RECONSTRUCTING THE BENGUELA ECOSYSTEM FOR A TIME BEFORE MAN'S INTERVENTION

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DECLARATION

I hereby declare that all the work in this thesis is my own, except where otherwise stated in the text. This thesis has not been submitted in whole or in part for a degree at any other university.

Signed by candidate

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22/11/2007

Date

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Abstract:

Humans have been present in the Benguela region for at least 1 my, although exploitation of marine resources only began in earnest in the 1400s, with the arrival of European seafarers. *Ecopath* with *Ecosim* was used to construct and compare mass-balanced models of the southern and northern Benguela ecosystems representing each of the following eras of human influence: aboriginal (10,000 BP–1652), preindustrial (1652–1910), industrial (1910–1975) and postindustrial (1975–present). The 'pristine' models of the two ecosystems were compared, and the effects of fishing investigated by simulating industrial-era fishing pressure on these models. In the southern Benguela, biomass at higher trophic levels (TLs) decreased over the periods examined, while that of sardine and anchovy increased in the current (2000s) model, as reflected by the decline in weighted TL of the community (excluding plankton). Fishing became an important predator, taking over consumption of small pelagics and horse mackerel from declined natural predators such as hake. Harvesting of apex predators, such as seals and seabirds, during the preindustrial era meant that the mean trophic level (TL) of the catch declined substantially as between the preindustrial (1900) and industrial (1960) models, although a slight increase occurred between the 1960 and 2000s models. Removals have increased substantially over time. Total biomass, consumption, respiration, production and throughput decreased from the pristine model to 1960 and then increased again in the 2000s model, probably due to the abnormally high and unsustainable small pelagic biomass in the 2000s. For the northern Benguela, biomass of most groups, especially sardine, hake and seabirds, declined over time. The few dominant small pelagic fish, characteristic of upwelling systems, were replaced by a wider range of species, and biomass of gelatinous zooplankton increased dramatically in recent decades. Catches declined, although mean TL of the catch increased from 1970 to 1990, as did the weighted TL of the community (excluding plankton), after the collapse of small pelagic stocks in the 1970s. Environmental anomalies experienced in the 1990s negatively affected a number of stocks, both directly and indirectly, compounding any effects of fishing and preventing mitigation of declining stocks by management measures implemented after Namibian independence in 1990. Pristine southern and northern Benguela models displayed greater similarities in structure and function than their modern counterparts. Total biomass, consumption and respiration were higher in the pristine northern Benguela. Hake and horse mackerel were responsible for a greater proportion of piscivorous consumption, while in the southern Benguela apex predators played a bigger role. Simulated fishing on pristine models resulted in higher-than modern biomasses per TL in the northern Benguela, and lower-than-modern biomasses per TL in the southern Benguela. Models resulting from simulations were not identical to the models for the modern era, but diverged from the pristine ecosystem structure. Although fishing did influence ecosystem structure and functioning, environmental events have had a considerable, and possibly even greater, impact. Ecosystem stress and the collapse of small pelagic stocks may lead to a shift toward a bottom-up trophic control mechanism, increasing the impact of environmental events. It is possible that pristine systems were not as severely affected by environmental anomalies as are modern systems.

Contents

Chapter 1

Introduction and General Methods

1.1. Introduction:

1.1.1. The impacts of fishing and an Ecosystem Approach to Fisheries (EAF):

That fishing pressure should have direct effects on the abundance of target species populations is not disputed. Any significant change to target populations, however, also tends to translate into altered energy flows within the system, and ultimately into changes in the structure and functioning of the community as a whole (Jackson *et al.*, 2001; Blaber *et al.*, 2000; Goñi, 2000; Pitcher & Pauly, 1998). Globally there are numerous examples of fishing pressure causing commercial stock collapse and eventual community structure adjustment: between 1950 and 1990 the California sardine (*Sardinops sagax*), the North Sea herring (*Clupea harengus*), the Peruvian sardine (*Sardinops sagax*) and the Atlantic cod (*Gadus morhua*) all suffered stock collapses (Hilborn & Walters, 2001); in the North Sea, benthic community structure has been shown to have changed significantly in a total of three areas (Frid *et al.*, 2000); in the Gulf of Thailand in the space of 20 years almost all large fish became commercially extinct and the trophic level of the entire fishery decreased as a result (Goñi, 2000). Although these are extreme examples, with evidence of fishery-induced changes in communities such as these it becomes questionable whether any community that has been subjected to any degree of fishing pressure can still exist in something resembling its pristine state.

Fishing impacts ecosystems and communities, either directly or indirectly. Direct impacts include fishing mortality of target and other species (e.g. bycatch species), as well as any habitat alteration or destruction resulting from fishing practices, as is often the case in areas where bottom-trawling has occurred (Gislason *et al.*, 2000; Goñi, 2000). These direct effects are relatively easy to measure, and hence monitor, using either direct sampling techniques in the field or catch and effort data. Tracking the indirect effects of fishing, however, poses a greater problem. Altered population structure of directly affected species with regard to both abundance and size distribution has a knock-on effect, in turn altering the structure and functioning of all trophically-linked groups, and ultimately of the community as a whole (Gislason *et al.*, 2000; Goñi, 2000; Pauly *et al.*, 1998; Blaber *et al.*, 2000).

It is the monitoring and prediction of these indirect effects that present both a key and a quandary to fisheries management science today. Fisheries management has commenced the necessarily slow move forward from the traditional single-species approach to management toward a multi-species or ecosystem approach to fisheries (EAF) management. An EAF is a more holistic approach to management and would allow for more realistic consideration of possible indirect impacts in the policy-making process and monitoring procedures (Cury *et al.*, 2005b; Shannon *et al.*, in press). The shift of focus from target-resource oriented management to an EAF was formalized in 2001 by the Reykjavik Declaration, which states that national marine resource-use policies are required to be formulated with an ecosystem-based approach in mind (Cury *et al.*, 2005b). This change in perspective is the result of increased awareness and knowledge of the role played by the various trophic interactions within a functioning ecosystem. It is now evident that in order to manage an ecosystem at any level, some understanding of the intra- and interspecific processes occurring within it is necessary (Botsford *et al.*, 1997; Gislason *et al.*, 2000; Cury *et al.*, 2003).

If an EAF is to become viable though, multi-species ecosystem models must become part of the policy-maker's toolbox (Cury, 2004; Shannon *et al.*; in press). Models facilitate what would otherwise be impossible: some form of quantitative understanding of the network of energy flows within the ecosystem, as well as the ability to predict the possible effects of changes that may occur as a result of management decisions or even a changing environment. Unfortunately at present it is still not feasible to use multi-species models as a primary tool for formulating management strategies, as models can only be as good as the input data and there is still a marked deficit of knowledge where most non-commercial and many commercial species are concerned. But although the many unavoidable assumptions and uncertainties associated with any multi-species models are something that the modeller must keep in mind during model construction and interpretation, a well-researched, best-fit model based on the data available can nevertheless provide useful insight into species interactions and possible future outcomes. South Africa has now begun to move towards the implementation of an EAF by proposing the use of ecosystem models as testing grounds for management strategies based on single-species models (Shannon *et al.*, 2004a).

While these steps in themselves are fairly revolutionary, a further suggestion has been made: that sustainable utilization of the resources currently available, customarily the goal of fisheries managers, should not be the end objective. Rather we should seek to rebuild ecosystems so that an exploitation potential closer to that of the pristine ecosystem can be reached (Pitcher, 1998; Pitcher & Pauly, 1998). This stems from the idea that the level of harvesting that can be sustained by an optimally exploited ecosystem is much higher than could be supported by many ecosystems as they stand today, most of which had been depleted by overexploitation, mismanagement, or various combinations of the two before any management strategies could be put into place (Ludwig *et al.*, 1993). If, instead of reconciling ourselves to what is left, we concentrated on regaining what has been lost, the optimal sustainable utilization level would be much higher than is currently possible (Pitcher & Pauly, 1998). While rebuilding an ecosystem to its pristine state seems to be something of an unattainable goal, it would nonetheless be a healthy standpoint from which to approach management - at least allowing the idea of restoration to enter the picture, if only as a background to the decision-making process. But for this to be possible some sort of reference point is needed as to what a pristine environment should look like. To this end retrospective models, based on fisheries records and knowledge of the fishery concerned, can be created (Jackson *et al.*, 2001). At the very least these models allow us to investigate the effects of fishing on an ecosystem, which in itself would serve to provide useful information for managing fisheries so as to avoid previously encountered detrimental effects resulting from overfishing. Retrospective ecosystem models have already been constructed in several areas where fishing has historically been important, some examples being the North Sea (Mackinson, 2000), Newfoundland (Heymans & Pitcher, 2002), and the Strait of Georgia (Dalsgaard *et al.*, 1998). HMAP (Historical Mapping of Animal Populations), the historical component of the Census of Marine Life (CoML) project, has a number of projects globally focusing on the collection and synthesis of catch and effort data from initial exploitation until present, which will ultimately be represented in retrospective ecosystem models.

In 1994 the Consortium for Oceanographic Research and Education and the Alfred P. Sloan Federation established CoML as a means of assessing and describing the diversity, distribution and abundance of organisms existing within marine environments globally (Decker & O'Dor, 2003). CoML aims to generate a resource of information including contemporary data as well as historical descriptions and future estimations of marine communities and their structure. The past and future branches of the project will be dealt with by HMAP and Future of Marine Animal Populations (FMAP) divisions of CoML respectively. HMAP is designed to investigate and describe the state of ecosystems and communities from a time prior to their exploitation, in their 'pristine' states, over the entire history of the fishery. As a by-product of this process it is hoped that reference points and perspectives for contemporary ecosystem research and management decisions will also be obtained. The data gathered will then be incorporated into the Ocean Biogeographical Information System (OBIS), which will serve as a global online database for marine systems (Grassle, 2000; Decker & O'Dor, 2003). The Benguela Project, of which this thesis forms part is one of 13 HMAP projects globally that are currently in the process of developing historical models. Only ecosystems with a history of fishing pressure, some habitat or biodiversity change, and good historical catch and effort data have been selected for historical model development. The other 12 projects are based in southeast Asia, the Caribbean Sea, the North Sea, the Baltic Sea, the northwest Atlantic, the northwest Pacific, the southeast Australian Shelf, the southwest Pacific, the White and Barent Seas, the Wadden Sea, the Mediterranean and Black Sea, New Zealand, and on world-wide whaling and mega mollusks (www.hmapcoml.org).

1.1.2. Introduction to the Benguela ecosystem:

The Benguela ecosystem is one of the world's four major upwelling systems, along with the California, Canary and Peruvian systems. All are characterised by an eastern boundary current, and are typically dominated by an equatorward and offshore flow of surface water, as well as the resultant high levels of primary productivity associated with coastal upwelling. This upwelling of deeper water masses is the result of a process called Ekman transport: prevailing winds force coastal water offshore and a deficit of water develops at the surface. Colder, nutrient-rich water is then drawn up from greater depth to replace that transported offshore. In this way nutrients are moved into the euphotic zone and become available to producers and hence consumers. As in the other three major eastern boundary currents, commercially valuable fisheries have developed in the Benguela as a result of the increased productivity relative to other non-upwelling areas (Crawford *et al.,* 1987; Shillington, 1998).

The Benguela is effectively divided into two regions, northern and southern, by differing ecological and oceanographic conditions. The Lüderitz permanent upwelling cell off Namibia is usually adopted as the barrier between the two regions, acting as a semi-permeable barrier to many marine species (Shannon, 1985; Shillington, 1998). Management (historical and current) and commercially important stocks both also vary between the regions, reinforcing the need for dealing with the northern and southern Benguela separately (Griffiths & Branch, 1997).

In 1910 the Union of South Africa was formed after Britain relinquished its colonies. The Benguela came under the governance of a single authority for the first time in 1915, after the capture of German Southwest Africa during the First World War. This remained the status quo until Southwest Africa became independent as the Republic of Namibia in 1990, although Walvis Bay was only restored to Namibia in 1994.

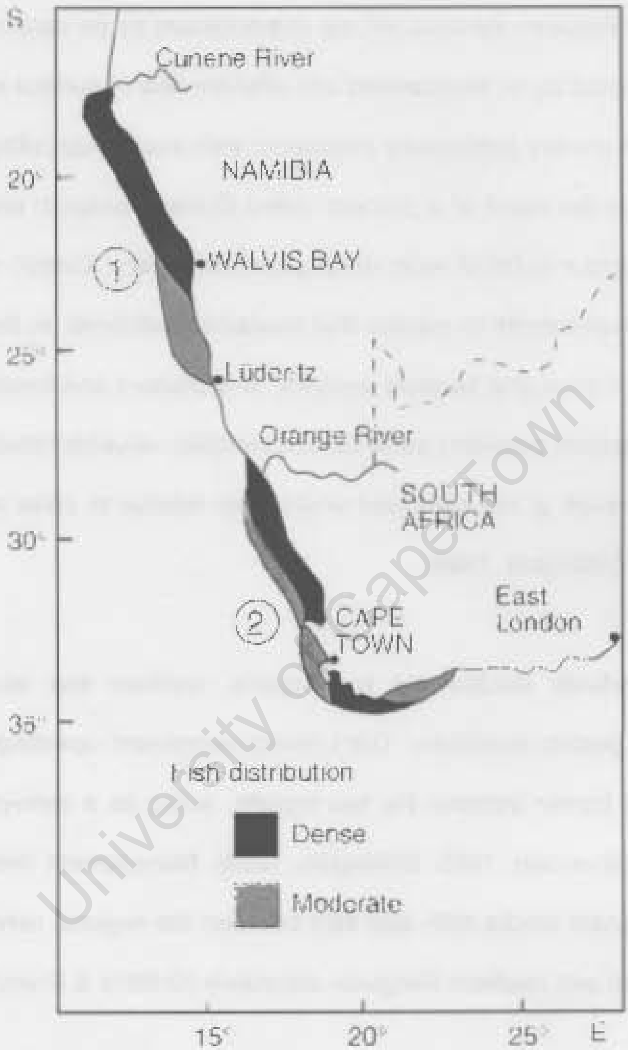


Figure 1.1: Map of the Benguela ecosystem showing division into 1.) the northern and 2.) the southern Benguela regions (Shannon *et al.*, 2003).

It was during this period of single governance that most of today's commercially important fisheries began. Large-scale commercial fisheries in the Benguela ecosystem are relatively young in terms of the global industry, having been operating for approximately 50 years only, since the 1950s brought about the expansion of the purse-seine fishery (Crawford *et al.*, 1987).

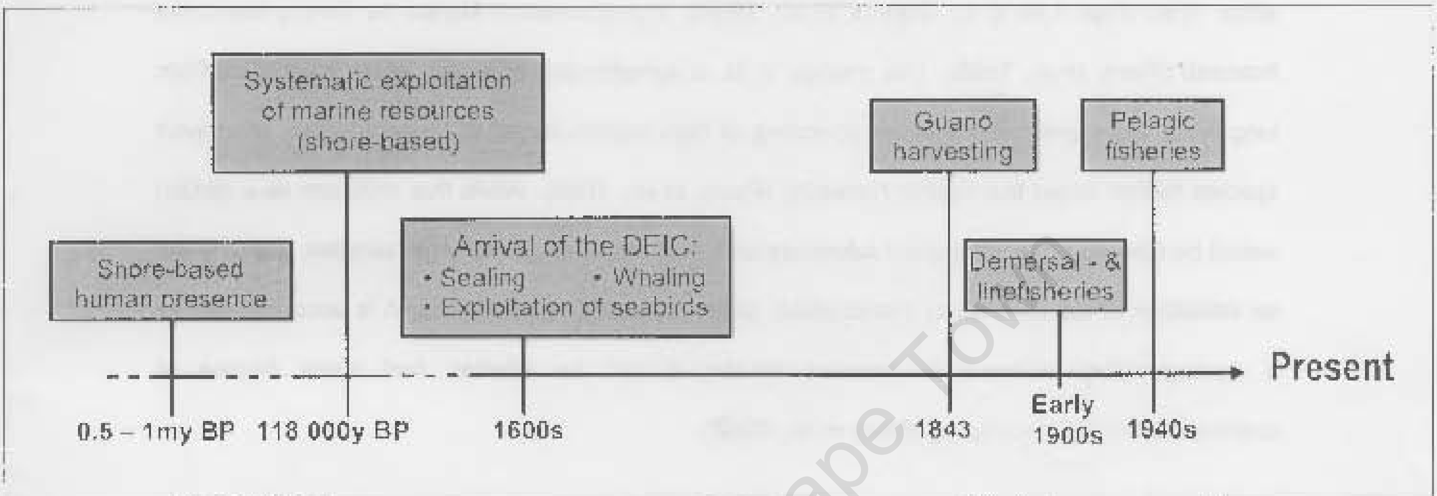


Figure 1.2: Timeline of human involvement and use of marine resources in the Benguela ecosystem, from 0.5 - 1 mya to the present day. Only large-scale changes of use are depicted, such as the arrival of the Dutch East India Co. (DEIC) in the mid-1600s and the starting points of most economically important fisheries.

Yet although this may have been the starting point of large-scale exploitation, archaeological evidence shows that man has been utilizing the marine resources within the Benguela ecosystem since approximately the last interglacial, 120 000y BP (Parkington, 2001). Man's growing involvement in the Benguela ecosystem and the advent of most large fisheries in the region are depicted in Fig. 1.2. The northern and southern Benguela have separate exploitation histories, and these will be dealt with separately and in more detail in Chapters 2 and 3 respectively.

Findings from the preceding phase of the Benguela HMAP project (the collection and synthesis of historical fishing data, presented in Griffiths *et al.* (2004)) show an exponential increase in the decadal biomass removal from the system over the period from 1790 to the 1990s (Fig. 1.3) (Griffiths *et al.*, 2004). The declines in removals after the late 1960s resulted from the collapse of various stocks and the implementation of more restrictive management tactics, but still only represent a regression to roughly the level of the biomass being removed in the 1950s. The mean trophic level (TL) of the total catch in the Benguela has been shown to have decreased markedly since 1790 (Figs 1.4a & b, Griffiths *et al.*, 2004), a phenomenon known as fishing down the foodweb (Pauly *et al.*, 1998). This change in TL is symptomatic of a shift of target species from long-lived, large, predatory species operating at high trophic levels, to those smaller, short-lived species further down the trophic hierarchy (Pauly *et al.*, 1998). While this shift can to a certain extent be blamed on technological advances and intended changes in target species, it also gives an indication of the community composition. Unless declining TL of the catch is accompanied by a corresponding increase in biomass landed, it can be inferred that some degree of overexploitation was occurring (Pauly *et al.*, 2002).

