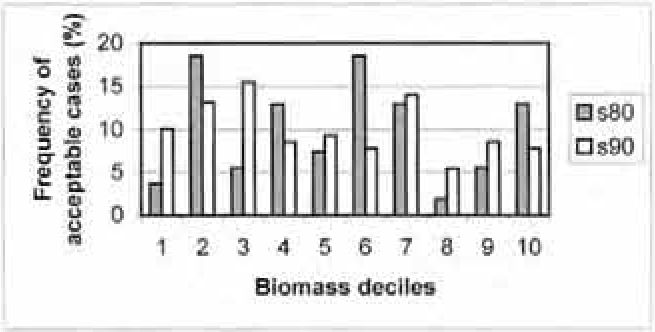

Fig. B12 Large *M. paradoxus*

APPENDIX C

INPUT DATA FOR MODEL OF THE NORTHERN BENGUELA ECOSYSTEM DURING THE 1980S

Tables C.1-C.8 contain input data and their sources for each group used in the *Ecopath* models. Where the value used differs from the original value, the revised value is given and comments included. B is biomass (t), P is annual production ($t.y^{-1}$), Q is annual consumption ($t.y^{-1}$) and U is the percentage of Q that is not assimilated. Unless otherwise stated, parameter values are presented in tons wet mass. Where biomass, production or consumption values were given in carbon equivalents in the literature, a conversion factor of 14.25 was used. This value lies between the upper (17.2) and lower (10) limits estimated by Ryther (1969) and Cushing (1971), respectively.

Table C.1 PLANKTON: Input data for northern Benguela *Ecopath* model (1980s).

Parameter	Original Value	Source	Value used	Comments
PHYTOPLANKTON				
B	2.6X10^6 t C	Brown *et al.* 1991		
P/B	77.4 y^{-1}		35.7 y^{-1}	Primary production in Brown *et al.* (1991) increased by 18% to account for particulate dissolved organic C (1989 workshop).
Sedimentation	228 t.km^{-2}.y^{-1}	Pitcher *et al.* 1991		Sedimentation estimated to be 3.7% of daily production (Pitcher *et al.* 1991).
MICROZOOPLANKTON *2-200μm equivalent spherical diameter; nanoflagellates, ciliates, zooplankton larvae*				
B	50 120 t C	Estimated from Brown *et al.* (1991) and Painting *et al.* (1992)	Estimated	Using *Ecopath*, estimated B required during each decade.
P/B	354 y^{-1}			
U	20%	Stoecker 1984		
MESOZOOPLANKTON 200-2 000μm; copepods				
B	179 000 t C	Hutchings *et al.* 1991;	Estimated	Using *Ecopath*, estimated B required during each decade.
P/B	40 y^{-1}		40 y^{-1}	B estimated from carbon assuming ratio of carbon:wet mass is 0.04, as in Hutchings *et al.* 1991.
P/Q	30%	Omori and Ikeda 1984		
U	35%	Verheye *et al.* 1992 Probyn *et al.* 1990 H. Verheye , MCM, pers. comm.		
MACROZOOPLANKTON 2-20 mm; mainly euphausiids (on which most of the macrozooplankton estimates are based), but also includes amphipods and fish larvae				
B	107 400 t C	Hutchings *et al.* 1991	Estimated	Using *Ecopath*, estimated B required during each decade.
P/B	13 y^{-1}			
P/Q	41%			
U	35%	Jarre-Teichmann *et al.* 1998		
GELATINOUS ZOOPLANKTON Cnidaria, Ctenphora, tunicates, chaetognaths				
B	5X10^6 t	Assumed to be 5 times B estimate for southern Benguela.	10^6 t	Biomass more likely in the range of 10-50% of combined meso- and macro-zooplankton biomass (L. Hutchings, MCM, pers. comm.).
P/B	0.371 y^{-1}	Calculated by converting to carbon equivalents (Jarre-Teichmann *et al.* 1998)		
P/Q	41%	H. Verheye, MCM, pers. comm.		
U	20%	Purcell 1983		This is from assimilation efficiency of siphonophores.

Table C.2. SMALL PELAGIC FISH: Input data for northern Benguela *Ecopath* model (1980s).

Parameter	**Original Value**	**Source**	**Value used**	**Comments**
CAPE ANCHOVY (ENGRAULIS CAPENSIS)				
B	252 000 t	Hewitson and Cruickshank 1993		
P/B	1.16 y^{-1}			
P/Q	9.98%			
SARDINE (SARDINOPS SAGAX)				
B	134 000 t	Hewitson and Cruickshank 1993		
P/B	1.1 y^{-1}			
P/Q	10%			
PELAGIC GOBY (SUFFLOGOBIUS BIBARBATUS)				
B	600 000 t	Hewitson and Cruickshank 1993	Estimated	B required estimated using *Ecopath*.
P/B	0.9 y^{-1}			
P/Q	10%			
OTHER SMALL PELAGIC FISH SAURY (Scomberesocidae), FLYING FISH (Exocoetidae), PELAGIC GOBY (*SUFFLOGOBIUS BIBARBATUS*)				
B	33 000 t	1989 Workshop	Estimated	There is little information available on other small pelagic fish in the northern Benguela (Hewitson and Cruickshank 1993). B required estimated using *Ecopath*.
P/B	0.9 y^{-1}			
P/Q	10%			Assumption, Jarre-Teichmann *et al.* 1998

Table C.3. HORSE AND CHUB MACKEREL AND LARGE PELAGIC FISH: Input data for northern Benguela *Ecopath* model (1980s).

Parameter	**Original Value**	**Source**	**Value used**	**Comments**
*HORSE MACKEREL (*TRACHURUS TRACHURUS CAPENSIS*)*				
B	2.5 X10^6 t	Babayon *et al.* 1986; Vaske *et al.* 1987; Scherbich *et al.* 1986		
P/B	0.52 y^{-1}	Jarre-Teichmann *et al.* 1998		Assumed same as in southern Benguela.
Q/B	5.2 y^{-1}			Corresponds to P/Q of 10%
U	30%			Zooplankton comprise more than 80% of diet.
*CHUB MACKEREL (*SCOMBER JAPONICUS*)*				
B	62 500 t			Chub mackerel thought to migrate between the southern and northern Benguela (Crawford and De Villiers 1984). Assumed they spend equal time in each region, i.e. B equivalent to that in Jarre-Teichmann *et al.* (1998).
P/B	0.6 y^{-1}	Jarre-Teichmann *et al.* 1998		Assumed same as values in southern Benguela
P/Q	10%			
U	25%			Heavy exploitation left more small, zooplanktivorous fish in 1980s.
LARGE PELAGIC FISH (TUNA THUNNUS *SPP., SNOEK* THYRSITES ATUN, *KOB* AGYROSOMUS INODORUS*)*				
B	154 000 t	Penney *et al.* 1991a		
P/B	0.49 y^{-1}			Combined estimate weighted by relative biomass estimates.
P/B Tuna	0.47 y^{-1}	Shannon and Jarre-Teichmann 1999		Estimated from sum of natural and fishing mortalities.
P/B Snoek	0.5 y^{-1}	Shannon and Jarre-Teichmann 1999		Estimated from sum of natural and fishing mortalities.
P/B kob	0.36 y^{-1}	1989 Workshop		
P/Q	9.9%	1989 Workshop		
U	20%			Large pelagic fish assumed efficient predators.

Table C.4 CEPHALOPODS AND MESOPELAGIC FISH: Input data for northern Benguela *Ecopath* model (1980s).

Parameter	**Original Value**	**Source**	**Value Used**	**Comments**
CEPHALOPODS *Mostly squids* LOLIGO *SPP. and* TODARODES *SPP.*				
B	30 000 t	1989 Workshop (M. Lipinski, MCM, pers. comm.)	50 000 t	Estimated range of B of *Todarodes angolensis* is 8 401t – 25 600t from 1983-1988 (Lipinski 1992). Also considering other cephalopod species, B likely twice this.
P/B	1.5 y^{-1}			
P/Q	10%			
U	20%			
MESOPELAGIC FISH (LANTERNFISH *LAMPANYCTODES HECTORIS* AND LIGHTFISH *MAUROLICUS MUELLERI*)				
B	810 000 t	Hewitson and Cruickshank 1993	Estimated	*Ecopath* used to estimate B required.
P/B	1.2 y^{-1}			
P/Q	10%			
U	35%			Assumed same as U of other zooplanktivorous fish.

Table C.5. HAKE, OTHER DEMERSAL FISH AND CHONDRICHTHYANS: input data for northern Benguela *Ecopath* model (1980s).

Parameter	**Original Value**	**Source**	**Value used**	**Comments**
HAKE *SHALLOW-WATER HAKE* MERLUCCIUS CAPENSIS *AND DEEP-WATER HAKE* M. PARADOXUS				
B	$1.3X10^{6}$ t	Schumacher 1987; Abelló *et al.* 1988; Gordoa and MacPherson 1989		
P/B	1.0 y^{-1}			Assuming P/B equivalent to the sum of natural (M) and fishing (F) mortality (Allen 1971); M estimates from Gasyukov and Dorovskikh 1989a and b; F estimates from Schumacher 1987.
Q/B	4.5 y^{-1}			From daily ration (Andronov 1987), and from P/B and P/Q, assuming P/Q=22% (Shannon and Jarre-Teichmann 1999).
U	20%			Assumed similar to other predatory fish
OTHER DEMERSAL FISH *WEST COAST SOLE* AUSTROGLOSSUS MICROLEPIS, *KINGKLIP* GENYPTENUS CAPENSIS, *RATTAILS (E.G.* MALACOCEPHALUS LAEVIS *AND* CAELORINCHUS SIMORHYNCHUS*)*, GURNARD CHELIDONICHTHYS *SPP.*, *JACOPEVER* HELICOLENUS *SPP.*, *RIBBONFISH* LEPIDOPUS *SPP. AND MONKFISH*, LOPHIUS *SPP.*				
B	155 834 t	1989 Workshop	Estimated	*Ecopath* used to estimate B required.
P/B	1.0 y^{-1}			Assumed same as that of hake.
P/Q	10%		15%	Increased as in Jarre-Teichmann *et al.* 1998.
U	20%			Assumed similar to other predatory fish and carnivores.
CHONDRICHYANS				
B	67 180 t			No B estimates available for northern Benguela. Assumed same B concentration as on west coast in southern Benguela model (Jarre-Teichmann *et al.* 1998), scaling by size of region.
P/B	0.5 y^{-1}	Jarre-Teichmann *et al.* 1998		Assumed same values as those used in southern Benguela model.
P/Q	25%			
U	20%			

Table C.6. MARINE MAMMALS AND BIRDS: input data for northern Benguela *Ecopath* model (1980s).

Parameter	**Original Value**	**Source**	**Value used**	**Comments**
*SEALS (*ARCTOCEPHALUS PUSILLUS PUSILLUS*)*				
B	51 763 t	1989 Workshop		
P/B	0.94 y^{-1}			
P/Q	4.9%			
U	20%			Furness (1984) for carnivorous mammals.
CETACEANS				
B	4 880 t	B of Dusky and Heavyside dolphins estimated at 1989 workshop. B quadrupled to account for other dolphin species and migratory whales.		
P/B	1.6 y^{-1}	1989 Workshop	1.0 y^{-1}	P/B estimated to be higher than southern
Q/B	7.5–10 y^{-1}	Jarre-Teichmann *et al.* 1998	10 y^{-1}	From daily rations of bottlenose and humpback dolphins (Smale *et al.* 1984) and Bryde's whales (Best and Rickett 1984). Within Tamura and Ohsumi 's (1999) range for whales.
U	21%	Gaskin 1982		
MARINE BIRDS				
B 1980s	3 257 t	Crawford *et al.* 1991		1990s B estimated from unpublished data, MCM; Crawford *et al.* 1991, 1995, 1999.
B 1990s	2 616 t			
P/B	0.123 y^{-1}			
Q/B	118 y^{-1}			
U	26%			

Table C.7. BENTHOS: input data for northern Benguela *Ecopath* model (1980s).