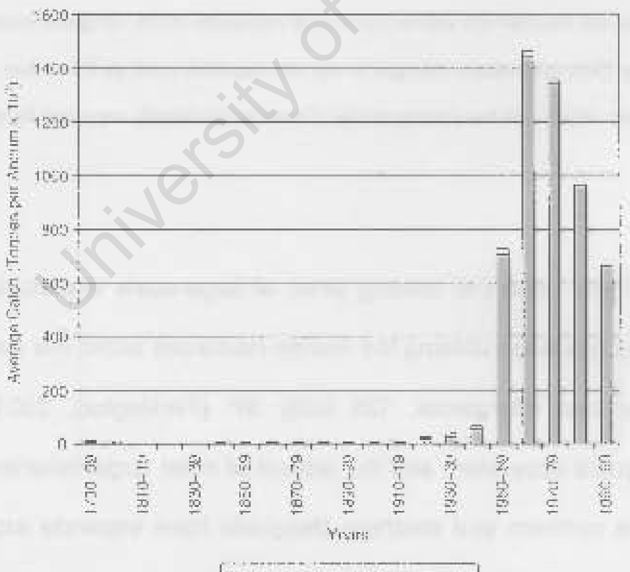


Figure 1.3: Average annual animal biomass removed from the Benguela system each decade since 1790 (Adapted from Griffiths *et al.*, 2004)

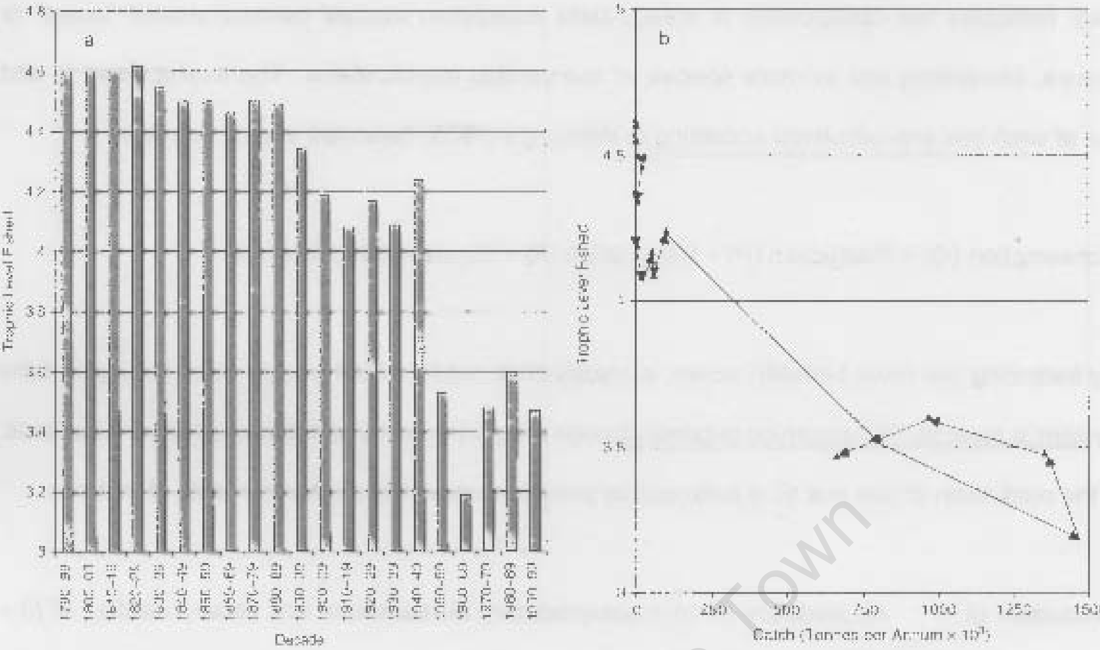


Figure 1.4: a) Mean trophic level (TL) of total removals from the Benguela system per decade since 1800; b) The relationship between mean TL and biomass of removals in the Benguela region per decade from 1790 until 2000. The decline in TL is only matched by an increase in biomass during the 1940s and 1950s (Griffiths *et al.*, 2004).

The data represented above and other data relating to historical fishing pressures and population sizes were used to construct retrospective ecosystem models of the Benguela using the modelling software *Ecopath* with *Ecosim* (Christensen *et al.*, 2000). The examination of 'pristine', interim and present-day *Ecopath* models of the northern and southern Benguela ecosystems should yield insight into the nature and root of trophic changes that have occurred in the Benguela.

1.1.3. *Ecopath* with *Ecosim* (EwE):

Ecopath:

EwE facilitates the construction of steady-state ecosystem models centred around 'boxes' or groups, comprising one or more species of comparable trophic status. The trophic flows in and out of each box are calculated according to Winberg's (1956) balanced energy equation:

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

By balancing the flows between boxes, a steady-state model of the energy flows throughout the system is created. Relationships between groups are portrayed by simultaneous linear equations. If the production of one box (i) is balanced by predation, export and other mortality of that box:

Production (i) = All predation on (i) + non-predatory biomass loss and fishery catches of (i) + other exports of (i),

then all aspects of the relationship between box/ group (i) and predator (j) can be described as follows:

Production by (i) = $B_i \,.\, P/B_i$

Predatory losses of (i) = $\sum_j (B_j \,.\, Q/B_j \,.\, DC_{j,I})$

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

where

i	=	a box/ 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
Q/B_j	=	the average fraction of i in the diet of j (in terms of mass)

EE_i = the ecotrophic efficiency of *i* (the fraction of total production consumed by predators or exported from the system, including as catches)

$(1 - EE_i)$ = other mortality for *i* (i.e. deaths as a result of disease or starvation, for example).

So for box *i* (and similarly for every other box/ group in the ecosystem):

$$B_i \,.\, P/B_i \,.\, EE_i - \sum_j (B_j \,.\, Q/B_j \,.\, DC_{j, I}) - Ex_i = 0$$

Where

Ex_i = export of i by harvesting or emigration, for example.

Ecopath requires that for each group, three out of the following four variables must be entered: biomass (*B*), production per unit biomass (*P/B*), total consumption per unit biomass (*Q/B*), and ecotrophic efficiency (*EE*). Solving the linear equations then allows for the fourth variable to be estimated. Respiration is used purely as a means of balancing the boxes, and is taken as the difference between assimilated consumption and production not thought to result from primary production. In the *Ecopath* approach, waste and dead matter accumulates in the detritus box unless consumed by detrivores. To complete the input data, the modeller must enter diet compositions, assimilation efficiency, and exports (Christensen *et al.,* 2005).

Once input data have been entered, the resulting model must be balanced so that ultimately all ecotrophic efficiencies are $0 < EE < 1$ (i.e. growth and mortality do not exceed production). A number of factors make this unlikely to be the case initially, largely due to the uncertainty that characteristically surrounds input data. Estimates of input parameters are often based on sparse or patchy data series, or there are not data for all species in a particular box/group, so estimates for those species that are available must be assumed to apply to the others in their group. In some cases the estimates themselves may be unsound, due to errors or inconsistencies in sampling. Balancing of the model can be accomplished manually, usually by revising diet compositions until all *EE*'s <1. This method relies on the fact that less confidence is generally placed in the diet composition estimates than in those for biomass, which have generally been directly acquired from field samples (although this is by no means always the case) (Kavanagh *et al.*, 2004). The model can also be balanced using the automatic balancing function found in more recent versions of EwE, which uses either random or gradient descent alterations to diet compositions and/ or biomasses and selects the optimal mass-balanced models (Kavanagh *et al.*, 2004), although this method was not used to construct models in this dissertation.

Outputs from EwE models may be used to calculate various indices that allow for the comparison of form and function between ecosystems. Shannon's and Simpson's diversity indices were calculated as measures of system diversity (Magurran, 2004). Shannon's diversity index (H) was calculated as the proportion of species i relative to the total number of species (pi), and multiplied by the natural log. of this proportion. This product is then summed for all species, and multiplied by -1:

$$H = -\sum_{i=1}^{s} p_i \ln p_i$$

In Simpson's diversity index (D), the proportion of species i relative to the total number of species (pi) is squared. The squared proportions are summed for all species, and the reciprocal is taken:

$$D = \frac{1}{\sum_{i=1}^{s} p_i^2}$$

Finn's cycling index (the proportion of throughput that is recycled within the ecosystem) and mean path length (total number of trophic links divided by the number of pathways between groups) (Christensen *et al.,* 2000) were also used as indicators of ecosystem state.

Ecosim:

The *Ecopath* software includes a dynamic simulation routine, *Ecosim*, which allows for the dynamics within a system to be examined over time (Walters *et al.*, 1997). Simulations using *Ecosim* can be performed once a balanced, steady state *Ecopath* model has been created. The linear equations on which the *Ecopath* model is based are used to derive the coupled differential equation expressing basic dynamics in *Ecosim*:

$$dB_i/dt = g_i \sum_j C_{ij} - \sum_j C_{ij} + I_i - (M_i + F_i + e_i)\ B_i$$

where

dB_i/dt = the growth rate of group *i* in terms of its biomass

g_i = growth efficiancy of group *i*

F_i = the fishing mortality rate of group *i*

I_i = the immigration rate

C_{ij} = the consumption rate of group i by group j.

Ecosim also allows for user-specified prey vulnerabilities, which in turn makes it possible to incorporate various hypotheses regarding trophic flow control, e.g. bottom-up or top-down control (Walters *et al.,* 1997). Default vulnerability for a given predator-prey interaction is set as 2, signifying mixed trophic controls, bottom-up control is characterised by a vulnerability closer or less than 1, and top-down, by a vulnerability much higher than 2. The consumption rates are thus calculated according to:

$$C_{ij} = v_{ij}\ a_{ij}\ B_i\ B_j\ /\ (v_{ij} + v'_{ij} + a_{ij}B_j),$$

where the rates of behavioural exchange between invulnerable and vulnerable groups are shown by v and v' parameters, and aij is the rate of effective search by predator j for prey group i (Christensen *et al.,* 2000).

Ecosim also allows the user to specify multi-stanza groupings of a species, allowing for juvenile and adult groups to be linked during time dynamics by way of parameters describing growth and recruitment into adult groups.

1.2. Aims and general methods:

In partial fulfilment of the Benguela region HMAP project, available data documenting man's historical exploitation of marine resources in the Benguela by way of catch and effort data have been summarized in Griffiths *et al.*, 2004. The concluding step in this project is the construction of ecosystem models of the Benguela region at various stages along the continuum from pristine to the current level of exploitation, based on these data. The aim of this thesis is thus to explore and describe any ecosystem-level changes that may have occurred since fishing and exploitation began in the Benguela, in terms of both structure and function. This will be investigated using *Ecopath* with *Ecosim* (EwE) There are currently available, models of the Benguela ecosystem based on modern catch and biomass data that cover the period from the 1970s or '80s, until the 2000s (Shannon *et al.*, 2003; Heymans *et al.,* 2004, Roux & Shannon, 2004). These will be used as the post-industrial models and as the basis for the construction of industrial (1910 – 1975), pre-industrial (1652 – 1910) and aboriginal models. EwE version 5.1 software will be used in the construction of all models, firstly because the existing models for the northern and southern Benguela on which these historical models are based were constructed using this software, and secondly because of its widespread usage globally as a means of modelling aquatic systems. It is hoped that these models can facilitate a better understanding of the Benguela ecosystem as it functions today, as well as if, how, and to what extent it has been altered as a result of fishing. A more in-depth knowledge of the responses of various populations to historical fishing levels allows for more informed management decisions in the future (Harvey *et al.*, 2000).

Chapter 2

Retrospective models of the Southern Benguela region

2.1. Introduction:

2.1.1. The southern Benguela ecosystem:

As described in the previous chapter, the Benguela can effectively be divided into northern and southern regions, based on management and more importantly biogeographic variations. The southern Benguela region, dealt with in this chapter, extends from its northern boundary, a permanent upwelling cell near Lüderitz in Namibia (between 25 and 27°S) that is thought to preclude the north-south migration of many fish species, around the coast of South Africa to 28°E at East London. The easterly extent of the system serves to include the Agulhas Bank region off the south coast, an important spawning and feeding site that cannot be excluded due to the important role played by this area in the life-cycles of many of the species found on the west coast. The modelled area extends offshore to the 500 m isobath, covering 220 000 km^2. The physical environment in the southern Benguela is characterised by pulsed seasonal upwelling, due to the prevailing south-east wind over the summer months, resulting in the high productivity typical of upwelling systems. This in turn supports a relatively large exploitable fish biomass and the associated commercially valuable fisheries. Small pelagics, namely the anchovy *Engraulis encrasicolus* and the sardine *Sardinops sagax,* predominate in the fish community, both with regard to community biomass and proportion of catch, forming the mainstay of the purse-seine fishery. Other important pelagic species include the round herring *Etrumeus whiteheadi* and horse mackerel *Trachurus trachurus capensis.* which also have relatively high biomasses and contribute to landings although to a lesser extent (Crawford *et al.,* 1987; Griffiths *et al.,* 2004). Small pelagics in the Benguela, as in other upwelling systems, are now recognised as undergoing shifts in abundance, as dominance oscillates over time between two or more species. Recorded patterns in the southern Benguela dating back to the 1920s show an initial anchovy dominance, followed by horse mackerel in the 1940s and 1950s, after which sardine biomass increased, outweighing other species contributions from the late 1950s until succeeded in turn by chub mackerel (*Scomber japonicus)* and anchovy, returning to dominance in the mid-1990s (Crawford *et al.*, 1987; Schwartzlose *et al.*, 1999). This decadal-scale phenomenon of alternating abundance levels, often described as a 'regime shift', has been demonstrated in a number of regions around the globe where sardine and anchovy co-exist (Lluch-Belda *et al.,* 1992; Schwartzlose *et al.*, 1999). A regime shift is defined as an altered state of a marine ecosystem produced by a change in form and function (Cury & Shannon, 2004). The shifts in the small pelagic community in the southern Benguela over the past few decades cannot necessarily be termed a regime shift, as though species abundances may have changed the structure and functioning of the system itself did not significantly (Cury & Shannon, 2004). This was not the case in the 1950s and 1960s, when the structure of the ecosystem was indeed altered and a regime shift occurred, while more recent changes may be better referred to as 'species replacement' (Cury & Shannon, 2004). Although many of the regions globally that have experienced regime shifts are in fact subject to high fishing pressure (e.g. the Humboldt, Californian, Japanese and Benguela ecosystems), fishing in itself has been ruled out as the primary driver of these shifts, as fish scales in oceanic sediment deposits off California and southern Africa give evidence of alternating regimes prior to the initiation of any large-scale fishing operations in the area (Soutar & Isaacs, 1969; Shackleton 1986; Baumgartner *et al.*, 1992). The shift from one dominant species to another appears to be influenced primarily by climatic changes and biological interactions, with fishing pressure, though relevant, playing a secondary role (Schwartzlose *et al.*, 1999; Cury, 2004; Shannon *et al.*, 2004b).

Although small pelagic fish are the largest contributors to fish community biomass, the most commercially valuable stocks in the system are the two species of Cape hake found in the region, shallow water *Merluccius capensis* and deep water *M. paradoxus*. The hakes are largely targeted by the demersal fishery.

2.1.2. Exploitation in the four epochs examined:

2.1.2.1. Pre-contact and aboriginal era (<1600):

Although archaeological evidence places humans in the coastal regions of the Benguela as early as 1 million years BP, these early inhabitants only began to utilize marine resources from around 120 000 years BP, during the last interglacial (Parkington, 2001). This exploitation was predominantly limited to the intertidal zone, and anthropogenic impacts on the offshore resources only began with the arrival of the early European seafarers. Seabirds, for the most part the African penguin *Spheniscus demersus,* were an easy target and served to provide sailors with food and even fuel in some cases. Harvesting of these birds was first recorded in 1487 by Bartholomew Diaz and continued as the southern African islands became provisioning points for passing ships (Shelton *et al.*, 1984, Griffiths *et al.*, 2004). The Cape fur seal *Arctocephalus pusillus pusillus* was the next species to be targeted, initially by the Dutch in the early 1600s (Griffiths *et al.*, 2004). Although the Benguela prior to 1600 cannot be termed 'pre-contact' with complete accuracy, the low levels of utilization occurring before this time are unlikely to have affected populations significantly until the early 1600s. Thus for the purposes of this thesis the period will be considered as essentially pristine.

2.1.2.2. Pre-industrial era: (1652-1910):

The establishment of the first permanent European settlement in the Cape by the Dutch East India Company (DEIC) in 1652 signalled an abrupt increase in harvesting effort on Cape fur seals and sea birds, especially in Table Bay and the surrounds. Once established in the Cape, the DEIC and its colonies continued to spread up the west coast, reaching what is now Namibia by the late 1700s (Van Duin & Ross, 1987). Exploitation levels remained comparatively low until the 1780s, when New England whalers began to overwinter at the Cape, targeting southern right whales (*Eubalaena australis*). The impact of these foreign whalers, combined with that of the shore-based operation that was established in the Cape in 1792 (targeting a more diverse range of species including Bryde's whales *Baleanoptera edeni*) led to a swift decline in abundance of baleen whales in general, particularly affecting southern right whales (Griffiths *et al.*, 2004). 1909 heralded the start of modern whaling off southern Africa's west coast, with steam-ships and cannon-fired harpoons replacing the traditional sail or oar-powered boats and hand-held harpoons. This new industry shifted its target species from southern right to humpback whales (*Megaptera novaeangliae*) as southern right populations had been severely impacted by this stage (Griffths *et al.*, 2004). Sealing, the other significant fishery at the time, did not intensify until after the British had unseated the DEIC in 1806. From this time until the Cape Fish Protection Act, which required permits for sealing, was introduced in 1893, unchecked efforts by British and American sealers on the southern African west coast and islands is believed to have caused the extinction of 23 colonies (Rand, 1972). The Cape line fishery also began to intensify over the period from 1800, targeting mainly snoek (*Thyrsites atun*), and collection of guano commenced in the Benguela in the mid-1800s. Although initiated in the northern Benguela where the majority of guano was initially collected, the valuable fertilizing material was also removed in large quantities from islands off South Africa. This resulted in declines in breeding success of island birds in many instances as guano is a crucial nesting material for species including the African penguin and the Cape gannet *Morus capensis* amongst others (Crawford *et al.*, 1983; Best *et al.*, 1997; Crawford & Jahncke, 1999; Griffiths *et al.*, 2004).

2.1.2.3. Industrial era (1910-80):

The demersal trawl fishery, which initially targeted Agulhas sole (*Austroglossus pectoralis*) and west coast sole (*A. microlepus*), began operating in the early 1900s (Lees, 1969). After the First World War however, the extent of the hake stocks off the west coast of South Africa was realised. Following this discovery the fishery began to target the Cape hakes *Merluccius capensis* and *M. paradoxus*. Improving technology served to increase catches in the 1950s. In the 1960s the waters off Namibia were increasingly targeted after exploratory fishing showed even richer stocks existed there (Payne & Punt, 1995; Gordoa *et al.*, 1995). The increased foreign interest that this raised lead to peak catches of almost 250 000 t off South Africa in the early 1970s (Rademan &

Butterworth, 2001). The targeting of small pelagic fish species off southern Africa only began in earnest during the 1940s after World War 2, after which purse-seine operations, initially based in St Helena Bay, spread rapidly to the rest of the west coast. Peak catches of around 500,000 t were recorded in 1962, the majority of which comprised the sardine *Sardinops sagax* (Crawford *et al.*, 1987). Record landings were, however, followed swiftly by the collapse of the sardine stock in the southern Benguela in the mid- to late 1960s, due to the combined effects of increased fishing pressure and irregular recruitment (Beckley & van der Lingen, 1999). Sardine was subsequently replaced by the anchovy *Engraulis encrasicolus* as the dominant small pelagic fish. The ensuing increase in the biomass of anchovy combined with a switch to a smaller net mesh size in 1964 to allow these stocks to be targeted, resulted in anchovy becoming the dominant pelagic species in catches (Beckley & van der Lingen, 1999). Modern whaling saw peak landings of humpbacks in 1913, and by 1915 catches had dropped dramatically, causing effort to be transferred to other species, and by the late 1960s legal whaling had ceased off South Africa (Best *et al.*, 1997; Griffiths *et al.*, 2004). Exploitation of seals continued to increase fairly steadily through the 1900s. In 1965 the government began to privatize sealing, giving rights to various colonies to private individuals. Harvest rates increased fairly rapidly from the late 1960s to reach a peak of 23 000 bulls taken in the early 1970s.

2.1.2.4. Post industrial era (1975- present):

Anchovy have maintained their dominance in pelagic landings since the 1960s, although stocks of both anchovy and sardine have been on the increase in the southern Benguela since the 1990s, increasing to what is estimated to be triple the biomass during the 1980s (Beckley & van der Lingen, 1999; Griffiths *et al.*, 2004; Shannon *et al.*, 2004b). The sudden increase in foreign interest in South Africa's demersal hake fishery during the late 1960s and early 1970s ultimately resulted in the government declaring a 200-nautical mile exclusive economic zone in 1977. This effectively reduced catches by eliminating most foreign effort. Catches have subsequently been in the region of 100 000 t per year (Rademan & Butterworth, 2001; Griffiths *et al.*, 2004). After peak harvests in the 1970s, sealing in South Africa declined severely when European embargos on importing seal products caused the South African market to crash in 1983. Harvesting continued at a lower level until finally being banned in 1990 (David, 1989; Griffiths *et al.*, 2004).

2.2. Methods:

The *Ecopath* with *Ecosim* (EwE) software (Walters *et al.,* 1997) was used to construct models for each of the eras described above. A detailed description of EwE is provided in Chapter 1.

2.2.1. Model construction:

Where values for P/B and Q/B are given, these are used in all models. Unaltered diet composition, Appendix A., Table A.1, was obtained from the 1978 EwE model for the southern Benguela referred to in Shannon *et al.* (2004). Input parameters are in line with those suggested in Moloney & Jarre (2003), so as to be comparable to models of other upwelling systems.

2.2.1.1 Input data by group for 1600, 1900 & 1960 models:

Input parameters were as follows, listed according to the group number as they appeared in the models:

1.) Phytoplankton: Primary production in the system was assumed to be 76.396t.km $^{-2}$, the same as in the 1978 model of the southern Benguela (Shannon *et al.*, 2004b), as no estimates are available for 1960, 1900 or 1600. The P/B ratio of 154.4 yr^{-1} used in the 1980s and 1990s model of Shannon *et al.* (2003), sourced from Brown *et al.* (1991), was assumed. As phytoplankton is a primary producer, Q/B and P/Q were not required for this group.

2.) Benthic producers: No estimates of benthic producer biomass are available for 1960, 1900 or 1600, so biomass was estimated using an ecotrophic efficiency of 50%. A P/B of 15 yr^{-1} was used (Jarre-Teichmann *et al.*, 1998).

3-5.) Zooplankton: Zooplankton was modelled as three separate groups according to size and a fourth containing salps and jellyfish: macro-, meso-, micro- and gelatinous zooplankton. As no biomass estimates are available for any zooplankton groups for 1960, 1900 or 1600, biomasses were estimated assuming an ecotrophic efficiency of 95% in all three models. The figure of 95% was decided on as this provides a conservative estimate of the B of the group in question, that would have been required to sustain the level of predation on that group. The microzooplankton group comprised nanoflagellates, ciliates, and zooplankton larvae with an equivalent spherical diameter of 2 – 200 µm. Estimates of P/B (482 yr^{-1}) and Q/B (1928 yr^{-1}) were obtained from the 1980s model (Jarre-Teichmann *et al.*, 1998). The mesozooplankton group includes copepods, predominantly *Calanoides carinatus* and *Calanus agulhensis*, of 200 - 2000 µm diameter. A P/B of 40 yr^{-1} and a Q/B of 133.33 yr^{-1} were used as in the 1980s and 1990s models in Shannon *et al.* (2003). Macrozooplankton has been defined as primarily consisting of euphausiids of 2 – 20 mm, although amphipods, fish larvae, and similar groups are also included. A P/B of 13 yr^{-1} and a Q/B of 31.707 yr^{-1} were used for the macrozooplankton group (Jarre-Teichmann *et al.*, 1998). Gelatinous zooplankton includes Cnidaria, Ctenophora, tunicates and chaetognaths, and was allocated, as for the 1980s and 1990s models, a P/B of 0.584 yr^{-1} and a Q/B of 1.669 yr^{-1} (Shannon *et al.*, 2003).

7&8) Anchovy and sardine: Biomass of sardine in the southern Benguela derived from catch data and VPA is estimated as having been 1 615 000 t in 1960 (Schwartzlose *et al.*, 1999). Biomass was estimated in the 1900 and 1600 models assuming an ecotrophic efficiency of 95%, as no estimates are available for these periods. Landings of 318 000 t are recorded in 1960 (Schwartzlose *et al.*, 1999), and no catch was assumed in the 1900 and 1600 models. A P/B of 1.2 yr^{-1} and a Q/B of 12.371 y^{-1}, obtained from the 1978 model in Shannon *et al.* (2004), were used. No biomass estimates were available for the anchovy for any of the three historic periods modelled in this study, so in all cases biomass was estimated by the model assuming an ecotrophic efficiency of 95%. As with sardine, P/B (1.4 yr^{-1}) and Q/B (14.4 y^{-1}) values from the

1978 model, initially derived from Armstrong *et al.* (1991) and Hewitson & Cruickshank (1993) were used. Minimal landings of anchovy were recorded between 1958 and 1963, significant catches only being made from 1964 onwards off South Africa (Crawford *et al.,* 1987).

9.) Redeye: Although biomass redeye does not rival that of sardine and anchovy, it is still significant and makes up a percentage of the purse-seine catch. It is therefore modelled as a separate group from 'Other small pelagics' in the southern Benguela. No biomass estimates for redeye are available for 1960, 1900 or 1600, and biomass was estimated assuming an ecotrophic efficiency of 95%. A P/B of 1.3 yr^{-1} and P/Q of 13 yr^{-1} were obtained from 1978 and 2000s models (Shannon *et al.*, 2004b). A catch of 100 t is recorded for 1960, and as the first recorded landings are in 1958, catch was presumed to be zero in 1900 and 1600 (Crawford *et al.*, 1987).

10.) Other small pelagic fish: The group 'other small pelagics' includes the less abundant species of small pelagic fish: saury (*Scomberesox saurus*), flying fish (Exocoetidae) and pelagic goby (*Sufflogobius bibarbatus*). No biomass estimates are available for any of these species for 1960, 1900 or 1600, so biomass was estimated in all three models assuming an ecotrophic efficiency of 95%. A P/B of 1.0 yr^{-1} and a Q/B of 10.0 yr^{-1} were used (Jarre-Teichmann *et al.*, 1998). No landings of any of the component species are recorded prior to the 1970s (Crawford *et al.*, 1987).

11.) Chub mackerel: Biomass of chub mackerel (*Scomber japonicus)* was estimated assuming an ecotrophic efficiency of 95% as no estimates of this stock were available for the historical periods modelled. P/B (0.8 yr^{-1}) and Q/B (8.0 yr^{-1}) were obtained from the 1978 model (Shannon *et al.*, 2004b). Chub mackerel has formed a small proportion of purse-seine landings in the southern Benguela since 1954, with landings of 29 100 t recorded for 1960 (www.fao.org).

12&13.) Horse mackerel: Cape horse mackerel, *Trachurus trachurus capensis*, has been modelled as two separate groups due to differences in diet and habitat between juvenile (<20 cm) and adult (>20 cm, older than 2 years) fish: juvenile horse mackerel (group 12) are zooplanktivorous and pelagic, while adult horse mackerel (group 13) are partially piscivorous, and midwater feeders (Shannon, 2001). Biomass of adult horse mackerel was estimated as 230 000 t in 1960 (Crawford, 1989). No estimates are available for 1900 or 1600 for adult horse mackerel, or for juveniles for any of the historical periods modelled. Biomass in these cases was therefore estimated by the model, assuming an ecotrophic efficiency of 95%. P/B and P/Q ratios for both juvenile (1.2 yr^{-1} and 0.1) and adult groups (1.5 yr^{-1} and 0.15) were obtained from the 1978 model. Horse mackerel appears in purse-seine catches from 1950 onwards, and landings of 62900 t and 429 t were recorded in 1960 in the purse-seine and demersal trawl fisheries respectively (Johnston & Butterworth, 2001). In recent decades any catches of horse-mackerel by the purse-seine fishery were assumed to comprise pelagic-feeding juvenile fish. The 1960 model, however, was prior to the collapse of the sardine stock and the subsequent lowering of mesh sizes in the mid 1960s which allowed for increased catches of juvenile fish (Crawford, 1989; Shannon, 2001), hence catch in 1960 is assumed to have been composed of adult fish.

14.) Mesopelagic fish: The lanternfish *Lampanyctodes hectoris* and the lightfish *Maurolicus muelleri* are grouped as 'mesopelagic fish'. Biomass of this little known group was estimated for all models, assuming an ecotrophic efficiency of 95%. P/B (1.2 yr^{-1}) and Q/B (12 yr^{-1}) were obtained from Jarre-Teichmann *et al.* (1998), originally derived from Hewitson & Cruickshank (1993). There is no record of either species in catches until 1968 (www.fao.org; Crawford *et al.*, 1987).

15.) Snoek: Thyrsites atun is the most abundant and hence commercially important large pelagic fish in the region, estimated to comprise 65% of the total large pelagic fish biomass (Penney *et al.*, 1991). No absolute biomass estimates are available, so biomass was estimated in all models using an ecotrophic efficiency of 95%. A P/B of 0.5 yr^{-1} and P/Q of 5.0 yr^{-1} were used, obtained from Jarre-Teichmann *et al.* (1998). A small-scale semi-directed demersal trawl fishery for snoek has operated off the Western Cape since the mid 1960s (Crawford *et al.*, 1987) and snoek is also caught as bycatch in the hake-directed fishery (although only retained since 1972) (Griffiths *et al.*, 2004). Despite this, the only recorded landings of snoek for the historic periods modelled are by the linefishery, one of the oldest fisheries operating in the region. Catches of 10300 t in 1960 and 275 t in 1900 are recorded (www.fao.org; Griffiths *et al.*, 2004).

16.) Other large pelagic fish: This group includes kob *Argyrosomus inodorus*, geelbek *Atractoscion aequidens*, yellowtail *Seriola lalandi*, carpenter *Argyrozona argyrozona*, hottentot *Pachymetopon blochii*, and tuna *Thunnus* spp. No biomass estimates are available for this group, so biomass was estimated using an ecotrophic efficiency of 95%. P/B (0.493 yr^{-1}) and P/Q (0.1) ratios were obtained from the 2000s and 1978 models. Landings of these species can be almost entirely attributed to the line fishery, which has been targeting these species since its beginning in the early 1800s, although some kob has been taken by the bottom-trawl fleet since 1917 (Crawford *et al.*, 1987). Landings for the group as a whole are recorded as 5249.3 t and 400 t by the linefishery and demersal trawl fleets respectively in 1960, and 3778.4 t by the linefishery in 1900 (Crawford *et al.*, 1987; Griffiths *et al.*, 2004).

17.) Cephalopods: Several species of cephalopod inhabit the southern Benguela, although no estimates of biomass exist for the historic periods modelled. The model was therefore allowed to estimate biomass assuming an ecotrophic efficiency of 95%. A P/B of 3.5 y^{-1} and P/Q of 0.35 were used as per Shannon et al. (2003). Landings of squid were reportedly 100 t (www.fao.org), with no catches recorded prior to 1958.

18-21.) Hakes: As mentioned previously, two species of Cape hake are found in the southern Benguela: the shallow water Cape hake *Merluccius capensis*, and the deep water Cape hake *M. paradoxus*. Hake were modelled as four discrete groups with regard to size and species (small *M. capensis,* large *M. capensis*, small *M. paradoxus* and large *M. paradoxus*), to allow for cannibalism and differences in diet between small (0-2 yr) and large (3 yr +) hakes (Shannon, 2001). Biomass of adult hake is estimated to have been 538 709 t in 1960 (Rademeyer & Butterworth, 2001). The proportion of the two species of hake found off South Africa was shown to be 25% *M. capensis* and 75% *M. paradoxus* on the west coast, and 91% *M. capensis* and 9% *M. paradoxus* on the south coast during the 1980s (Jarre-Teichmann *et al.*, 1998). The percentage of hake biomass on each coast during the 1970s and 1980s based on survey estimates and production models in Punt (1994) was 75% on the west coast and 25% on the south coast. These proportions were assumed to apply in 1960 as well, and the biomass of each species was calculated accordingly. No biomass estimate for adult hake was available prior to 1917, and of small hake for any of the years modelled, so in these cases biomass was estimated assuming an ecotrophic efficiency of 95%. P/B and Q/B, taken as 2.5 .y^{-1} and 0.15 for small hake, 0.8 y^{-1} and 0.182 for large *M. capensis* and 0.8 y^{-1} and 0.182 for large *M. paradoxus* were obtained from the 1978 and 2000s models. In 1960, landings by the demersal fishery of both species combined were recorded as 159 900 t. As the ratio of *M. capensis* to *M. paradoxus* during the 1980s and 1990s was shown to have been 1:3 in research cruise surveys (Shannon, 2001), this proportion was also assumed for 1960 in the absence of any other indications. In 1960, landings were only recorded off the west coast (ICSEAF division 1.6) as opposed to the south (Crawford *et al.*, 1987), and were attributed to each species accordingly. Hake landed were assumed to be large, as a market for small hake only developed in the 1980s, subsequent to large hake becoming more scarce (Griffiths *et al.*, 2004). No landings are recorded prior to 1955 (Crawford *et al.*, 1987).

22 & 23) Other demersal fish: Other demersal fish were modelled as two groups: pelagic-feeding species (group 22) and benthic-feeding species (group 23), as in previously constructed models of the region (Shannon *et al.*, 2003). Species were divided according to Meyer & Smale (1991a & b). Species included in the pelagic-feeding group are ribbonfish (*Lepidopus cordatus*), Cape John Dory (*Zeus capensis*), southern rover (*Emmelichhthys nitidus nitidus*), pencil cardinal (*Epigonus denticultatus*), cutlass fish (*Trichuiurus lepturus*), jutjaw (*Parascorpis typus*) and angelfish (*Brama brama*). As there are no estimates of biomass available for this group, the 1960, 1900 and 1600 models were used to estimate B at the time assuming an ecotrophic efficiency of 95%. A P/B of 0.7 $y^{-1}$and Q/B of 3.5 y^{-1} from the 1978 model were used for both demersal fish groups (Shannon *et al.,* 2004b). Of the pelagic-feeding demersal fish, only angelfish is commercially important today. The FAO reports a catch of 0.3 t of Cape John Dory in 1960 and no landings prior to 1958. As no other species appear in catch records for the time, 0.3 t was assumed as the catch for this group. Benthic-feeding demersal fish comprise kingklip (*Genypterus capensis),* Cape gurnard (*Chelidonichthys capensis),* African gurnard (*Trigloporus l. Africanus*), lesser gurnard (*Chelidonichthys queketti)*, redspotted tonguefish (*Cynoglossus zanzibarensis)*, beaked sandfish (*Gonorhynchus gonorhynchus)*, spinenose horsefish (*Congipodus spinifer)*, smooth horsefish (*Congiopodus torvus)*, large-scaled rattail (*Coelorinchus fasciatus)*, smooth-scaled rattail (*Malacocephalus* laevis), panga (*Ptreogymnus laniarius)*, jacopever (*Helicolenus dactylopterus)*, monkfish (*Lophius sp.)*, bank steenbras (*Chirodactylus grandis)*, hairy conger (*Bassanago albescens)*, and Agulhas and west coast soles (*Austroglossus spp.).* Biomass of this group was also estimated assuming an ecotrophic efficiency of 95%, due to a lack of other estimates. The FAO reports 1100 t kingklip, 2900 t panga, 1000 t west coast sole, and 700 t of jacopever landed in 1960, giving a total catch of 5700 t for benthic-feeding demersal fish (www.fao.org). As most of these species were only landed in numbers significant enough to be recorded only from the 1920s onward, no catches were assumed to have occurred in 1900 (Crawford *et al.*, 1987).

24 – 26) Chondrichthyans: Following Shannon *et al.* (2003), chondrichthyans were divided into pelagic feeders, benthic feeders, and apex predators. This was in order to contend with cannibalism difficulties in diet assimilation that arise if all are grouped together (see Table 2.1. for species). No biomass estimates for chondrichthyans were available for any of the time periods modelled, so biomass of all three groups was estimated assuming an ecotrophic efficiency of 95%. P/B and Q/B for all three groups were obtained as follows from Shannon (2001) and subsequent models: pelagic-feeding chondrichthyans 0.5 y^{-1} and 4.545 y^{-1}, benthic-feeding chondrichthyans 1.0 y^{-1} and 10.0 y^{-1}, and apex chondrichthyans 0.5 y^{-1} and 5.0 y^{-1}. Sharks and rays may not have raised much interest as a resource in the southern Benguela in the past (although a shark-directed longline fishery developed in the 1990s). However, they have not escaped the effect of increasing fishing pressure, as many species became by-catch in fisheries targeting other more lucrative resources, such as the demersal trawl fishery and the line fishery. As a result, what records there are of landings tend to be somewhat vague or lacking entirely. FAO catch statistics for 1960 purport landings of 1800 t of chondrichthyans as a group. As there is no record of which species this figure includes, the catch was split in the same proportion as that of 1978, when approximately 80% of chondrichthyans landed were benthic-feeding species and the remaining 20% pelagic-feeding. Catch in 1900 was assumed to be zero.

Table 2.1: Chondrichthyan species comprising the benthic-feeding and pelagic-feeding groups (Shannon, 2001).

Benthic feeders	Pelagic feeders
Electric ray *Torpedo fuscomaculata*	Mako sharks *Isurus oxyrhincus*
Blancmange skate *Raja wallacei*	Blue sharks *Prionace glauca*
Spearnose 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*
Thorntail stingray *Dasyatis thetidis*	Other skates and rays
Ragged-tooth shark *Carcharius taurus*	
Spotted gully shark *Triakis megalopterus*	
Puffadder shyshark *Haploblepharus edwardsii*	
Spotted catshark *Porodera africanum*	
Striped catshark *Porodera pantherium*	
Yellowspotted catshark *Scyliorhinus capensis*	
St Joseph's shark *Callorhincus capensis*	

27) Seals: The only species of seal breeding in the Benguela is the Cape fur seal *Arctocephalus pusillus pusillus*, currently breeding at 10 colonies in South Africa and 15 in Namibia (Griffiths *et al.*, 2004). Wickens *et al.* (1991) give the annual rate of increase in pup numbers in South Africa as 3.2% pa from 1972-1989, based on data from aerial surveys only available from 1972. Assuming this rate applied uniformly until 1960, and using a population: pup ratio of 5,2:1 (Wickens *et al.*, 1991), the South African population of Cape fur seals in 1960 can be calculated as approximately 250 300 individuals. However, this number was insufficient to support the trophic demands on seals in the system. As the aerial counts on which this figure was based are thought to be minimum estimates, a less conservative estimate derived from a total (southern

African) population estimate for the time was used in favour of this figure. The total population of Cape fur seals in 1960 was estimated as approximately 795 000 individuals by Best *et al.* (1997). Of these, 40% of individuals were assumed to have been located in South Africa and 60% in Namibia, as was the case in the 1980s and 1990s (Griffiths *et al.*, 2004; Heymans *et al.*, 2004; Shannon, 2001). Mass per individual was obtained using the total population and total biomass estimates for the 1990s (Best *et al.*, 1997; Shannon, 2001) and this was used to convert the 1960 population estimate to a biomass of 10128.5 t (0.046 $t.km^{-2}$). In the same way a southern Benguela biomass of 1650 t (0.0076 $t.km^{-2}$) was obtained for 1900 by using the total population estimate from Best *et al.* (1997), but this time assuming 50% of the population to be in South Africa as at this time the large colonies currently found in Namibia had yet to be established. The biomass of 29260 t (0.133 $t.km^{-2}$) used in the 2000s model was used for 1600, since although 23 colonies have become extinct since exploitation began, four of the mainland colonies that have since been established are of such size that they may well offset the loss of the other 23 colonies (David, 1989; Griffiths *et al.*, 2004). Although this is not certain, no other data exist and the biomass estimated by the model is far too low, due to the small number of predators consuming seals within the system. Therefore, the 2000s estimate was used as the best estimate available for the 1600 model as well. P/B (0.25 y^{-1}) and Q/B (19.306 y^{-1}) were obtained from Shannon (2001) and the 1978 model (Shannon *et al.*, 2004b). With Dutch sealers first recording a harvest of 45 000 individuals in 1610 (David, 1989; Griffiths *et al.*, 2004), seals appear to have been the first resource exploited at any significant level in the Benguela. A lack of any controls on harvesting until the late 1800s meant that increasing numbers of colonies were harvested to extinction. Those close to Cape Town were the first to be affected, but by 1900 at least 23 colonies, both in South Africa and Namibia, had become extinct (David, 1989; Griffiths *et al.*, 2004). By 1960 a permit system and limited season had been instituted, but harvesting continued to increase despite the introduction of a TAC in 1974, only dropping off after the market collapsed in 1983. Sealing activities ceased altogether in South Africa in 1990, although they continue even today at low levels in Namibia (David, 1989; Griffiths *et al.*, 2004). The majority of seals harvested are pups, because of the high value placed on their skins, but a smaller number of bulls are also taken and utilized for other by-products (e.g. seal oil). Landings were calculated assuming an average mass of 22.7 kg for pups (David, 1987) and 150 kg for bulls (Griffiths *et al.*, 2004). Using recorded numbers of pups and bulls harvested in South Africa, this translated into 254 t removed in 1960 and 196.5 t in 1900.