Parameter	**Original Value**	**Source**	**Value used**	**Comments**
		BENTHIC PRODUCERS		
B	?		Estimated	Using *Ecopath*, required B estimated; EE assumed 50% because benthic producers often consumed as detritus.
P/B	15.0 y^{-1}	Jarre-Teichmann *et al.* 1998		
		MEIOBENTHOS		
B	?		Estimated	Using *Ecopath*, required B estimated.
P/B	4.0 y^{-1}	Jarre-Teichmann *et al.* 1998		
P/Q	12%			
U	20%			
B	?		Estimated	Using *Ecopath*, required B estimated.
P/B	1.2 y^{-1}	Jarre-Teichmann *et al.* 1998		
P/Q	12%			
U	20%			

Table C.8 Balanced diet composition (%) in the northern Benguela ecosystem during the 1980s. Prey groups are listed in rows, predators in columns. An asterisk indicates that a prey group comprises less than 0.5% of the predator's diet. Shaded cells indicate dietary compositions altered during the balancing of the model, in which case the revised value is tabulated below the original value.

Prey/ predator	Microzoo.	Mesozoo.	Macrozoo	Gel Zoo.	Anchovy	Sardine	Goby	H. Mack.	Mesopel.	Small Pel.	Cephalop.	Chub Mack.	Hake	Demersals	Large Pel.	Birds	Seals	Cetaceans	Chondrich.	Meioben.	Macroben.
Phytoplankton	40 50	50 75	60	25	33	56	93														
Benthic producers																				5	5
Microzooplankton	20 10	50 20		25	4	8															
Mesozooplankton		0 5	40	25	31	18	1	18	40	81		1	2	8		*					
Macrozooplankton					32	18	6	79	60	14	10	80	49	32	17 19	4					
Gelatinous zooplankton										3			3								
Anchovy												2	1		47 7	21 18	4 2	1	9 7		
Sardine															4 7	1 5	3 4	1	1 4		
Pelagic Goby								1			10		4	2	* 39	47	53	7			
Horse Mackerel											10		5		2	1	24		1		
Mesopelagics								3			55 59	16	18	2	5	5	1	19			
Small pelagics												1		5 2	6 4	3 4		12			
Cephalopods								*			10 1		*	13 *	*	4	8 1	32	*		

Prey/ predator	Microzoo.	Mesozoo.	Macrozoo	Gel. Zoo.	Anchovy	Sardine	Goby	H. Mack.	Mesopel.	Small Pel.	Cephalopods	Chub Mack.	Hake	Demersals	Large Pel.	Birds	Seals	Cetaceans	Chondrich.	Meioben.	Macroben.
Chub mackerel															*	*			2		
Hake											5 10		5	10	8 6	10	4 12	28	11		
Other demersal fish													5	11 5	11	2			42		
Large pelagic fish													*		*	*	4		*		
Marine birds																* 0			* 0		
Seals																					
Cetaceans																					
Chondrichthyans																			23		
Meiobenthos																					8
Macrobenthos										2			9	15 38	1				10		7
Detritus	40			25																95	80

APPENDIX D

ADDITIONAL RESULTS OF SIMULATED EFFECTS OF ALTERED FISHING SCENARIOS IN THE SOUTHERN BENGUELA ECOSYSTEM

Tabulated in Appendix D are detailed results of some of the simulated fishing scenarios investigated in Chapter 10 and referred to in the text.

Table D.1 Biomasses and catches in year 50, expressed as a proportion of original levels in 1980s and 1990s models, when the purse seine fishery is closed (year 0-50), the line fishery increased fourfold year 10-50, and the demersal fishery is increased two-fold from year 10 to year 50.

	1980s		1990s	
Group modeled	Biomass	Catch	Biomass	Catch
Anchovy	4.37	0.00	1.39	0.00
Sardine	3.82	0.00	1.50	0.00
Redeye	0.71	0.00	1.35	0.00
Chub mackerel	0.01	0.01	0.40	0.55
Horse mackerel	0.60	1.10	1.05	0.73
Large pelagic fish (including snoek)	2.34	7.03	1.00	3.01
Mesopelagic fish	1.22	0.00	1.47	0.00
Hakes	0.22	0.47	0.43	0.93
Pelagic-feeding demersal fish	0.51	1.03	0.86	1.70
Benthic-feeding demersal fish	1.30	2.47	1.20	2.38
Avian and mammalian predators	1.57	-	1.08	-
System total (excluding detritus)	1.05	0.45	1.04	0.57

Table D.2 Biomasses and catches in year 50, expressed as a proportion of original levels in 1980s and 1990s models, when the line fishery is enlarged two-fold from year 10 to year 50.

	1980s		1990s	
Group modelled	Biomass	Catch	Biomass	Catch
Anchovy	1.06	1.06	0.99	0.99
Sardine	1.06	1.06	1.05	1.05
Redeye	0.89	0.89	0.91	0.91
Chub mackerel	1.19	1.19	1.11	1.11
Horse mackerel	1.42	1.42	1.40	1.40
Large pelagic fish (including snoek)	0.73	1.08	0.69	1.05
Mesopelagic fish	0.97	0.97	0.98	0.98
Hakes	1.00	1.00	1.02	1.03
Pelagic-feeding demersal fish	0.98	0.98	0.95	0.95
Benthic-feeding demersal fish	1.00	1.00	0.99	0.99
Avian and mammalian predators	1.06	-	1.05	-
System total (excluding detritus)	1.00	1.05	1.00	1.03

Table D.3 Biomasses and catches in year 50, expressed as a proportion of original levels in 1980s and 1990s models, when the demersal trawl fishery is increased two-fold from year 10 to year 50.