28) Cetaceans: The cetacean group comprised marine mammals such as Heavyside's dolphin *Cephalorhynchus heavisidii*, common dolphin *Delphinus delphis*, dusky dolphin *Lagenorhynchus obscurus*, bottlenose dolphin *Tursiops truncates* and Bryde's whale *Balaenoptera edeni*, all of which feed in South African waters. Other baleen whales are present in the system, with the southern right whale *Eubalaena australis* and humpback whale *Megaptera novaeangliae* amongst others having been heavily targeted by the whaling industry off South Africa. These whales are, however, highly migratory, for the most part feeding elsewhere and generally only moving into the southern Benguela to breed. While southern right whales have been recorded as consuming mesozooplankton in the southern Benguela (Verheye *et al.*, 1992), these two species are nonetheless not regarded as regular consumers in the Benguela (Smale *et al.*, 1994) and so have been excluded from the modelled cetacean group, as in previous models of the region (Jarre-Teichmann *et al.*, 1998; Shannon, 2001; Shannon *et al.*, 2004b). No biomass approximations are available for cetaceans for any of the periods modelled, and thus a rough estimate was generated by adding the biomass of cetaceans removed from the system between models to the current estimate. The model could not be allowed to merely estimate cetacean B, as the resulting figure would be based on the minimum B needed to sustain any catches and predation on the cetacean group and both of these are minimal for this group. As a result estimated B would be far below that which could be supported by the system and would not give an accurate representation of actual population levels, hence this method, although not precise, provided a less incorrect estimate. Approximately 543 Bryde's whales (the only exploited cetacean feeding within the system) are recorded as landed off South Africa (Best *et al.*, 1997) and approximately 1012 between 1900 and 1959. The 20% of recorded mass removed was added to this total, as in Heymans & Pitcher (2002), to account for fishery-related mortality. An average mass of 10.77 t per individual was assumed (Best & Rickett, 1984). Biomass was thus estimated as 25579.69 t in 1960 and 43045.31 t in 1900. The 1900 estimate was assumed to apply in 1600 as well, as no removals are recorded prior to 1900. Diet was adjusted proportionally in each model. Exploitation of cetaceans began as use of beached whales and dolphins and their products, with little active hunting taking place. Although European settlers arriving in 1652 made some efforts at whaling, they were not successful enough to have impacted populations, preferring to concentrate their efforts on sealing (Best & Ross, 1989). By 1900 foreign whalers, the first large-scale exploiters of whales in the south Atlantic, had been operating in the Benguela for over a hundred years, and a number of shore-based whaling stations had been set up by colonizers along the coast of South Africa and Namibia. Both shore- and boat-based operations initially targeted southern right whales, and later, as catches began to decline, focus was shifted to humpback whales. Although Bryde's whales were exploited during the 1900s, the last landing taking place in 1967, there are no records of landings in 1900 or 1960 (Best *et al.*, 1997).

29) Seabirds: The 15 species of seabird breeding in the southern Benguela region include the African penguin *Spheniscus demersus*, Cape gannet *Morus capensis*, four cormorants *Phalacrocorax* spp., three gulls *Larus* spp., great white pelican *Pelicanus onocrotalus*, four terns *Sterna* spp. and Leach's storm petrel *Oceanodroma leucorhoa* (Berruti, 1989; Whittington *et al.*, 1999), with other migrant species also feeding within the Benguela. To obtain biomass estimates for seabirds as a group, total biomass of the eight most abundant species (African penguin, Cape gannet, Cape cormorant, bank cormorant, white-breasted cormorant, crowned cormorant, great white pelican, kelp gull, Hartlaub's gull & swift tern) in 1960 and 1900 relative to that in the 1990s was established, based on population estimates (Berruti, 1989; Crawford *et al.*, 1983; Shannon and Crawford, 1999; Underhill & Crawford, 2005). The population target minima suggested for these eight species in Underhill & Crawford (2005) were taken as the 1600 population sizes, except in the case of African penguins, where the population target minimum of 400 000 individuals is less than a quarter of that of the already exploited 1900 population. In this case the 1900 population of approximately 1 612 700 individuals was assumed in 1600 as well (Crawford *et al.*, 1983). Using the biomass estimate for seabirds in the 1990s southern Benguela model (2640 t) from Crawford *et al.* (1991) and used by Shannon *et al.* (2003), and the theoretical population sizes described above, estimates of the total biomass in 1960 and 1900 were generated. In 1960 the seabird biomass was taken as 3740 t, approximately 1.42 times greater than in the 1990s. 1900 and 1600 biomasses were both assumed to be 7920 t, approximately three times that of the 1990s. Although human impacts on seabird populations are varied, ranging from exploitation of birds, to habitat modification, guano harvesting and by-catch mortality, only the effects of direct exploitation in the form of harvesting of eggs or birds themselves can be taken into account by the model, due to the trophic basis of these models. The harvesting of penguin eggs and sometimes the birds themselves had been practiced since the arrival of the first seafaring European visitors to Southern Africa, who used them as provisioning for their ships (Randall, 1995). Lack of any monitoring or regulation resulted in the loss of a number of breeding colonies (Crawford *et al.*, 1995), although later the majority of eggs were taken from Dassen Island near Saldanha Bay, off the west coast of South Africa, with 13 million eggs harvested there between 1900 and 1930 (Randall, 1989). Records of egg harvests since 1871 are available (Best *et al.*, 1997). The small number of eggs recorded as harvested in 'southern Africa' over and above those from Dassen Island was divided between the northern and southern Benguela, as no indication of origin was available. The potential number of penguins these eggs could have produced was then calculated assuming hatching success of 0.548 and fledging success of 0.37 (Shannon & Crawford, 1999). Assuming the average mass per individual to be approximately 3.2 kg (Crawford & Whittington, 2005), removals of seabirds were taken as 7.95 t in 1960 and 60.3 t in 1900.

2.2.2. Balancing of the models:

2.2.2.1. Biomass:

Apex chondrichthyans:

The unbalanced 1960s model could not estimate a biomass of apex chondrichthyans, as this group is not consumed within the system. The biomass used in the 1978 and 2000s models (0.045 $t.km^{-2}$) was therefore assumed in the 1960, 1900 and 1600 models.

Gelatinous zooplankton:

Gelatinous zooplankton is likely to be approximately 10-50% of the combined meso- and macrozooplankton biomass (Shannon, 2001). When the models were allowed to estimated biomass for this group, estimates for all historic periods fell far below this range, owing to the low degree to which gelatinous zooplankton is consumed within the system. As the estimate of 5 t/km^2 used in the 1978 (Shannon *et al.*, 2004b) and 2000s models falls well within these limits for the three historical periods modelled, this estimate was used for all models.

Hake:

Biomass estimates for hake are only available from 1917 onwards, but the 1917 estimate of 972 000 t of adult hake remains approximately constant from 1917 until the 1940s (Rademeyer & Butterworth, 2001). Since biomass estimates provided by the 1900 and 1600 models were far below the stock assessment model estimates for 1917 – 1940 (prior to direct exploitation), the estimate of 972 000 t was therefore also assumed for the 1900 and 1600 models.

2.2.2.2 Balancing the 1600 model:

EE for all groups was < 1, but as in the 1900 model the biomass of mesopelagic fish (13.6 $t.km^{-2}$) was conspicuously higher than the estimated maximum for the 1980s. Therefore, the proportion of mesopelagic fish in the diet of other groups was reduced (see Appendix A., Table A.2 for balanced diet).

2.2.2.3 Balancing the 1900 model:

Ecotrophic efficiency (EE) of seals was initially calculated as 8.684. The contribution of seals to the diet of apex chondrichthyans was consequently decreased from 3 to < 1%, while the benthic-feeding chondrichthyans and adult horse mackerel components were correspondingly increased (see Appendix A., Table A.3 for balanced diet). B of mesopelagic fish estimated by the model was 12.738 $t.km^{-2}$, outside the range estimated for this group in the 1980s by Armstrong *et al.* (1991). As a result the proportion of mesopelagic fish in the diets of predators was decreased until the biomass required was inside the upper limit of the suggested biomass for this group (approximately 10.9 $t.km^{-2}$).

2.2.2.4. Balancing the 1960 model:

The unbalanced model calculated ecotrophic efficiencies of 6.454 and 1.05 for anchovy and seals respectively. The unbalanced diet was based on the ecosystem as it stood in 1978, at which time anchovy dominated the small pelagic community. In 1960 sardine were the dominant small pelagic fish. To account for this shift in abundance, the proportion of anchovy and sardine in the diets of all predator groups were substituted for one another, so that sardine were consumed in a greater proportion than anchovy. The EE of anchovy remained > 1 however, and minor adjustments to its contribution to the diets of its main predators were made to rectify this (see Appendix A., Table A.4 for balanced diet). The contribution of seals to the diet of apex chondrichthyans was reduced from 3 to 2.5%, with a compensatory increase from 2.5 to 3% in the proportion of adult horse mackerel consumed.

2.2.3. Network analysis:

Most outputs are estimated by *EwE* according to the equations outlined in Chapter 1. Network analyses performed using routines in *Ecopath* produce indices such as total system throughput and aggregated trophic level. Total throughput is described by Ulanowicz (1986) as the 'size of the entire system in terms of flow'. The trophic level (TL) of selected groups was calculated relative to their biomass contribution in the system as the weighted trophic level (TLw), according to the following equation:

$$TLw_i = TL_i\left(\frac{B_i}{B_T}\right)$$

where TLw_i is the weighted trophic level of group i; TL_i is the trophic level of group i; B_i is the biomass of group i; and B_T is the total biomass of all groups in the model excluding phytoplankton and detritus (Neira, 2007). TL of the community, excluding detritus and planktonic groups was calculated, with the TL of each group weighted according to its biomass contribution to the community. Similarly the TL of the piscivorous groups was also calculated.

2.2.4. Sensitivity analysis:

The sensitivity of the models to their parameters was tested by means of a mixed trophic impact assessment and sensitivity analysis built into the EwE software. The mixed trophic impact assessment, initially developed as a measure of interactions within the USA economy by Leontief (1951) has been adapted for use in ecology (Hannon, 1973), so that the influence of changes in the biomass of one group on that of other groups in the system can be measured. This process has been incorporated into *Ecopath* based on the routine developed by Ulanowicz and Puccia (1990). Mixed trophic impact in *Ecopath* is calculated according to the following equation:

$$MTI_{ij} = DC_{ij} - FC_{j,i}$$

Where i represents the impacting group, j the impacted group. DC_{ij} is the contribution of j to the diet composition of i and $FC_{j,i}$ gives the proportion of predation on j due to i (Christensen *et al.*, 2000).

The sensitivity analysis routine in *Ecopath* alters the basic input parameters in 10% steps to +50% and -50% of their original values. The effects of these alterations are then reported as the proportion of the original value by which the affected parameter has changed.

2.3. Results:

2.3.1. Internal indices:

2.3.1.1. Biomass:

The change in biomass of selected groups (some have been aggregated) over the period 1600 - 2000 are presented in Fig. 2.1. The following groups showed an increasing trend in biomass over time: phytoplankton, micro- and mesozooplankton, anchovy, sardine, chub mackerel, horse mackerel, snoek, other large pelagic fish, chondrichthyans and seals. Those groups that demonstrated a decreasing trend include the following: macrozooplankton, benthic producers, redeye, other small pelagic fish, mesopelagic fish, cephalopods, hake (adult and juvenile), pelagic- and benthic feeding demersal fish, cetaceans and seabirds. Although a number of species depicted in Fig. 2.1 that have been impacted either directly or indirectly by fishing actually show an increasing trend (sardine, anchovy, horse mackerel and snoek), the biomass of many of those that have felt the effect of fishing over time has declined (redeye, cephalopods, other demersal fish, hake, cetaceans and seabirds). In the 1600 and 1900 models, anchovy is the dominant small pelagic, while sardine biomass was estimated to have been low if the structure of the small pelagics in the 1978 model is adopted and these diet compositions used as the source of unbalanced diet composition for 1600 and 1900. Small pelagics communities are characterised by having one dominant species and one or more much less abundant species at a time, and though the dominant species can and does change in what are termed 'regime shifts' (Schwartzlose *et al.*, 1999), no evidence exists as to which species dominated during these time-periods. As a result the diet in 1978, when anchovy happened to be dominant, was used to determine the relative biomass of each species in 1600 and 1900.

Biomass of the non-planktonic consumers within the system (Fig. 2.2) decreased from <1600 until 1960, subsequently showing a marked increase in the 2000s, resulting in an overall increasing trend. If one excludes sardine and anchovy from the groups examined, however, the decreasing trend carries through to the 2000s which show only a small increase in the biomass of other predator groups since 1960.

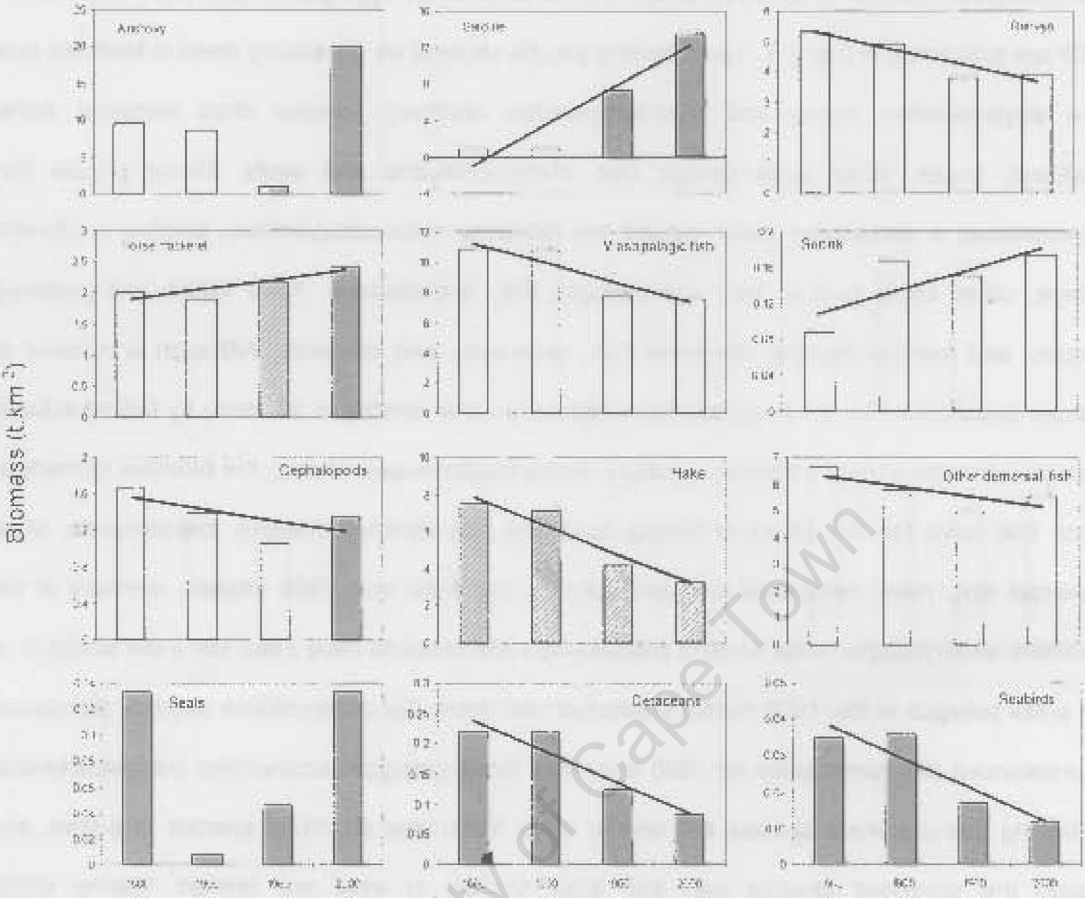


Figure 2.1: Biomass of selected groups over the time-period modelled. ▇ = B obtained from input data (measured data/ stock assessment estimate); ▨ = aggregate of groups, B of some obtained from input data, some estimated by the model. ▭ = B estimated by the model. The biomass depicted for horse mackerel, hake and other demersal fish is comprised from two or more component groups (e.g. juvenile and adult).

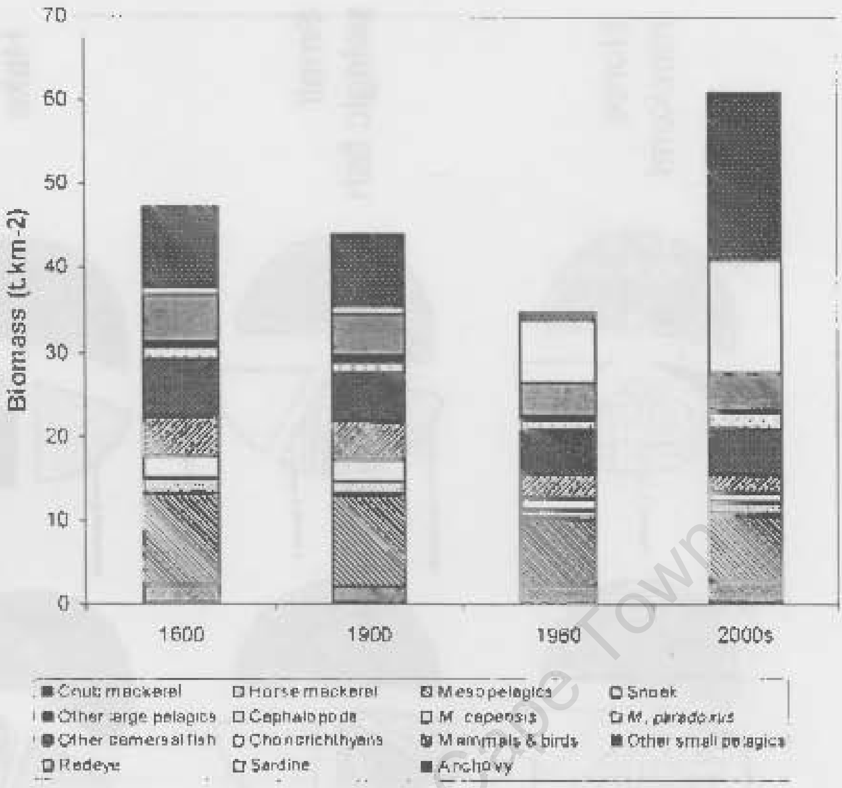


Figure 2.2: Biomass of non-planktonic consumers in the southern Benguela in each of the periods modelled. Seals, cetaceans and seabirds have been aggregated into 'mammals and birds'.