	1980s		1990s	
Group modelled	Biomass	Catch	Biomass	Catch
Anchovy	1.44	1.44	1.39	1.39
Sardine	1.23	1.23	1.50	1.50
Redeye	1.32	1.32	1.35	1.35
Chub mackerel	0.03	0.05	0.40	0.68
Horse mackerel	1.27	2.35	1.04	1.73
Large pelagic fish (including snoek)	1.02	1.41	1.00	1.42
Mesopelagic fish	1.55	1.55	1.47	1.47
Hakes	0.40	0.81	0.52	1.09
Pelagic-feeding demersal fish	0.98	1.94	0.86	1.75
Benthic-feeding demersal fish	1.20	2.21	1.20	2.42
Avian and mammalian predators	1.04	-	1.08	-
System total (excluding detritus)	1.04	1.35	1.04	1.36

Table D.4 Biomasses and catches in year 50, expressed as a proportion of original levels in 1980s and 1990s models, when fishing mortality of adult horse mackerel is increased.

Fishing scenario	Fishing mortality of adult horse mackerel increased fourfold year 10-50				(Fishing mortality of adult horse mackerel increased eightfold year 10-50			
	1980s		1990s		1980s		1990s	
Group modelled	Biomass	Catch	Biomass	Catch	Biomass	Catch	Biomass	Catch
Anchovy	0.81	0.81	0.98	0.98	0.64	0.64	1.09	1.09
Sardine	1.12	1.12	0.99	0.99	1.56	1.56	1.28	1.28
Redeye	1.34	1.34	0.98	0.98	2.18	2.18	1.49	1.49
Chub mackerel	2.47	2.47	1.67	1.67	1.71	1.71	1.27	1.27
Horse mackerel	0.20	0.20	0.41	0.41	0.00	0.01	0.05	0.05
Large pelagic fish (including snoek)	1.11	1.10	0.93	0.92	1.16	1.17	0.99	0.97
Mesopelagic fish	0.60	0.60	0.73	0.73	0.35	0.35	0.52	0.52
Hakes	0.83	0.85	0.91	0.92	0.70	0.75	0.83	0.86
Pelagic-feeding demersal fish	1.72	1.72	1.55	1.55	2.00	2.00	1.72	1.72
Benthic-feeding demersal fish	0.97	0.97	0.95	0.95	1.00	1.00	0.97	0.97
Avian and mammalian predators	0.90	-	0.95	-	0.86	-	1.00	-
System total (excluding detritus)	0.98	0.87	0.98	0.95	0.98	0.82	0.98	1.04

Table D.5 Simulated biomasses of fish boxes at the start (year 0), 10 years after the implementation of an altered fishing strategy (year 20) and at the end of the simulation period (year 50) when i) anchovy fishing mortality rate is increased twofold from year 10 onwards and the 1980s model is used and ii) sardine fishing mortality is increased fourfold from year 10 onwards and the 1990s model is used.

	Scenario i (anchovy; 1980s model)			Scenario ii (sardine; 1990s model)		
Model box	Year 0	Year 20	Year 50	Year 0	Year 20	Year 50
Anchovy	5.216	0.742	0.018	3.573	4.122	4.539
Sardine	0.586	0.669	0.699	2.091	0.105	0.000
Redeye	5.555	7.023	6.829	6.230	6.987	8.015
Other small pelagics	0.364	0.448	0.366	0.364	0.472	0.891
Chub mackerel	0.284	0.448	0.703	0.455	0.447	0.272
Juvenile horse mackerel	0.200	0.273	0.332	0.484	0.555	0.597
Adult horse mackerel	1.618	2.139	2.718	1.937	2.200	2.410
Mesopelagic fish	8.651	9.023	6.828	10.249	10.468	11.267
Snoek	0.240	0.120	0.051	0.337	0.238	0.224
Other large pelagics	0.131	0.110	0.116	0.131	0.109	0.110
Cephalopods	1.364	1.383	1.304	1.364	1.277	1.202
Small *M. capensis*	0.595	0.637	0.703	0.641	0.616	0.551
Large *M. capensis*	0.823	0.877	0.957	1.127	1.148	1.145
Small *M. paradoxus*	1.700	1.806	1.622	1.880	1.857	1.650
Large *M. paradoxus*	0.684	0.711	0.670	1.067	1.121	1.120
Pelagic-feeding demersals	3.450	4.388	5.688	3.696	3.490	2.796
Benthic-feeding demersals	3.512	3.456	3.258	3.720	3.703	3.794

Table D.6 Simulated biomasses of fish boxes at the start (year 0), 10 years after the implementation of an altered fishing strategy (year 20) and at the end of the simulation period (year 50) when the redeye fishing mortality rate is increased fourfold from year 10 onwards and i) the 1980s and ii) the 1990s models are used.

	Scenario i (1980s model)			Scenario ii (1990s model)		
Model box	Year 0	Year 20	Year 50	Year 0	Year 20	Year 50
Anchovy	5.216	5.797	7.468	3.573	4.160	5.313
Sardine	0.586	0.591	0.675	2.091	2.115	2.250
Redeye	5.555	2.993	2.315	6.230	2.915	1.901
Other small pelagics	0.364	0.376	0.677	0.364	0.388	0.573
Chub mackerel	0.284	0.372	0.286	0.455	0.610	0.688
Juvenile horse mackerel	0.200	0.205	0.151	0.484	0.499	0.385
Adult horse mackerel	1.618	1.655	1.229	1.937	1.996	1.539
Mesopelagic fish	8.651	9.782	11.745	10.249	11.843	13.147
Snoek	0.240	0.250	0.285	0.337	0.354	0.387
Other large pelagics	0.131	0.132	0.143	0.131	0.134	0.148
Cephalopods	1.364	1.396	1.387	1.364	1.414	1.437
Small *M. capensis*	0.595	0.591	0.523	0.641	0.642	0.629
Large *M. capensis*	0.823	0.810	0.774	1.127	1.121	1.102
Small *M. paradoxus*	1.700	1.780	1.726	1.880	1.958	2.013
Large *M. paradoxus*	0.684	0.690	0.719	1.067	1.075	1.105
Pelagic-feeding demersals	3.450	3.505	2.459	3.696	3.717	2.980
Benthic-feeding demersals	3.512	3.469	3.588	3.720	3.676	3.734

Table D.7 Simulated biomasses of fish boxes at the start (year 0), 10 years after the implementation of an altered fishing strategy (year 20) and at the end of the simulation period (year 50) when the purse seine fishery is closed from year 0 onwards, fishing mortality from the demersal trawl fishery is increased twofold from year 10 onwards and fishing mortality from the line fishery is increased fourfold from year 10 onwards, when i) the 1980s and ii) the 1990s models are used.

	Scenario i (1980s model)			Scenario ii (1990s model)		
Model box	Year 0	Year 20	Year 50	Year 0	Year 20	Year 50
Anchovy	5.216	19.241	20.613	3.573	4.090	4.991
Sardine	0.586	2.065	2.329	2.091	2.519	3.147
Redeye	5.555	2.942	4.106	6.230	6.579	8.447
Other small pelagics	0.364	0.141	0.138	0.364	0.544	1.321
Chub mackerel	0.284	0.041	0.012	0.455	0.388	0.183
Juvenile horse mackerel	0.200	0.091	0.062	0.484	0.663	0.489
Adult horse mackerel	1.618	0.821	0.523	1.937	2.697	2.027
Mesopelagic fish	8.651	7.963	8.074	10.249	13.011	15.095
Snoek	0.240	0.606	0.646	0.337	0.235	0.306
Other large pelagics	0.131	0.259	0.277	0.131	0.137	0.164
Cephalopods	1.364	1.284	1.271	1.364	1.339	1.301
Small *M. capensis*	0.595	0.374	0.325	0.641	0.444	0.342
Large *M. capensis*	0.823	0.635	0.588	1.127	0.787	0.707
Small *M. paradoxus*	1.700	0.863	0.727	1.880	1.126	0.869
Large *M. paradoxus*	0.684	0.470	0.427	1.067	0.601	0.523
Pelagic-feeding demersals	3.450	1.711	1.524	3.696	4.004	3.145
Benthic-feeding demersals	3.512	4.026	4.210	3.720	4.063	4.462

Table D.8 Simulated biomasses of fish boxes at the start (year 0), 10 years after the implementation of an altered fishing strategy (year 20) and at the end of the simulation period (year 50) when fishing mortality from the line fishery is increased twofold from year 10 onwards, when i) the 1980s and ii) the 1990s models are used.

	Scenario i (1980s model)			Scenario ii (1990s model)		
Model box	Year 0	Year 20	Year 50	Year 0	Year 20	Year 50
Anchovy	5.216	5.353	5.519	3.573	3.620	3.557
Sardine	0.586	0.618	0.620	2.091	2.202	2.203
Redeye	5.555	5.406	4.937	6.230	6.079	5.670
Other small pelagics	0.364	0.376	0.405	0.364	0.400	0.439
Chub mackerel	0.284	0.319	0.334	0.455	0.490	0.505
Juvenile horse mackerel	0.200	0.245	0.279	0.484	0.583	0.666
Adult horse mackerel	1.618	1.986	2.302	1.937	2.345	2.722
Mesopelagic fish	8.651	8.283	8.434	10.249	9.857	10.031
Snoek	0.240	0.199	0.198	0.337	0.250	0.253
Other large pelagics	0.131	0.073	0.073	0.131	0.076	0.073
Cephalopods	1.364	1.357	1.337	1.364	1.356	1.344
Small *M. capensis*	0.595	0.608	0.627	0.641	0.660	0.680
Large *M. capensis*	0.823	0.831	0.862	1.127	1.153	1.191
Small *M. paradoxus*	1.700	1.672	1.632	1.880	1.877	1.845
Large *M. paradoxus*	0.684	0.682	0.667	1.067	1.091	1.076
Pelagic-feeding demersals	3.450	3.492	3.385	3.696	3.617	3.498
Benthic-feeding demersals	3.512	3.485	3.510	3.720	3.665	3.683

Table D.9 Simulated biomasses of fish boxes at the start (year 0), 10 years after the implementation of an altered fishing strategy (year 20) and at the end of the simulation period (year 50) when fishing mortality from the demersal trawl fishery is increased twofold from year 10 onwards, when i) the 1980s and ii) the 1990s models are used.