2.3.1.2. Consumption:

The relative consumption of hake, small pelagic fish and horse mackerel by their predators (Fig. 2.3.) was shown to be dominated in all instances by hake itself, although decreasingly with time in all three groups., For example, 54% of horse mackerel was consumed by hake in the <1600s models, whereas in the 2000s model, predatory fish (35.3%) consumed almost the same proportion of horse mackerel as did hake (36.3%). For all three groups, mortality as a result of fishing became apparent only in the 1960 models, but for these and the 2000s models, fishing 'consumed' a significant proportion of production. Some 55 % of hake was cannibalised in the <1600 model, compared with 34% in the 2000s model when 14% of hake was estimated to be consumed by fishing. Cephalopods also played an increasingly significant role in the consumption of hake, being responsible for 27% of its consumption in the 2000s model. Hake and predatory

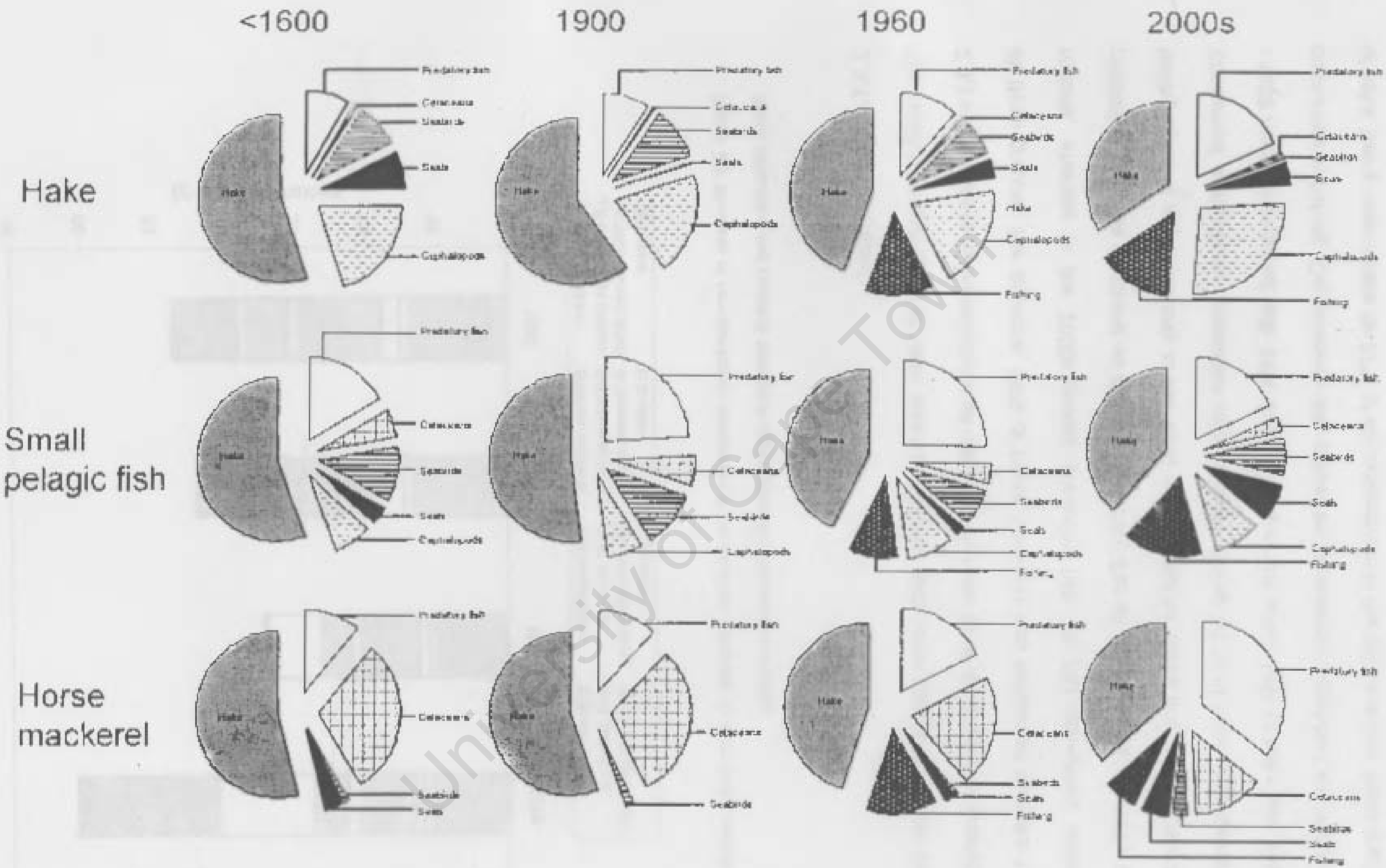


Figure 2.3: The proportion of production of the hakes, small pelagic fish (includes anchovy, sardine, redeye and other small pelagics) and horse mackerel (adult and juvenile combined) consumed by their various predators in the southern Benguela for each period modelled.

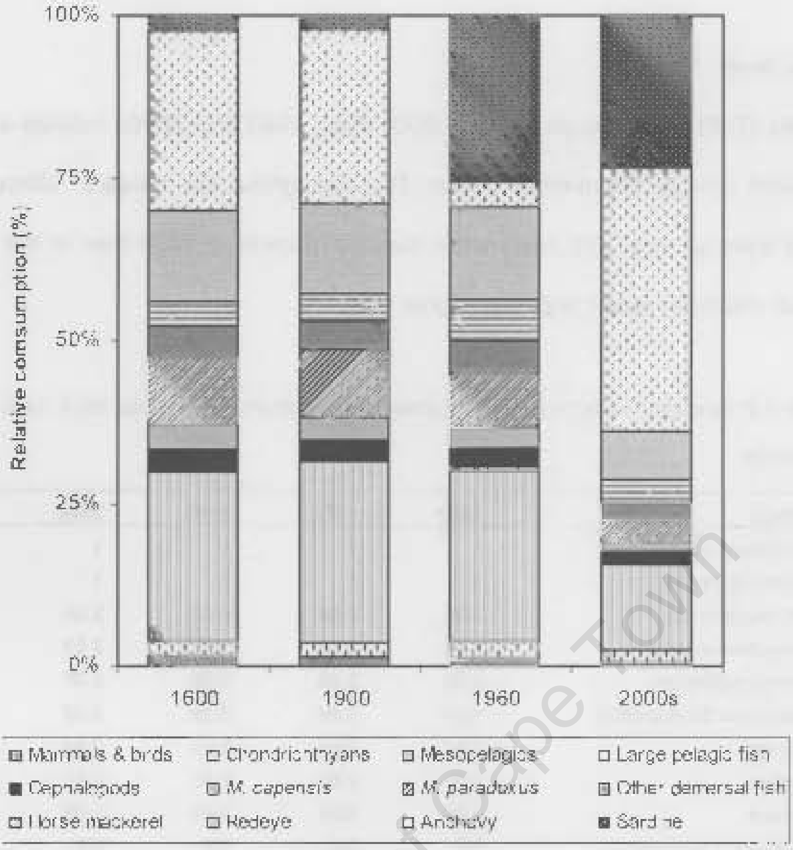


Figure 2.4: The relative consumption by key groups in the southern Benguela in each of the periods modelled. Consumption by chondrichthyan groups was aggregated, as was that of seals, cetacean and seabirds, juvenile and adult horse mackerel, and juvenile and adult groups for both hake species.

fish predated the highest proportions of small pelagic fish in the <1600 model (55% and 17% respectively), and although they were still the top consumers of this group in the 2000s model it was by a smaller margin, contributing 39% and 18% respectively, while fishing consumed 16%.

A comparison of the consumption of production by key groups relative to one another (Fig. 2.4) shows small pelagics to be the chief consumers within the system, responsible for up to 71% of consumption in the 2000s model. Mesopelagic fish contributed the highest consumption of any single group, followed by sardine. Consumption by top predators such as seabirds and marine mammals remained low in all models.

2.3.1.3. Trophic level:

The trophic levels (TLs) of all groups in the <1600, 1900, 1960 and 2000s models are presented in Table 2.2. Most groups maintained similar TLs throughout the models, although those of cephalopods, all hake groups, and seals were marginally lower in 2000 than in the 1600 model, while that of chub mackerel was marginally higher.

Table 2.2: Estimated trophic level of each group in the southern Benguela for 1600, 1900, 1960 and the 2000s.

Group	1600	1900	1960	2000
Phytoplankton	1	1	1	1
Benthic producers	1	1	1	1
Microzooplankton	2.05	2.05	2.05	2.05
Mesozooplankton	2.53	2.53	2.53	2.53
Macrozooplankton	2.86	2.86	2.86	2.86
Gelatinous zooplankton	3.29	3.29	3.29	3.29
Anchovy	3.54	3.54	3.54	3.54
Sardine	2.91	2.91	2.91	2.91
Redeye	3.66	3.66	3.66	3.66
Other small pelagics	3.6	3.6	3.6	3.6
Chub mackerel	4.01	4.01	4	4.08
Juvenile horse mackerel	3.61	3.61	3.61	3.61
Adult horse mackerel	3.79	3.79	3.78	3.79
Mesopelagic fish	3.73	3.73	3.73	3.73
Snoek	4.54	4.54	4.25	4.5
Other large pelagics	4.51	4.51	4.43	4.51
Cephalopods	3.93	3.93	3.89	3.91
Small *M. capensis*	4.17	4.17	4.06	4.11
Large *M. capensis*	4.75	4.75	4.56	4.65
Small *M. paradoxus*	4.01	4.03	3.99	4.01
Large *M. paradoxus*	4.62	4.61	4.6	4.61
Pelagic-feeding demersals	4.17	4.17	4.16	4.17
Benthic-feeding demersals	3.43	3.46	3.46	3.46
Pelagic-feeding chondrichthyans	4.97	4.97	4.94	4.96
Benthic feeding chondrichthyans	3.56	3.56	3.56	3.56
Apex chondrichthyans	4.8	4.77	4.79	4.8
Seals	4.73	4.74	4.57	4.55
Cetaceans	4.6	4.6	4.6	4.58
Seabirds	4.58	4.58	4.35	4.38
Meiobenthos	2	2	2	2
Macrobenthos	2.16	2.16	2.16	2.16
Detritus	1	1	1	1

2.3.1.4. Fishing:

The total catch the contribution by various species and mean TL of catch are shown in Fig. 2.7. 3.50 $t.km^{-2}$ of biomass were removed annually from the southern Benguela by fishing during the 2000s, compared with 2.76 $t.km^{-2}$ in 1960 and 0.02 $t.km^{-2}$ in 1900. Sardine constituted the greatest proportion of landings in 1960 (1.45 $t.km^{-2}$). While still the second largest constituent of catch in the 2000s with 0.991 $t.km^{-2}$ landed, sardine had in the interim (1970s and 1980s) been overtaken by anchovy and in the 2000s 1.17 $t.km^{-2}$ anchovy was landed annually. Hake (both species) were landed in similar quantities in 1960 (0.73 $t.km^{-2}$) and the 2000s (0.72 $t.km^{-2}$), although in 1960 landings consisted entirely of large hake and by the 2000s small hake also formed part of the catch. The average trophic level of the catch dropped from 4.52 in 1900, to 3.53 in 1960, increasing slightly to 3.63 by the 2000s.

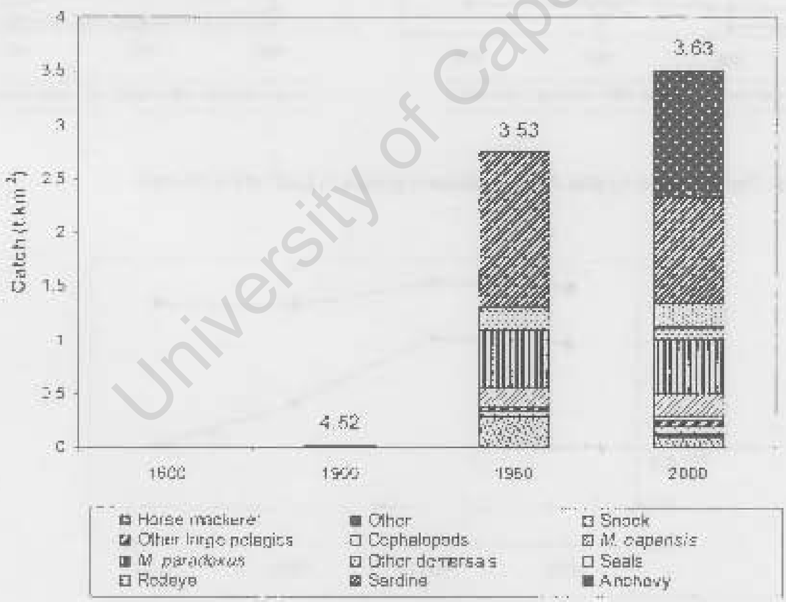


Figure 2.7: Total removals and catch composition by group for each of the periods modelled. The mean TL of the catch is indicated above the column depicting total catch for that model.

2.3.1.5. Mortality:

.In 1900, fishing comprised a fairly substantial proportion of the mortality of large pelagic fish and seals, and by 1960 fishing mortality (F) was playing a more significant role in the overall mortality of many species, such as hake (large *M. capensis* and to a greater extent large *M. paradoxus*), sardine, chub mackerel and horse mackerel (see Fig. 2.8 for coefficients of mortality). The pattern in the 2000s was similar to 1960, with snoek, other large pelagics and large hakes still having the greatest proportions of mortality resulting from fishing. On the other hand, the proportion of chub mackerel and sardine mortality ascribed to fishing had dropped by the 2000s. A number of previously unexploited species (e.g. small hakes and horse mackerel, anchovy, redeye, other small pelagic fish, pelagic-feeding demersal fish) began to show a relatively low proportion of fishing mortality in the 2000s. Although a high proportion of predation mortality is expected, this must also be considered to some extent an artefact of the high EE (95%) applied to most groups,

2.3.2. System indices:

Table 2.3 shows the summary statistics for the models. Total biomass, consumption, throughput, production and respiratory flows all decreased from <1600 to 1960 and then increased again to varying degrees in the 2000s. Exports (catches, emigration, or consumption by predators not resident in the system) (Christensen,*et al.*, 2000) and flows to detritus both show the inverse – increasing from <1600 to 1960, after which they decrease in the 2000s. Net primary production decreased from <1600 to a minimum in the 2000s. Finn's cycling index, shown in Fig. 2.9, decreased from the <1600 model to 1960, increasing to a maximum in the 2000s model. The same pattern was exhibited by Finn's mean path length (Fig. 2.9). Shannon's and Simpson's diversity indices both showed similar results, decreasing from 1600 to 1960, then increasing again in the 2000s, although in both cases not to the same level as the 1600 model (Fig. 2.10). Transfer efficiency (TE) between trophic levels was constant in the 1600 and 1900 models. TE's in the 1960 model followed the same pattern, then increased at higher TLs. TE's in the 200s model were the lowest at low TLs, then increased to match those of the 1960 model between the higher TLs. Odum (1985) suggested a suite of indices to be used as an indication of whether or not a system is stressed. Selected indices and the expected and actual trends from the 1600 model until the

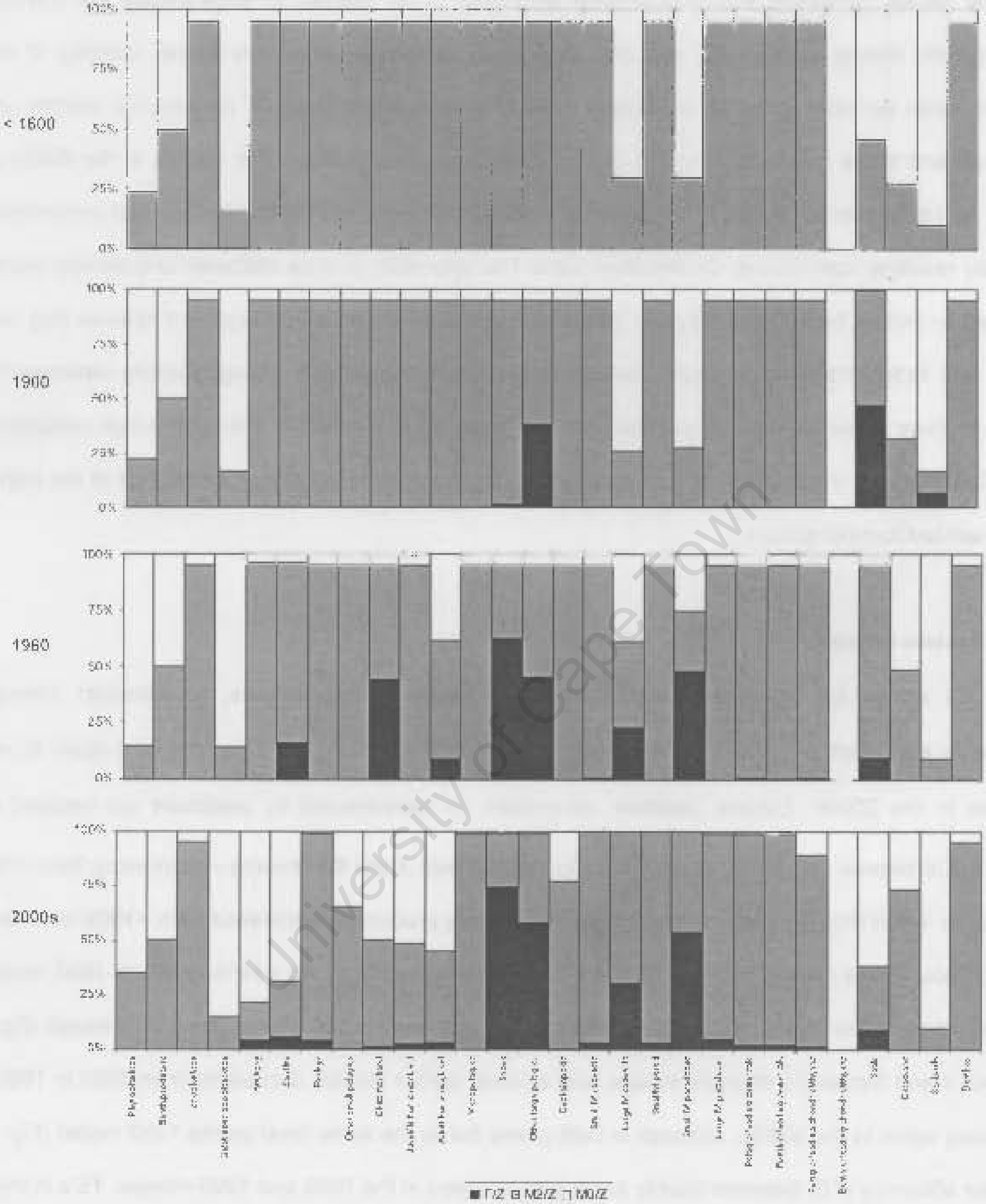


Figure 2.8: Coefficients of mortality by group in the southern Benguela for each period modelled. Zooplankton groups and benthos have been aggregated. F/Z is the proportion of mortality resulting from fishing, M2/Z is the proportion as a result of predation, and M0/Z is other mortality.

Table 2.3: Summary statistics for each southern Benguela model. All statistics are in $t.km^{-2}.y^{-1}$, except for biomass, which is in $t.km^{-2}$.

	1600	1900	1960	2000s
Total biomass (excluding detritus)	230	214	187	274
Sum of all consumption	7959	7362	5062	5355
Sum of all exports	7731	8053	9124	6682
Sum of all flows into detritus	10716	10759	10955	9065
Total system throughput	30650	30083	27887	29676
Sum of all production	13930	13778	13084	13080
Sum of all respiratory flows	4244	3910	2746	5256
Calculated total net primary production	11975	11962	11870	10611

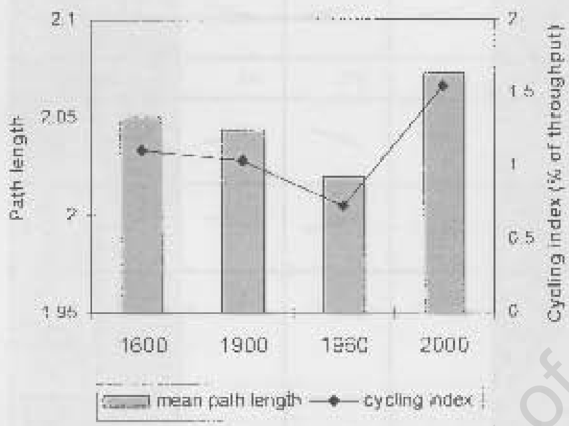


Figure 2.9: Finn's mean path length and cycling index for each period in the southern Benguela

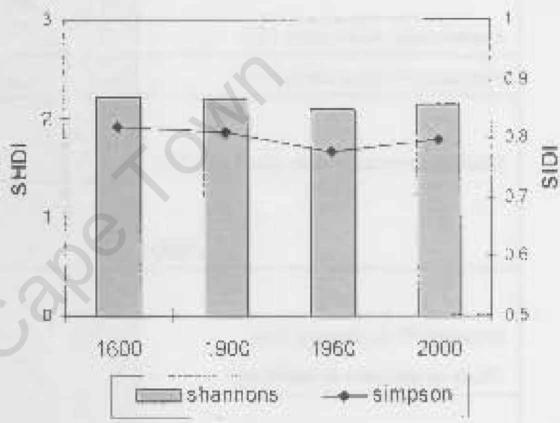


Figure 2.10: Diversity indices for each period in the southern Benguela. SHDI is Shannon's diversity index, SIDI is Simpson's diversity index.

Table 2.4: Transfer efficiencies (all flows) between trophic levels (TL) in each of the southern Benguela models

TL	2000s	1960	1900	1600
1				
2	19.9	19	19.7	19.6
3	25.1	26.1	27.2	27.1
4	14.3	18.6	18.5	18.6
5	8.2	11.2	10.2	10.3
6	11.5	11.2	8.2	8.4
7	8.5	8.5	6	6
8	6.9	7.3	5.3	5.3
9	5.1	6.5	4.5	4.5
10	0.6	0.6	0.6	0.6
11				

present, as well as between each successive model, are displayed in Fig. 2.11. Only the overall trend in community respiration and diversity indices are those expected of a stressed ecosystem. In most cases however the trend from 1600- 1900 and 1900-1960 are those of a stressed system, and opposite to the trend from 1960- 2000s, which for the most part exhibits the same trend as found overall.

System indices (Odum, 1985)	Expected trend (stressed ecosystems)	1900	1960	2000s	Overall trend (1600-2000s)
Community respiration (R)	↗	↘	↘	↗	↗
Production/ respiration (P/R)	<1 or >1	>1	>1	>1	>1 (↓)
Maintenance:biomass structure(P/B)	↗	↗	↗	↘	↘
(R/B)	↗	↘	↘	↗	↘
Unused PP & nutrient loss *(Sum of all flows to detritus)*	↗	↗	↗	↘	↘
Vertical cycling of nutrients *(Finn's cycling index)*	↘	↘	↘	↗	↗
Proportion of r strategists. Size & lifespan of organisms *(B/P)*	↘	↘	↘	↗	↗
Length of food chain *(Finn's mean path length)*	↘	↘	↘	↗	↗
Species diversity *(SIDI)*	↘	↘	↘	↗	↘
(SHDI)	↘	↘	↘	↗	↘

Figure 2.11: Trends in selected indices, as from Odum (1985), indicating ecosystem stress in the southern Benguela. For indices of species diversity *SIDI* is Simpson's diversity index and *SHDI* is Shannon's diversity index.

2.3.3. Sensitivity analyses:

Results from the mixed trophic impact assessment are presented in Appendix A., Figs 1-4. In all models the dominant small pelagic of the time had relatively large impacts on other groups, for the most part negative except with regard to the large pelagics and top predators which prey on them. The hake groups also had significant impacts on other groups, the majority of which were negative. As fishing became more prevalent in 1960 and the 2000s, it also had a noticeable impact on other groups. The larger of these impacts were negative and on those groups targeted by fishing, although the fisheries did exert positive impacts on groups such as juvenile horse mackerel, mesopelagic fish and the small hake groups. In the 2000s the fisheries exerted the largest influence over other groups.

The sensitivity analysis performed on each model showed that groups having a strong influence were relatively few whilst those affected were more numerous. Effects were considered 'strong' if a 40% or more change in the value of the estimated parameter was triggered by the change in the original parameter. In all but the 2000s model, pelagic chondrichthyans had a very strong influence on almost all other groups apart from top predators when its Q/B was increased by even 10%. Similarly, demersal-feeding chondrichthyans also had a wide-ranging influence in the same models, but only after input parameters, specifically P/B and Q/B, were altered by a minimum of 20%. Groups whose input parameters that had a significant influence on other parameters and the groups affected by each are listed in Table 2.4. For the full results of the sensitivity analysis including which parameters were affected see Appendix A., Tables A.8-11.

2.4. Discussion:

2.4.1. Internal indices:

The biomasses from the models appear to suggest that while top predators may have experienced a decline since their pristine levels, this is not necessarily true for those groups operating at lower trophic levels, namely the small pelagics. Sardine and anchovy biomasses in

Table 2.4: Results from sensitivity analysis, showing groups that had strong impacts and the affected groups in each time period modeled. For comprehensive results see Appendix A., Tables A.8-11

Group	1600	1900	1960	2000s
Microzooplankton	Phytoplankton	Phytoplankton	Phytoplankton	Phytoplankton
Mesozooplankton	Phytoplankton Microzooplankton	Phytoplankton	Phytoplankton Microzooplankton	- -
Macrozooplankton	- - -	Microzooplankton Mesozooplankton -	Phytoplankton Microzooplankton -	Phytoplankton Microzooplankton Mesozooplankton
Meiobenthos	-	-	-	Benthic producers
Macrobenthos	Meiobenthos	Meiobenthos	Meiobenthos	Benthic producers
Cephalopods	Meiobenthos Macrobenthos	Meiobenthos Macrobenthos	small hakes -	Juvenile horse mackerel -
Benthic-feeding demersals	Meiobenthos Macrobenthos - -	Meiobenthos Macrobenthos - -	Meiobenthos Macrobenthos Pelagic-feeding demersals Benthic-feeding chondrichthyans	Meiobenthos Macrobenthos Benthic producers -
Apex chondrichthyans	Other large pelagic fish Pelagic-feeding chondrichthyans Benthic-feeding chondrichthyans Cetaceans	Pelagic-feeding chondrichthyans Cetaceans - -	Pelagic-feeding chondrichthyans Benthic-feeding chondrichthyans - -	Cetaceans - - -

the southern Benguela have in recent years reached extraordinarily high levels, approximately three times that estimated for the 1980s, and not thought to be sustainable (Shannon *et al.*, 2004b). Nonetheless as the comparisons made in this thesis cover the time period from 'pristine state' to the current condition of the system, these unusually high biomasses have been included in the analyses, but should not prevent the observation of the underlying trends. For example, if sardine and anchovy are excluded when considering total non-planktonic biomass (Fig. 2.2) the increasing trend initially observed falls away and the biomass of predators within the models can be seen to have decreased since the pristine state. The decreased proportion of predation on important groups attributable to 'natural' predators e.g. hakes as opposed to fishing (Fig. 2.3) and the declining weighted trophic levels of predator groups (Fig. 2.5) are all symptomatic of the decline in predator biomass. While the biomass of the majority of fished groups in the models did decrease towards the present, as mentioned above the same cannot be said for the small pelagics. Evidence of 'wasp-waisted' control of trophic interactions by small pelagic fish has been postulated for some of the upwelling systems of which they are characteristic, e.g. Humboldt and Benguela Current systems (Cury *et al.*, 2000, Cury *et al.*, 2005a). 'Wasp-waist' control is the term used for trophic flow control where a trophically intermediate group, small pelagic fish, concurrently exerts top-down control on the lower trophic levels, such as zooplankton, and bottom-up control on top predators including fishers (Cury *et al.*, 2000). The recruitment of pelagic fish themselves is influenced by food availability and physical processes, environmental factors being seen as the major determinants (Bakun, 1996; Cury *et al.*, 2000). It is therefore unlikely that these increases in biomass result either directly or indirectly from fishing or the management thereof, but rather as a result of fluctuations in the state of the physical environment. The larger biomasses of several groups in the 2000s may also in part reflect the fact that biomasses in earlier periods modelled are conservative estimates of the minimum biomasses required to sustain catches and predation in earlier models, whereas actual biomass estimates are available for several groups in the 2000s model. The lower fishing mortality of groups such as chub mackerel and sardine in the 2000s are explained to some extent by the unconstrained nature of the biomass inputs in the 2000s model versus those estimated for 1960. Although a decrease in the relative abundance of small pelagics versus demersal fish and small pelagic predators in the southern Benguela over the 1980s and 1990s has been shown (Cury *et al.*, 2005b), this is representative of a much shorter time-scale, and thus is not necessarily contradictory of the increase in planktivorous fish relative to predatory fish portrayed here.

The changing patterns in the consumption of groups such as the hakes (Fig. 2.3) reflect the onset of the influence of fishing as a 'predator' and the more recent increase in small pelagic biomass and are compounded by the concurrent, although lesser, declines in biomass of other predators. The increasing contribution of small pelagics to the consumption within the system may be indicative of the increasing prevalence of lower trophic level groups as the proportion of higher level predators declines, largely due to fishing. Evidence of a change in the structure of an ecosystem such as this can be found in the mean trophic level (TL) of the fish landed by fisheries operating in the region (Pauly & Palomares, 2005). This phenomenon, otherwise known as 'fishing down the marine food web' (Pauly *et al.*, 1998) has been shown to occur globally in areas that have a history of fishing activity (Pauly & Palomares, 2005). In the southern Benguela this effect has been exaggerated by the abundance of both sardine and anchovy in the first half of the 2000s and their resulting increased contribution to overall landings. The small increase in mean TL of the catch between 1960 and the 2000s can be attributed to the increased contribution of anchovy, which operates at a slightly higher TL than the previous mainstay of the fishery, sardine, to small pelagic landings. Decreasing TL of catch over time could be explained merely as a change in the focus of fisheries from longer lived species operating at higher trophic levels (e.g. snoek, other large pelagics) to smaller, shorter lived species such as sardine and anchovy, and not necessarily a symptom of changes in the food web structure. If this were the case however, the declining trophic level of the catch would be accompanied by an increase in biomass removed, which certainly occurs from the 1900 model to the 2000s. Even considering the removals by whaling, which have not been included in these models due to the lack of trophic involvement of harvested whale species in the system, total biomass removed has drastically increased since the early 1900s (Griffiths *et al.*, 2004). The marked decline in the mean TL of both the community as a whole (excl. detritus and planktonic groups) and the piscivorous community (Fig. 2.6), particularly from 1900 to 1960, also appears to support the idea that smaller, shorter-lived species have become more predominant since the advent of industrial fishing. The decline in community TL from 1960 to the 2000s may be explained as an increase in the B of lower TL groups such as the small pelagic fish, rather than a decrease in that of the larger predators, and hence the pattern was not repeated in the piscivorous groups whose TL remained constant over this period. The same cannot be said for the period from 1900 to 1960 however, as no increase in small pelagic B accompanied this lowering of the community TL. While conclusive evidence of fishing down of the food web may not be forthcoming from catch statistics, and in any event one cannot use evidence from the fishery alone as proof of a change in ecosystem structure without far more data than was available for this study, if the declining biomass and TL of predators as estimated by the models is also considered it would seem that system-level changes have indeed occurred in the southern Benguela. This increased abundance of r-strategy species, shorter lived and of a smaller size, are also symptomatic of an ecosystem under stress (Odum, 1985). The marked differences in many indices over the period 1900 to the present would seem to implicate fishing either directly or indirectly as a major stressor and significant instigator of these changes. Large-scale changes in the southern Benguela, specifically with regard to zooplankton and small pelagic abundance, have been recorded since the 1950s (Verheye *et al.,* 1998; Verheye *et al.*, 1998; Schwartzlose *et al.,* 1999). These changes in the abundance and structure of the small pelagic fish community have in turn been linked to fluctuations in and changes to the diet composition of seabird populations and large pelagic predators (Crawford & Dyer, 1995; Crawford & Jahnke, 1999) as well as changes in the diet composition of predators such as snoek. Although fishing pressure has been modified many times over this period, this has not been the only variable – evidence that environmental forcing has been instrumental in these changes in community structure is also available. Increased upwelling over this period is thought to have resulted in the increase in zooplankton abundance observed on the west coast of South Africa since the 1950s (Verheye *et al.*, 1998). Different physical conditions result in divergent phytoplankton size structure and hence distinctive zooplankton community structures (Mitchell-Innes & Pitcher, 1992; Painting *et al.*, 1993). Differences in diet between sardine and anchovy mean that an environment dominated by smaller cyclopoid copepods would favour sardine, while one where large calanoid copepods were abundant would favour anchovy (Van der Lingen *et al.,* 2006a). It is therefore possible that physical changes in the environment have been responsible for the changes in sardine and anchovy abundance in the southern Benguela via bottom-up effects. Verheye *et al.* (1998), however, suggest that the increasing dominance of larger zooplankton was rather a result of top-down feeding pressure by the higher sardine population at the time on smaller zooplankton, The latter argument would imply a greater role to be played by fisheries in the structuring of the ecosystem.

2.4.2. System indices:

Although total biomass displayed an increasing trend from 1600 to present, this is an artefact of the extremely high small pelagic biomass of the early 2000s and model assumptions which restrict biomass of many groups in earlier models (i.e. high EE). Although the high biomass in the 2000s should not be ignored, comparisons with previous biomasses do not allow for a representative portrayal of changes within the system. The substantial decline in estimated total biomass from 1600 to 1960 possibly gives a more accurate, or at the least more explicit impression of the general trend. It should be noted however that even excluding the extreme small pelagic biomasses of late, the trend in total biomass from 1600 to the 1980s or 1990s, while still negative, is less pronounced than from 1600 to 1960, following the slow recovery of small pelagic stocks over these decades. Finn's mean path length was positively linked by Odum (1969) to system maturity. The decline in mean path length (Fig. 2.8) displays the expected trend of increasing stress and decreasing maturity from pristine state to the 1960s as fishing became a factor and food chains shorten as top predator abundance declines (Odum, 1985). The opposite trend from 1960 to the 2000s, as in many indices considered, is much stronger and again results in an overall positive trend, suggesting that the 2000s system is more mature than the pristine 1600 system. Nutrient cycling within the system follows the same pattern (Finn's cycling index, Fig. 2.8), also displaying the expected response to stress as proposed by Odum (1985) until 1960, then reversing for the 2000s. This interpretation of this index is unclear however, with Wulff and Ulanowicz (1989) suggesting that cycling may in fact be reduced as system maturity increases. Lower TE's between low TLs in the 2000s model may be ascribed to the high B found at these levels compared to higher TLs. Similarly the higher TE between higher TLS for bith the 1960 and 2000s model may reflect the lower relative B at these higher levels when compared to earlier models.

With few exceptions, the community indices examined in Fig. 2.11 between the 1600 and 1900 models and the 1900 and 1960 models display trends expected of stressed ecosystems, according to Odum (1985), where stress is defined as a 'detrimental or disorganising influence'. Although other stresses, of environmental origin, have doubtless been brought to bear upon the system over this time period, in all likelihood they either occurred over too short a time-scale to be distinguishable here, or are outside of the capabilities of a mass-balanced modelling routine such as *Ecopath* to adequately describe. As a result, any evidence of stress detected from the models is considered to be a result of fishing pressure. When one observes the overall trend from pristine to present, however, the southern Benguela does not appear 'stressed' as such. The opposite in fact – for the most part indicators suggests that the ecosystem has not been negatively affected since its pristine state. This unexpected result can largely be ascribed to the overriding influence of the anomalous 2000s system. The recovery and subsequent overabundance of the small pelagics in recent years appears to have masked the impacts of fishing as a stress. As other changes within the system were evident in the models, such as the altered community structure and the increased influence of fishing, it seems both intuitively and empirically unlikely that the system has 'recovered' from any impacts of fishing, especially when considering that the weighted community TL and that of piscivorous groups declined markedly by 1960 and has not increased since. Rather it seems more probable that the system is reacting either to an absence of top predators reduced by fishing, or, more likely, to environmental forcing. Increased zooplankton biomass (Verheye *et al.*, 1998, Verheye and Richardson 1998) and hence prey availability has been suggested as a driving factor, although whether this itself was a result of environmental forcing or top-down control by the heavily fished small pelagic groups is uncertain (Verheye *et al.*, 1998, Shannon *et al.*, 2004c). Included in the few indices not to have recovered themselves in the 2000s were the diversity indices. Species diversity has declined, one of Odum's (1985) indicators of a stressed system.

2.4.3. Sensitivity analysis:

From the mixed trophic impact assessment and sensitivity analysis performed it seems that while some influential groups such as the small pelagic fish, hake, and the fisheries are fairly well known, estimates of others that have a notable impact on the rest of the system are less robust. Negative impacts by the dominant small pelagic fish of the time on many groups reflect either direct or indirect competition, while positive effects affected their predators. Positive impacts by fishing on groups such as juvenile horse mackerel, mesopelagic fish and the small hakes illustrate how these groups benefit from reduced predation pressure as a result of removal of predatory fish through fishing. More accurate input data for groups such as zooplankton, cephalopods, demersal fish and chondrichthyans, although sadly unavailable for historical purposes, could be very useful in reducing some of the uncertainty inherently involved in the building of these models.

2.4.4. Conclusions:

The effect of man on the southern Benguela at an ecosystem level may not be as drastic as those observable fluctuations experienced by individual species, but it is evident nonetheless. Biomass at higher trophic levels has declined while that of species operating at low trophic level has in some cases increased. Fishing has become an important predator within the system, taking over the consumption of a proportion of the production of groups such as small pelagics and horse mackerel from declined predator groups such as hake. The biomass per trophic level is lower in later models than in the pristine with the exception of the 2000s model, where high small pelagic biomass also affected higher trophic levels. This is to be expected in the southern Benguela, like other upwelling systems, where small pelagics exert 'wasp-waisted' control over groups at both lower and higher trophic levels than themselves (Cury *et al.*, 2000). The trophic level of the catch has decreased drastically from 1900 to 1960, as fishing became industrialised and new fisheries were introduced, and the biomass removed has increased. Catches have diversified, although in the 1960 and 2000s models, after the commencement of purse-seine operations in the 1950s, by far the majority of the catch comprised small pelagics. While total system biomass has increased, species diversity has not, reflecting the increasing prevalence of the low trophic level r-selected species.