	Scenario i (1980s model)			Scenario ii (1990s model)		
Model box	Year 0	Year 20	Year 50	Year 0	Year 20	Year 50
Anchovy	5.216	6.210	7.461	3.573	4.132	4.998
Sardine	0.586	0.631	0.718	2.091	2.543	3.155
Redeye	5.555	5.989	7.290	6.230	6.623	8.458
Other small pelagics	0.364	0.637	1.634	0.364	0.569	1.325
Chub mackerel	0.284	0.149	0.008	0.455	0.380	0.183
Juvenile horse mackerel	0.200	0.297	0.242	0.484	0.664	0.489
Adult horse mackerel	1.618	2.407	2.041	1.937	2.710	2.027
Mesopelagic fish	8.651	11.593	13.330	10.249	13.092	15.111
Snoek	0.240	0.186	0.216	0.337	0.239	0.305
Other large pelagics	0.131	0.139	0.164	0.131	0.138	0.164
Cephalopods	1.364	1.303	1.246	1.364	1.334	1.301
Small *M. capensis*	0.595	0.365	0.288	0.641	0.442	0.341
Large *M. capensis*	0.823	0.482	0.453	1.127	0.788	0.703
Small *M. paradoxus*	1.700	0.760	0.596	1.880	1.120	0.864
Large *M. paradoxus*	0.684	0.263	0.235	1.067	0.600	0.519
Pelagic-feeding demersals	3.450	4.561	3.355	3.696	3.950	3.153
Benthic-feeding demersals	3.512	3.860	4.206	3.720	4.073	4.468

Table D.10 Simulated biomasses of fish boxes at the start (year 0), 10 years after the implementation of an altered fishing strategy (year 20) and at the end of the simulation period (year 50) when fishing mortality of large *M. capensis* is increased twofold from year 10 onwards, when i) the 1980s and ii) the 1990s models are used.

	Scenario i (1980s model)			Scenario ii (1990s model)		
Model box	Year 0	Year 20	Year 50	Year 0	Year 20	Year 50
Anchovy	5.216	5.333	5.627	3.573	3.526	3.321
Sardine	0.586	0.571	0.583	2.091	2.062	1.939
Redeye	5.555	5.454	5.628	6.230	6.035	5.587
Other small pelagics	0.364	0.390	0.526	0.364	0.369	0.334
Chub mackerel	0.284	0.325	0.208	0.455	0.509	0.528
Juvenile horse mackerel	0.200	0.323	0.367	0.484	0.644	0.783
Adult horse mackerel	1.618	2.731	3.168	1.937	2.704	3.368
Mesopelagic fish	8.651	8.115	8.812	10.249	9.519	9.580
Snoek	0.240	0.238	0.227	0.337	0.348	0.353
Other large pelagics	0.131	0.136	0.138	0.131	0.135	0.131
Cephalopods	1.364	1.351	1.301	1.364	1.382	1.364
Small *M. capensis*	0.595	0.468	0.463	0.641	0.525	0.564
Large *M. capensis*	0.823	0.553	0.596	1.127	0.814	0.875
Small *M. paradoxus*	1.700	1.788	1.664	1.880	2.006	1.976
Large *M. paradoxus*	0.684	0.781	0.785	1.067	1.179	1.174
Pelagic-feeding demersals	3.450	3.124	2.509	3.696	3.520	3.353
Benthic-feeding demersals	3.512	3.448	3.542	3.720	3.639	3.651

Table D.11 Simulated biomasses of fish boxes at the start (year 0), 10 years after the implementation of an altered fishing strategy (year 20) and at the end of the simulation period (year 50) when fishing mortality of large *M. paradoxus* is increased twofold from year 10 onwards, when i) the 1980s and ii) the 1990s models are used.

	Scenario i (1980s model)			Scenario ii (1990s model)		
Model box	Year 0	Year 20	Year 50	Year 0	Year 20	Year 50
Anchovy	5.216	5.683	6.408	3.573	4.055	4.834
Sardine	0.586	0.619	0.716	2.091	2.374	2.872
Redeye	5.555	6.023	7.722	6.230	6.774	8.409
Other small pelagics	0.364	0.548	1.330	0.364	0.487	0.908
Chub mackerel	0.284	0.241	0.051	0.455	0.438	0.268
Juvenile horse mackerel	0.200	0.195	0.135	0.484	0.463	0.285
Adult horse mackerel	1.618	1.602	1.105	1.937	1.885	1.140
Mesopelagic fish	8.651	11.292	12.311	10.249	12.979	13.582
Snoek	0.240	0.270	0.304	0.337	0.367	0.426
Other large pelagics	0.131	0.136	0.157	0.131	0.138	0.161
Cephalopods	1.364	1.287	1.252	1.364	1.327	1.315
Small *M. capensis*	0.595	0.508	0.409	0.641	0.545	0.456
Large *M. capensis*	0.823	0.789	0.714	1.127	1.067	0.972
Small *M. paradoxus*	1.700	0.722	0.604	1.880	1.001	0.878
Large *M. paradoxus*	0.684	0.243	0.205	1.067	0.489	0.449
Pelagic-feeding demersals	3.450	4.699	4.136	3.696	4.658	4.252
Benthic-feeding demersals	3.512	3.987	4.259	3.720	4.254	4.511

Table D.12 Simulated biomasses of fish boxes at the start (year 0), 10 years after the implementation of an altered fishing strategy (year 20) and at the end of the simulation period (year 50) when fishing mortality of large horse mackerel is increased fourfold from year 10 onwards, when i) the 1980s and ii) the 1990s models are used.

	Scenario i (1980s model)			Scenario ii (1990s model)		
Model box	Year 0	Year 20	Year 50	Year 0	Year 20	Year 50
Anchovy	5.216	5.243	4.188	3.573	3.716	3.500
Sardine	0.586	0.634	0.652	2.091	2.173	2.071
Redeye	5.555	6.246	7.412	6.230	6.607	6.145
Other small pelagics	0.364	0.319	0.063	0.364	0.340	0.099
Chub mackerel	0.284	0.332	0.734	0.455	0.495	0.756
Juvenile horse mackerel	0.200	0.082	0.044	0.484	0.279	0.205
Adult horse mackerel	1.618	0.582	0.317	1.937	1.027	0.777
Mesopelagic fish	8.651	8.172	5.050	10.249	9.950	7.512
Snoek	0.240	0.250	0.267	0.337	0.324	0.294
Other large pelagics	0.131	0.133	0.149	0.131	0.133	0.141
Cephalopods	1.364	1.425	1.430	1.364	1.411	1.443
Small *M. capensis*	0.595	0.516	0.447	0.641	0.585	0.525
Large *M. capensis*	0.823	0.763	0.685	1.127	1.075	0.992
Small *M. paradoxus*	1.700	1.690	1.380	1.880	1.895	1.755
Large *M. paradoxus*	0.684	0.683	0.600	1.067	1.073	1.023
Pelagic-feeding demersals	3.450	3.849	6.083	3.696	3.993	5.724
Benthic-feeding demersals	3.512	3.521	3.391	3.720	3.714	3.545