The focus of this investigation has been on the impacts of fishing rather than environmental factors. Fishing pressure has obviously played a major role in the ecosystem structure over the past century, but can by no means be perceived as the only factor affecting the system. Physical and environmental dynamics have been shifting ecosystem structure for centuries and will continue to do so. In fact, Odum (1985) suggests that a stressed ecosystem would be more susceptible to the effects of environmental changes. The collapse of small pelagic stocks could in fact lead to a shift in trophic control toward a bottom-up driven system, which would be more influenced by environmental fluctuations than the wasp-waist control system thought to operate in many upwelling systems (Shannon *et al.*, submitted). If this is the case, the southern Benguela today may be more at the mercy of its environment than ever.

Chapter 3

Retrospective models of the Northern Benguela

3.1. Introduction:

3.1.1. The northern Benguela ecosystem:

The Northern Benguela is considered to extend from the Angola-Benguela front at 14°S (although it does shift between 14° and 17°S seasonally), southwards to approximately 29°S, the vicinity of the perennial Lüderitz upwelling cell. It thus covers an area of about 179 000 km^2 (Shannon, 1985; Roux & Shannon, 2004). Upwelling in the northern Benguela is perennial and maximum in late winter and spring (Shannon, 1985). The region experiences large-scale environmental variability known as Benguela Ninõs, similar to the El Ninõ effect and originating in the tropics, when warmer water is introduced onto the shelf (Shannon *et al*, 1986; Boyd *et al.,* 1987). Documented Benguela Ninõ events have taken place in 1963, 1984 and 1995 (Gammelsrød *et al.*, 1998). As in the southern Benguela, the northern Benguela was in the past characterised by a high biomass of small pelagic fish species, mainly sardine, anchovy. The pelagic goby *Sufflogobius bibarbatus* is also abundant, unlike in the southern Benguela, where redeye is the third most abundant small pelagic. Important commercial stocks included sardine prior to the 1970s, hake, and horse mackerel, which currently constitute the bulk of the catch.

3.1.2. Exploitation in the four epochs examined:

3.1.2.1. Pre-contact and aboriginal era (<1600):

As in the southern Benguela, although humans were present in the Benguela during this period (see Chapter 2), exploitation took the form of utilization of the coastal zone and beach-cast mammals (Parkington, 2001). Any anthropogenic impact these activities had on marine species is thus not considered significant.

3.1.2. Pre-industrial era: (1750-1910):

Commercial use of resources in the northern Benguela began as colonists moved up the west coast from the Cape in the 18th century. Early exploitation concentrated on seals, but soon after there was an increased effort in whaling and exploitation of seabirds through the 18th and 19th centuries. The 1700s saw the arrival of both European and American whalers and sealers and colonisers in the form of the Dutch East India Company (DEIC). The Dutch initiated whaling, of first right whales and later sperm whales, in the 1720s near Walvis Bay (Best *et al.*, 1997). By the end of the 18th century, almost 150 years after the DEIC had set up a permanent settlement in Table Bay, their sphere of influence had expanded to include Walvis Bay, Lüderitz, and three other bays north of the Orange River. The British succeeded the DEIC in 1809 and went on to include in their territory the mainland south of the Orange River, then all the present-day Namibian islands, and finally Walvis Bay by 1879. Germany then took control of the current mainland Namibia (from the Orange to the Cunene Rivers) in 1884.

Records of sealing only exist from 1900, and though the government regulated harvests from islands from 1903, private sealing at Cape Cross persisted unconstrained until the 1970s (Best *et al.,* 1997). While the majority of African penguin eggs harvested on the west coast of southern Africa during the late 1800s and early 1900s originated from the southern Benguela, some harvesting activities can be assumed to have taken place in the northern Benguela, as the colonisers moved north. Another activity initiated over this period and which impacted seabird populations heavily was the harvesting of guano. Guano harvests began at Ichaboe Island in 1843 (Best *et al.*, 1997), around the same time that the linefishery in the northern Benguela, largely targeting snoek (*Thyrsites atun*), commenced (Griffiths *et al.*, 2004).

3.1.3. Industrial era (1910-1980):

In 1910 the Union of South Africa took over power from the British in the south. The Union of South Africa subsequently became the first ruling power to acquire authority over the whole Benguela in 1915, after taking over rule of German South West Africa in the First World War. Sealing and the collection of guano and penguin eggs continued over this period, although seal harvests were now regulated by the government (Roux & Shannon, 2004). Purse-seine fisheries began operating on a large scale in the Benguela after World War II, and sardine was initially targeted in both the northern and southern Benguela. After South African stocks collapsed in the 1960s, even more pressure was put on the northern sardine stocks, contributing to the decline in catches after 1968, and ultimately the collapse of the stock in the late 1970s (Griffiths *et al.*, 2004). As in South Africa, this resulted in a change of focus of the fishery to anchovy (*E. encrasicolus*) by way of a decrease of net mesh sizes (Griffiths *et al.*, 2004). Anchovy and juvenile horse mackerel subsequently dominated purse-seine catches (Roux & Shannon, 2004). The hake fishery, targeting the same species as the southern Benguela fishery (*M. paradoxus* and *M. capensis*), started in the 1960s after Japanese and Spanish fleets discovered larger stocks off present-day Namibia than those being fished off South Africa (Gordoa *et al.*, 1995). As hake stocks began to decline in the 1970s, however, some effort was directed by the mid-water trawl fishery at horse mackerel. Sealing continued over this period, becoming totally privatised by the early 1970s, and saw the introduction of TACs in 1974 after sufficient data on the sizes of colonies had been gathered (Shaughnessy, 1984; Griffiths *et al.*, 2004). Although guano was harvested throughout this period, these resources began to decline in the 1970s, after the collapse of the Namibian sardine stocks and disturbance of colonies began to result in severe declines in populations of seabirds such as the Cape gannet (*Morus capensis*), Cape cormorants (*Phalacrocorax capensis)* and African penguins (*Spheniscus demersus*) (Berruti, 1989; Roux & Shannon, 2004).

3.1.4. Post industrial era (1975- present):

Namibia gained independence in 1990, and since Walvis Bay was returned to Namibia by South Africa in 1994 the northern Benguela has been under Namibian administration. An EEZ could only be declared in the northern Benguela in 1990, after Namibia's independence made it an internationally recognized government, although reduced catches of species such as the hakes had discouraged some international effort prior to this (Griffiths *et al.*, 2004). Despite the rapid adoption of management and resource rebuilding strategies after 1990, resources failed to show significant signs of recovery, at least partly due to the environmental effects resulting from the 1995 Benguela Niño and other events experienced in the 1990s (Roux & Shannon, 2004). Sardine has remained at low levels following the collapse of the stock in the 1970s, and anchovy has not displayed a compensatory increase (Griffiths *et al.*, 2004). Catches of approximately 500000 t of horse mackerel over the 1980s made this species the largest contributor to landings off Namibia at the time (Boyer & Hampton, 2001). A small-scale longline fishery for hake was initiated in the 1980s and continues to operate (Griffiths *et al.*, 2004). After having been re-privatized in 1976, harvesting of guano on the islands off Namibia was discontinued in the 1990s, although it is still collected on a small scale from platforms constructed for this purpose off the coast from the 1930s (Best *et al.*, 1997). In contrast to South Africa, Namibian harvest of seals continues at Cape Cross and Lüderitz.

3.2. Methods:

3.2.1. Model construction:

Models were constructed based on that of Roux & Shannon (2004) for the 1990s, using *Ecopath* with *Ecosim* software (see Chapter 1) (Walters *et al.*, 1997; Christensen *et al.*, 2000). Where values for P/B and Q/B are given, these are used in all periods modelled. Unaltered initial diet composition for all groups (Appendix B., Table B.1) was obtained from the 1990s EwE model (Roux & Shannon, 2004). Input parameters are in line with those suggested in Moloney & Jarre (2003) so as to be comparable to models of other upwelling systems.

3.2.1.1. Input data by group for 1600, 1900 & 1970:

1.) Phytoplankton: Phytoplankton B of 214.29 t. km^{-2} used in the 1971-1977 *Ecopath* model of the northern Benguela (Jarre-Teichmann *et al.*, 1998) was assumed for the 1970 model. B in 1900 and 1600 is unknown, and in the absence of any other estimates the average of that used in the existing 1970s, 1980s and 1990s models (Jarre-Teichmann *et al.*, 1998; Shannon & Jarre-Teichmann, 1999; Roux & Shannon, 2004), calculated as 207.2 t.km^{-2}, was assumed in these models. A P/B of 35.7 y^{-1} was used instead of the original estimate (Brown *et al.,* 1991) of 77.4 y^{-1}, as adjusted in Shannon (2001) and Shannon and Jarre-Teichmann (1999), to account for particulate dissolved organic carbon.

2-5.) Micro-, meso- and macro- and gelatinous zooplankton: As in the southern Benguela and existing northern Benguela models (Jarre-Teichmann *et al.*, 1998, Shannon *et al.*, 2003), zooplankton was divided into four discrete groups. Microzooplankton comprises nanoflagellates, ciliates, and zooplankton larvae with an equivalent spherical diameter of 2 – 200 µm. A P/B of 482 y^{-1} as estimated from Brown *et al.* (1991) and Painting *et al.* (1992) by Shannon (2001) and a Q/B ratio of 1928 y^{-1} (Roux & Shannon, 2004) were used. U was assumed to be 20% (Stoeker, 1984). Mesozooplankton included copepods of 200 - 2000 µm diameter. A P/B of 40 y^{-1} (Hutchings *et al.*, 1991), Q/B of 133.333 y^{-1} (Shannon & Jarre-Teichmann, 1999), and U of 35% (Probyn *et al.*, 1990; Verheye *et al.*, 1992) were assumed. Macrozooplankton primarily consists of euphausiids of 2 – 20 mm, although amphipods, fish larvae, and similar groups are also included. A P/B of 13 y^{-1} (Hutchings *et al.*, 1991), Q/B of 31.707 y^{-1} (Shannon & Jarre-Teichmann, 1999), and U of 35% (Jarre-Teichmann *et al.*, 1998) were assumed. The fourth zooplankton group modelled was gelatinous zooplankton, which included Cnidaria, Ctenophora, tunicates and chaetognaths. A P/B of 0.44 y^{-1} (Shannon, 2001), Q/B of 1.467 y^{-1} (Roux & Shannon, 2004) and U of 20% (Purcell, 1983) were assumed in all models. As no estimates were available, a minimum biomass for all zooplankton groups was estimated assuming an EE of 0.999 for all zooplankton groups excepting gelatinous zooplankton. Due to the low utilisation of this group within the system, an EE of 0.5 was assumed.

6&7.) Benthos: No estimates of B for either meio- or macrobenthos were available, so mimimum B was estimated by the model assuming an EE of 0.999 for all periods modelled. P/B and P/Q were assumed as 8 y^{-1} and 33 y^{-1}, and 1.2 y^{-1} and 10 y^{-1} for meio- and macrobenthos respectively, as adopted by Roux & Shannon (2004).

8.) Anchovy: No B approximations for Cape anchovy (*Engraulis encrasicolus)* were available in the northern Benguela for 1970, 1900 or 1600, so biomass was estimated in all models assuming an EE of 0.999. P/B (1.8 y^{-1}) and Q/B (18 y^{-1}) were assumed to be the same as in the 1990s (Roux & Shannon, 2004). Anchovy was not initially targeted by the purse-seine fishery in the northern Benguela, which started in the 1950s and which focused predominantly on sardine *Sardinops sagax*. Anchovy were only recorded in the catch from the late 1960s, after sardine catches began to decline and smaller net mesh sizes were introduced. As a result no landings of anchovy are included in the 1900 or 1600 models, and 170 000 t were included in the 1970 model (Griffiths *et al.*, 2004).

9.) Sardine: The mainstay of the early Namibian purse-seine fishery, B of the sardine *Sardinops sagax* was estimated as 1 465 000 t in 1970 (Boyer & Hampton, 2001). For the 1900 and 1600 models, the earliest B estimate available was used (6 330 000t) (Griffiths *et al.*, 2004), as it pre-dated fishing on this stock. minimum likely biomass was estimated assuming an EE of 0.999. P/B (1.35 y^{-1}) and Q/B (14 y^{-1}) ratios assumed were the same as those used in the 1990s model (Roux & Shannon, 2004). Landings in 1970 were recorded as 595 000 t (Griffiths *et al.*, 2004). No catches were made in 1900.

10.) Pelagic goby: The pelagic goby *Sufflogobius bibarbatus*, although incorporated into the 'Other small pelagic fish' group in the southern Benguela models, is more prolific in the northern Benguela and for purposes of model aggregation, takes the place of redeye round herring, which stands as its own group in the southern Benguela but has been added into the northern models'

'Other small pelagic fish' group. No B estimates are available for pelagic goby in any of the years modelled, so biomass was estimated in all models assuming an EE of 0.999. P/B (0.9 y^{-1}) and Q/B (9.0 y^{-1}) were assumed to be the same as in the 1990s in all other models (Roux & Shannon 2004). No landings of pelagic goby were recorded for any of the periods modelled.

11.) Mesopelagic fish: The lanternfish *Lampanyctodes hectoris* and the lightfish *Maurolicus muelleri* were grouped as the mesopelagic fish group. No B estimates are available for either species for the time periods modelled, so biomass was estimated in all models assuming an EE of 0.999. P/B (1.23 y^{-1}) and Q/B (12.3 y^{-1}) and U (35%) for all periods modelled were obtained from Roux & Shannon (2004). No landings of either species are recorded prior to the 1970s (Crawford *et al.,* 1987).

12.) Cephalopods: The squids *Loligo* spp. and *Todarodes* spp. comprise the majority of the cephalopod group in the northern Benguela. No B approximations were available for this group in 1960, 1900 or 1600, therefore biomass was estimated in all models assuming an EE of 0.999. P/B (1.5 y^{-1}), Q/B (15.0 y^{-1}) and U (20%) were obtained from Roux & Shannon (2004) and assumed the same in 1960, 1900 and 1600. With the squid fishery only taking off in the 1970s, no landings were included in the 1970 model, nor in the 1900 or 1600 models.

13.) Other small pelagics: Saury *Scomberesox saurus*, flying fish Exocoetidae and round herring or redeye *Etrumeus whiteheadi* are the less prolific small pelagic fish species in the northern Benguela and are combined in the 'Other small pelagics' group, as in other northern Benguela models (Heymans *et al.*, 2004; Shannon & Jarre-Teichmann, 1999). No biomasses for these species are available for 1960, 1900 or 1600, therefore B was estimated in all models assuming an EE of 0.999. P/B (0.958 y^{-1}) and Q/B (9.349 y^{-1}) ratios were obtained from Roux & Shannon (2004). No landings of these species are recorded for any of these species prior to the 1970s (Crawford *et al.,* 1987).

14 & 15.) Horse mackerel: No estimate of B for either juvenile or adult horse mackerel (*Trachurus trachurus capensis*) were available, therefore B was estimated in all models assuming an EE of 0.999. P/B (1.2 & 0.8 y^{-1}) and Q/B (10 & 5.3 y^{-1}) for juvenile and adult groups respectively were obtained from Roux & Shannon (2004). Horse mackerel were only landed off Namibia from 1961 onwards (Crawford *et al.,* 1987), and no significant catches were made in 1900 or 1600. 51 400 t of adult horse mackerel are recorded in 1970 (Crawford *et al.*, 1987).

16.) Large pelagics: This group includes tuna *Thunnus spp.*, snoek *Thyrsites atun* and kob *Agyrosomus inodorus*. No biomass approximations were available for these species in 1970, 1900 or 1600; biomass was estimated in all models assuming an EE for the group of 0.999. P /B (0.5 y^{-1},) Q/B (5 y^{-1}) and U (20%) were obtained from the 1990s model (Roux & Shannon, 2004) and assumed to be the same in all models. Landings of 1160 t of snoek and 800 t of kob were recorded in the northern Benguela in 1970 (Crawford *et al.*, 1987).

17–19.) Hake: Two species of hake occur in the Benguela, namely the shallow water Cape hake *Merluccius capensis* occurring at an everage depth of 380 m, and the deep water Cape hake *M. paradoxus*, found at depths of 150 – 800 m (Payne, 1989). Hake were modelled as three discrete groups with regard to size and species: small *M. capensis* (0-2 yrs), large *M. capensis*, and large *M. paradoxus*, to allow for cannibalism and differences in diet between small and large hakes (Shannon, 2001). Small *M. paradoxus* was excluded from the northern Benguela models, as stocks are thought to be located in the southern Benguela, only migrating north later in life (Roux & Shannon, 2004). B of both adult hakes is estimated to have been an unchanging 3 666 000 t from 1964 to 1917 (Griffiths *et al.*, 2004), and as fishing on hake only began off Namibia in the early 1960s and there were no other large-scale fisheries in operation between 1900 and 1917, this estimate was also assumed in the 1900 and 1600 models. The proportion of large *M. capensis* to *M. paradoxus* was taken as 64% to 36%, as in the 1990s model (Roux & Shannon, 2004). B of small *M. capensis* was estimated for all periods modelled assuming an EE of 0.999. P/B and Q/B for small *M. capensis* (2 y^{-1}& 13.333 y^{-1}), large *M. capensis* (1.228 y^{-1}& 7.824 y^{-1}), and large *M. paradoxus* (1.14 y^{-1}& 7.278 y^{-1}) were obtained from Roux & Shannon (2004). 627 198 t of hake are recorded to have been landed in 1970 (Geromont *et al.*, 2000). This was assumed to have been large fish, and was apportioned between the species as 64% *M. paradoxus* and 36% *M. capensis*, as assumed for landings off Namibia in Roux and Shannon (2004).

20 & 21.) Demersal fish: Included in the benthic-feeding demersals group are kingklip *Genypterus capensis,* monkfish *Lophius spp.*, rattails *Caelorinchus fasciatus,* soles (Soleidae) and tonguefish (Cynoglossidae). Pelagic-feeding demersals include gurnards *Chelidonichthys spp.,* jacopever *Helicolenus spp.*,and Sparidae such as *Dentex.* No biomasses were available for these species in 1960, 1900 or 1600, thus conservative biomass was estimated in all models assuming an EE of 0.999. P/B (1.0 y^{-1}) and Q/B (5 y^{-1}) for both groups were obtained from Roux & Shannon (2004). A catch of 1 527 t of west coast sole was made in 1970, but otherwise no landings are recorded for any of the species included in these groups in any of 1970, 1900 or 1600 models (Crawford *et al.*, 1987).

21.) Chondrichthyans: No estimates of chondrichthyan B in the northern Benguela for the periods modelled were available, and there is very little consumption of chondrichthyans within the system. Thus any biomass estimated by assuming a high EE in the model would be unrealistically low, and the 1990s B of 0.36 $t.km^{-2}$ was assumed for all periods modelled. P/B (0.5 y^{-1}) and Q/B (3.333 y^{-1}) were also assumed the same as in the 1990s model (Roux & Shannon, 2004). No landings of any species included in this group have been recorded for any of the periods modelled.