APPENDIX E

SIMULATED CHANGES IN THE SOUTHERN BENGUELA ECOSYSTEM WHEN AVAILABILITY OF PLANKTON TO ANCHOVY AND SARDINE IS ALTERED

Figs E.1-E.4 Differences in biomass of groups (*B*) in models of the 1990s and 1980s, expressed as proportional changes (in percentages) of biomass of groups in models of the 1980s:

$$\frac{(B_{1990s} - B_{1980s})}{B_{1980s}} \times 100 \qquad \text{.......equation E.1}$$

"Original" refers to biomass ratios in the original models of the 1980s and 1990s described in Chapters 4 and 5. "Simulated 1990s" refers to ratios when the original model of the 1980s is used to simulate the 1990s situation, and "simulated 1980s" refers to ratios when the original model of the 1990s is used to simulate the 1980s situation. In simulations, forcing functions that alter susceptibility of prey to anchovy and sardine are applied as indicated in figure captions.

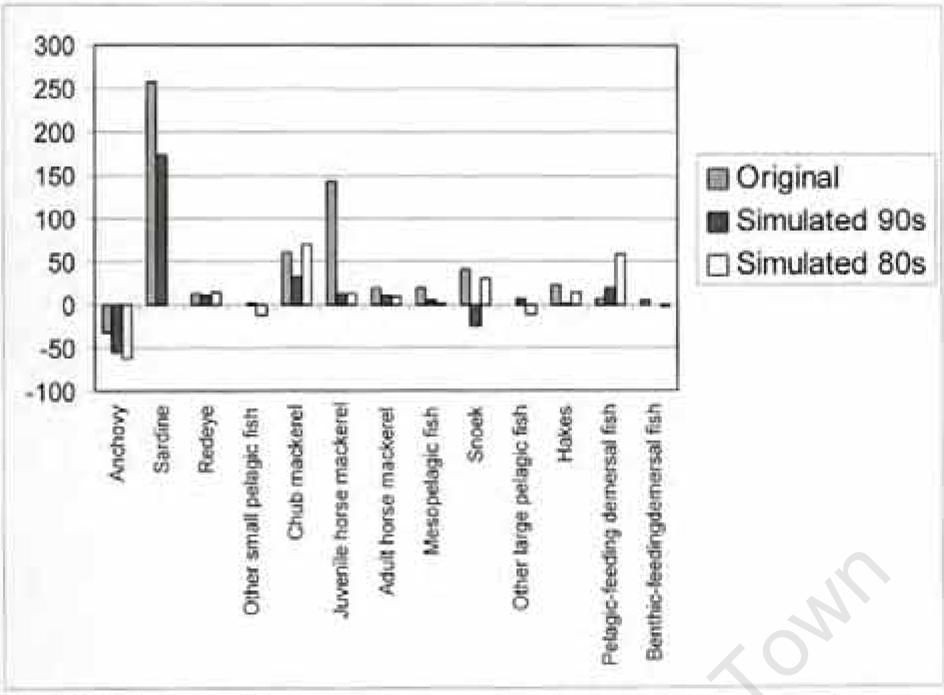

Fig. E.1 Using the 1980s model, a negative forcing function equivalent to 45% of the maximum is applied to the trophic links between anchovy and its phyto-and zooplankton prey, and a positive forcing function equivalent to 40% of the maximum is applied to sardine and its phyto-and zooplankton trophic links. Similarly, using the 1990s model, a positive forcing function equivalent to 14% of the maximum is applied to the trophic links between anchovy and its phyto-and zooplankton prey, and a negative forcing function equivalent to 38% of the maximum is applied to sardine and its phyto- and zooplankton prey, lowering susceptibility of prey to sardine.

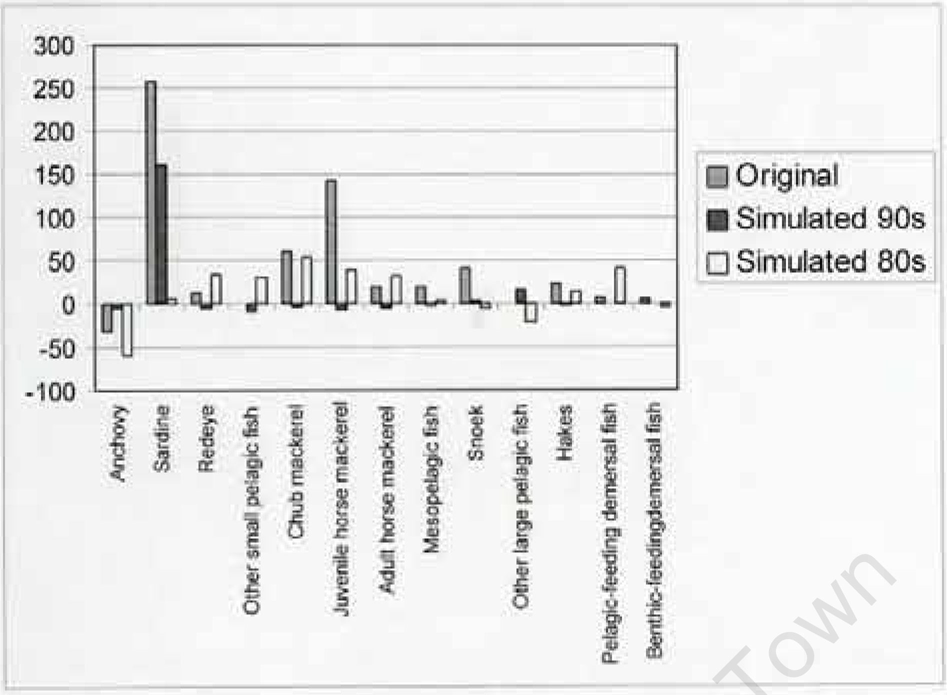

Fig. E.2 Using the 1980s model, a positive forcing function equivalent to 40% of the maximum is applied to trophic links between sardine and its phyto-and zooplankton prey and anchovy is unaffected. Similarly, using the 1990s model, a positive forcing function equivalent to 14% of the maximum is applied to trophic links between anchovy and its phyto-and zooplankton prey and sardine is unaffected.

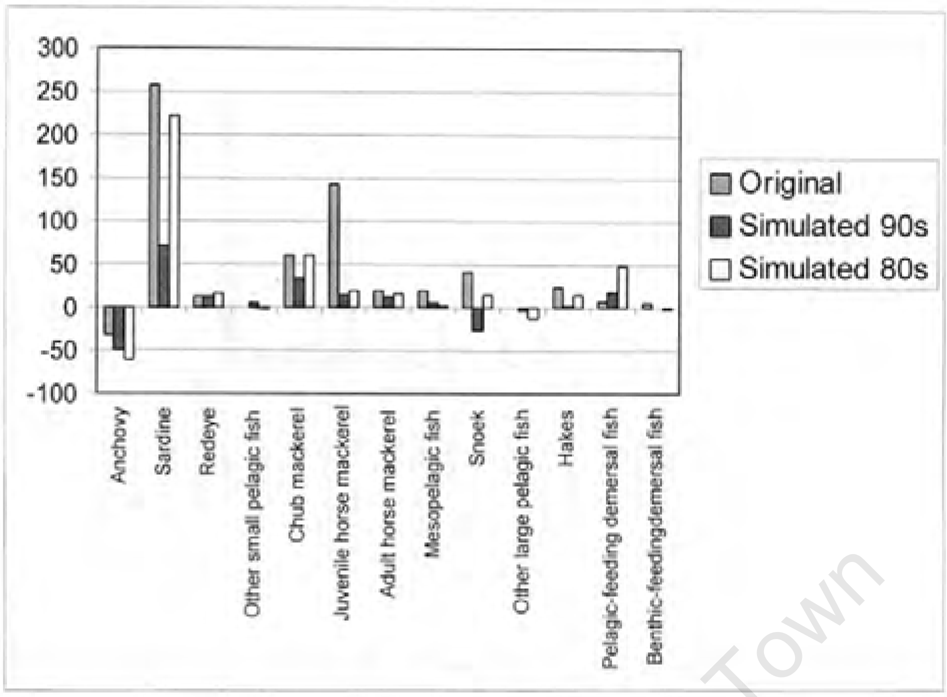

Fig. E.3 Using the 1980s model, a negative forcing function equivalent to 45% of the maximum is applied to the macro- and mesozooplankton-anchovy trophic links, and a positive forcing function equivalent to 40% of the maximum is applied to the macro- and mesozooplankton-sardine links. Similarly, using the 1990s model, a positive forcing function equivalent to 14% of the maximum is applied to the macro- and mesozooplankton-anchovy trophic links, and a negative forcing function equivalent to 38% of the maximum is applied to the macro- and mesozooplankton-sardine links.

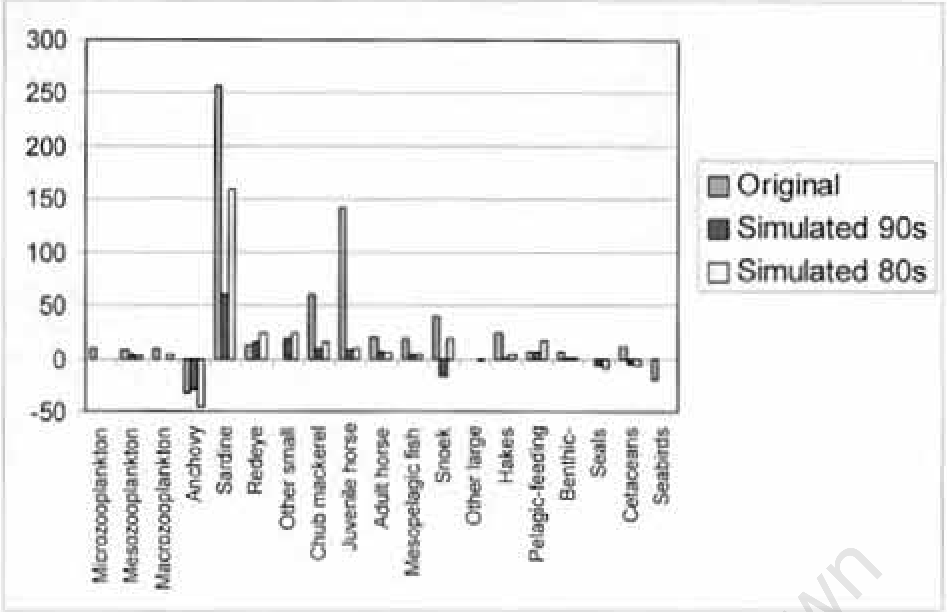

Fig. E.4 Using the 1980s model, a negative forcing function equivalent to 45% of the maximum is applied to the mesozooplankton-anchovy trophic link only, and a positive forcing function equivalent to 40% of the maximum is applied to the mesozooplankton-sardine link only. Similarly, using the 1990s model, a positive forcing function equivalent to 14% of the maximum is applied to the mesozooplankton-anchovy trophic link, and a negative forcing function equivalent to 38% of the maximum is applied to the mesozooplankton-sardine link.