23.) Seabirds: To obtain B estimates for seabirds as a group, total biomass of the eight most abundant species in 1960 and 1900 was established using population size data (Berruti, 1989; Crawford *et al.*, 1983; Underhill & Crawford, 2005). Where no other indications were found, B in 1600 was based on the theoretical minimum size of the populations of these species in a 'healthy' environment, as suggested in Underhill & Crawford (2005) based on past populations. B of those species in 1960, 1900 and 1970 were then related to that of the 1990s based on population estimates. Using the B input for the seabird group in the 1990s southern Benguela EwE model (0.004 $t.km^{-2}$) from Roux & Shannon (2004) and the Bs in previous periods based on population data relative to that of the 1990s, estimates of the total seabird B in 1970 (0.0139 $t.km^{-2}$), 1900 (0.01768 $t.km^{-2}$) and 1600 (0.01768 $t.km^{-2}$) were generated. P /B (0.156 y^{-1}) and P/Q (120.3 y^{-1}) and U (26%) were obtained from Roux & Shannon (2004). Although various factors such as guano harvesting and displacement by seals have influenced the seabird populations in the northern Benguela over the past centuries, due to the trophic nature of the models under discussion, only direct harvesting of seabirds can be included in the models. The majority of direct exploitation was of penguins eggs, which were harvested in large numbers during the late 1800s and early 1900s. Although from the early 1900s until 1970, African penguin eggs harvested were taken almost entirely from Dassen Island in the southern Benguela, assuming that half of those eggs harvested in 'southern Africa' in excess of those collected at Dassen were collected in Namibia, 17.89 t were removed in 1900 (Best *et al.*, 1997). Assuming hatching and fledging success from Shannon and Crawford (1999), biomass of birds lost to harvesting was estimated to have been 109.5 t in 1900.

24.) Seals: The Cape fur seal *Arctocephalus pusillus pusillus* is the only species of seal that breeds in the Benguela, with 15 of the 25 extant colonies in Namibia, the others being located in South Africa (Griffiths *et al.,* 2004). Seal biomass in the northern Benguela was calculated based on estimated total population size and distribution of colonies in the years modelled, with biomass per individual calculated using total population size and biomass estimates for the 2000s. In 1970 total Cape fur seal population was estimated as approximately 850 000 (Best *et al.*, 1997). 60% of this population was assumed to have been in Namibia, as was the case in the 1980s and 1990s, which translated into a B of approximately 16 262 t in 1970. In 1900, 50% of the total population biomass, approximately 1650 t, was assumed to comprise individuals inhabiting the northern Benguela. For 1600 the biomass was assumed to be the same as the 2000s biomass, as it is possible that the current large size of some colonies compared to those described in the 1800s and early 1900s may counteract the decrease in population that should be associated with the 23 colonies that became extinct prior to 1900 (David, 1989; Griffiths *et al.*, 2004). The P/B (0.29 y^{-1}) ratio, Q/B (18.25 y^{-1}) and U (20%) were obtained from the 1990s model (Roux & Shannon, 2004). Exploitation of seals is one of the longest operating fisheries in the Benguela, although reasonably reliable records are only available from about 1900 onwards (Best *et* *al.*, 1997). Assuming an average mass of 22.7 kg per pup (David, 1987) and 150 kg per bull (Griffiths *et al.*, 2004), removals were calculated to have been 196 t in 1900 and 1625 t in 1970.

25.) Cetaceans: Input parameters for cetaceans in the northern Benguela are largely based on dolphin species, as most baleen whale species found in the region are migratory and for the most part do not feed within the system. As no estimates of B were available for this group, and as any estimate by assuming a high EE in the model would be unrealistically low, due to the low levels of predation on cetaceans within the system, current B (0.019 $t.km^{-2}$) was assumed for all periods modelled for lack of a better estimate. P/B (0.15 y^{-1}) and Q/B (7.418 y^{-1}) were assumed the same as the 1990s model (Roux & Shannon, 2004). As species harvested are largely migratory baleen whales, no removals are included for any of the periods modelled.

3.2.2. Balancing the models:

While biomasses in southern Benguela were for the most part estimated using an EE of 95%, a figure used in previous models for both this system and others to provide a conservative estimate of biomass. For most groups in northern Benguela models, an EE of 99.9% was used, both because this was used in the previously constructed 1990s model referred to in this chapter, and due to difficulties in balancing the models. It should be kept in mind that an EE of 99.9% provides a conservative estimate of biomass.

3.2.2.1. Sardine biomass:

Due to the 1990s diet composition, reflecting the consumption of species during a period of very low small pelagic biomass, B of sardine in 1900 and 1600 was estimated by the unbalanced models at similar levels to those found in the 1990s. As this is highly unlikely to have been the case (as anchovy levels were also very low), the earliest B estimate for sardine, from 1952, was assumed in both models instead as a best-estimate. As the purse-seine fishery only took off after 1950 in the northern Benguela, the B estimate for 1952 (Griffiths *et al.,* 2004) is assumed to be that of a relatively unexploited stock.

3.2.2.2 Balancing the 1600 model:

The EEs of both phytoplankton (1.2) and detritus (2.28) indicated an unbalanced initial model.

The over-use of detritus was likely the result of unreasonably high Bs that were estimated for both benthos groups, pelagic goby (65.4 t.km^{-2}), and mesopelagic fish (35.8 t.km^{-2}), all of which had a high proportion of detritus in their diet. Diet compositions of predators were adjusted accordingly, also to incorporate the higher sardine B of the time relative to the 1990s, for which period the unadjusted diet was intended, and thus to decrease the consumption of the aforementioned groups (See Appendix B., Table B.2 for balanced diet composition).

3.2.2.3 Balancing the 1900 model:

The EE of seals (3.836) and detritus (1.763) both indicated an unbalanced initial model. The proportion of seals in the diet of chondrichthyans, cetaceans and seabirds was reduced accordingly until the EE was reduced to < 1. As in the 1600 model, B of benthos groups and pelagic goby were estimated to be very high initially, and diet compositions of predators of goby and consumers of detritus were again adjusted to reduce these and the EE of detritus to take into account the far higher B of sardine relative to the 1990s (see Appendix B., Table B.3 for revised diets).

3.2.2.4 Balancing the 1970 model:

Initially an EE of 1.356 was calculated for detritus based on the unadjusted input data. Biomass of benthos groups and pelagic goby (55.2 t.km^{-2}) were very large in the unbalanced model. Diet composition was thus adjusted with the effect that the B of these groups decreased and the EE of detritus decreased to < 1. Diet adjustments were made taking into consideration the higher B of sardine in 1970 relative to the 1990s (see Appendix B., Table B.4 for revised diets).

3.2.3. Analysis:

Data outputs and analyses were performed as described in Chapter 2 for the southern Benguela models.

3.3. Results:

3.3.1. Internal indices:

3.3.1.1. Biomass:

The B of selected groups for each of the four periods modelled is depicted in Fig. 3.1. Only two groups showed an increasing trend towards the present: large pelagics and gelatinous zooplankton. Although, as expected, all groups that have experienced high levels of fishing pressure such as anchovy, sardine, hakes, and horse mackerel, displayed varying degrees of decline, the B of cephalopods, mesopelagic fish, other demersal fish and seabirds also decreased over time. While some of the species included in these groups have been fished, the majority have not and are instead likely to have experienced the indirect effects of fishing and environmental change on prey populations. Seals, although they did not show a substantial overall change from pristine to present, suffered a collapse by 1900 after the advent of sealing, subsequently recovering after sealing was curtailed. B of pelagic goby also showed no great temporal trend, but this belies the increased B in 1970 compared to the other periods modelled. Sardine B was consistently higher than that of anchovy, although this was largely due to the specified input diet composition: as no estimates were available for anchovy B, and those for sardine were consistently high, it was assumed that sardine was the dominant small pelagic of the time and diets were adjusted accordingly in all periods modelled, so that comparatively little anchovy was consumed within the system and hence a low B was estimated. The biomass of non-planktonic consumers (Fig. 3.2) showed a marked overall decline as the B of almost all component groups decreased over time. Small pelagics and the hakes in particular, the most extensively fished groups, had a far lower B in the 1990s.

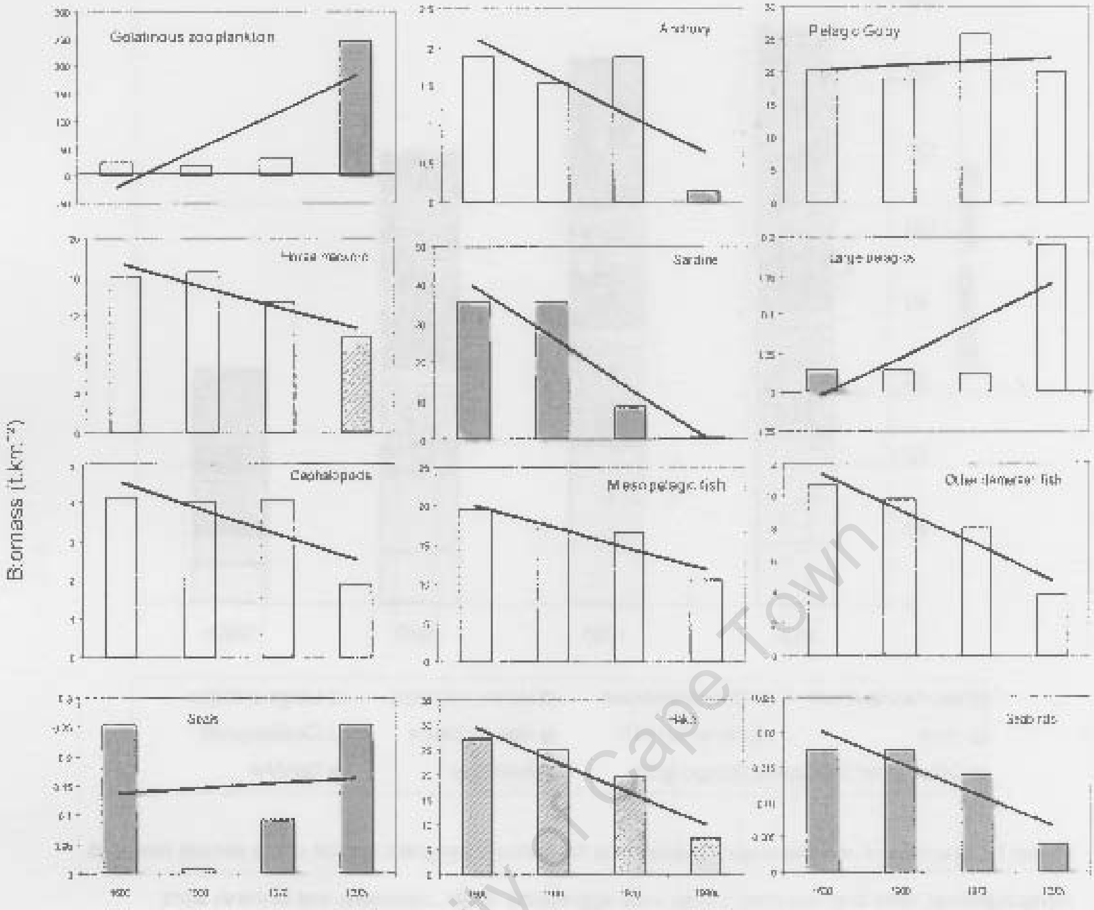


Figure 3.1. Biomass of selected groups over the time-period modelled = B obtained from input data (measured data/ stock assessment estimate); = aggregate of groups, B of some obtained from input data, some estimated by the model; = B estimated by the model. The biomass depicted for horse mackerel, hake and other demersal fish is compiled from two or more component groups (e.g. juvenile and adult).

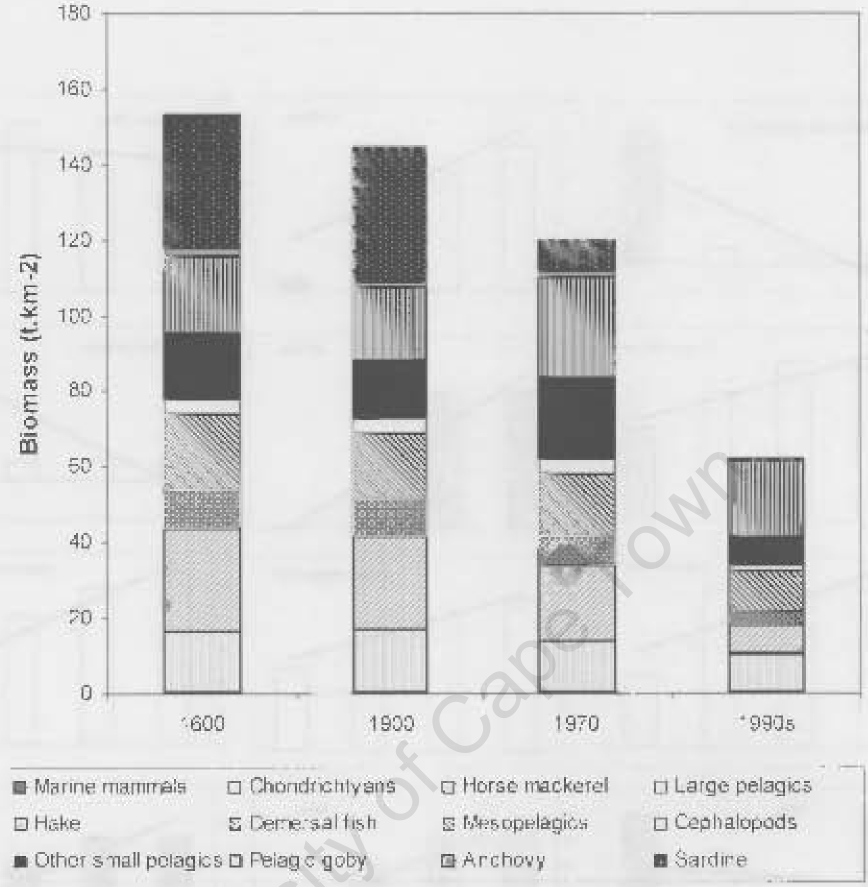


Figure 3.2 Biomass of non-planktonic consumers in the northern Benguela in each of the periods modelled. Horse mackerel, hake and demersal groups were aggregated. Seals, cetaceans and seabirds were aggregated into 'mammals and birds'.

3.3.1.2. Consumption:

Hake, small pelagic fish and horse mackerel were all consumed in the greatest part by hake for all periods modelled (Fig. 3.3). The proportion of production consumed by hake for each period did decrease over time, however. For example, hake initially cannibalised 85% of its total consumption, while by the 1990s hake only comprised 63% of its own diet. This was to some extent inter-specific predation of *M. paradoxus* by *M. capensis* and visa versa, but also illustrates the predation of small *M. capensis* by the large hake groups. Similarly, 56% of consumed horse mackerel production was ascribed to hake, compared with only 34% in the 1990s, the excess being taken up, or taken over, by fishing. Consumption by seals also increased relative to other

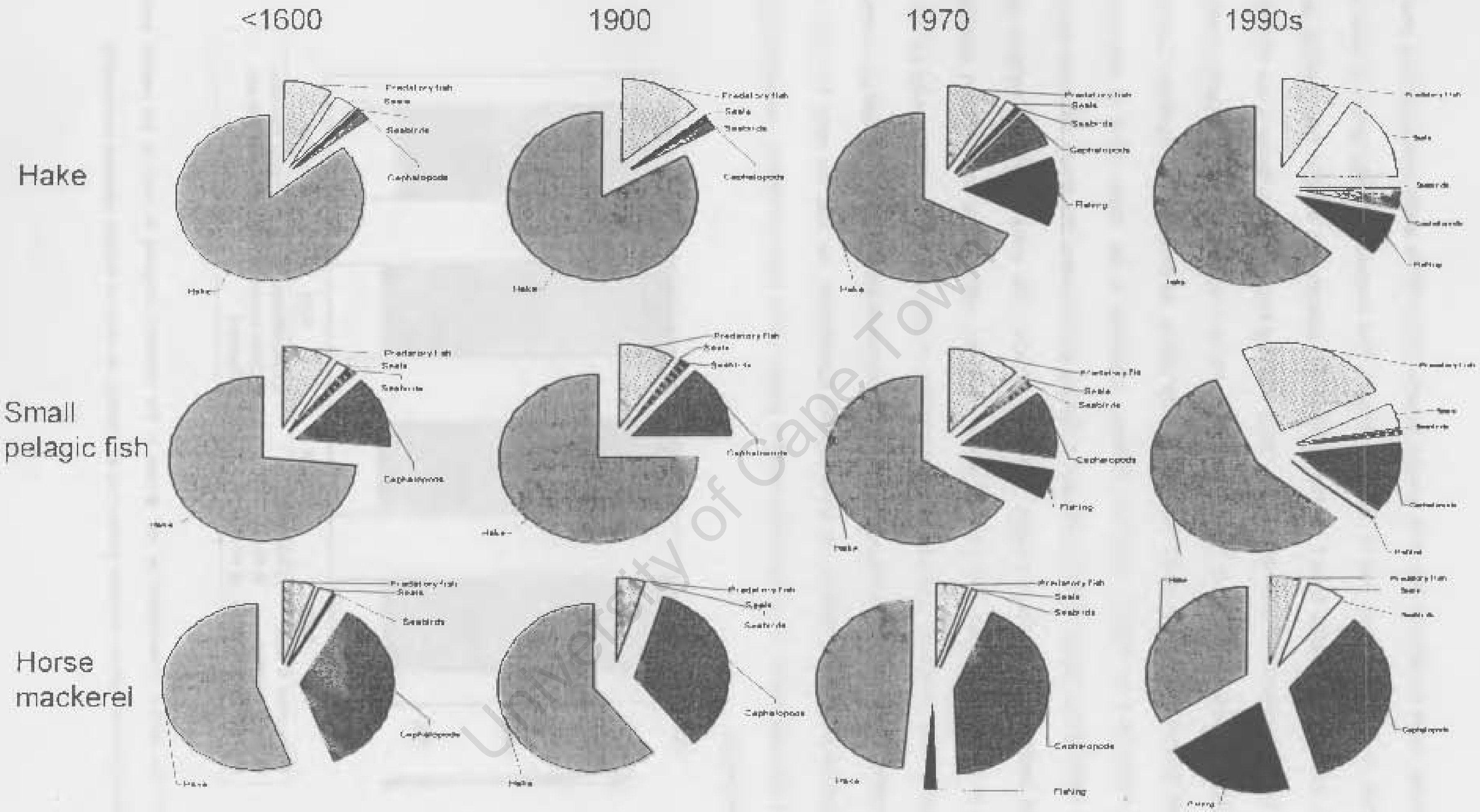


Figure 3.3: The proportion of production of the hakes, small pelagic fish (includes anchovy, sardine, pelagic goby and other small pelagics) and horse mackerel (adult and juvenile combined) consumed by their various predators in the northern Benguela for each period modelled

consumers, most notably for the hake groups, where by the 1990s seals consumed four times the proportion of hake that they had in the 1600 model. The increased consumption of hake in the modern era can to a large extent be attributed to the scavenging of hake from fishing vessels during trawling operations (Wickens *et al.*, 1992). Fishing began to be a factor in the 1970 model for all three groups presented in Fig. 3.3, although for both hakes and small pelagics production removed by fishing had decreased markedly by the 1990s, as these stocks declined. Conversely fishing removed a far higher proportion of horse mackerel in the 1990s (21% of consumption) than in 1970 (2%), reflecting the redirection of fishing effort toward this group after the respective collapse and decline of small pelagic and hake stocks. The consumption by various groups relative to one another (Fig. 3.4) displays similar patterns, with sardine and anchovy contributing significantly less to overall consumption in the 1990s (1.5%) versus the 1600 model (31%), with consumption by hakes also declining, but not to the same degree. All other groupings considered here showed either little change, or an increased contribution, as was the case for other small pelagics (an aggregate of pelagic goby and the group 'other small pelagics'), mesopelagics and horse mackerel.

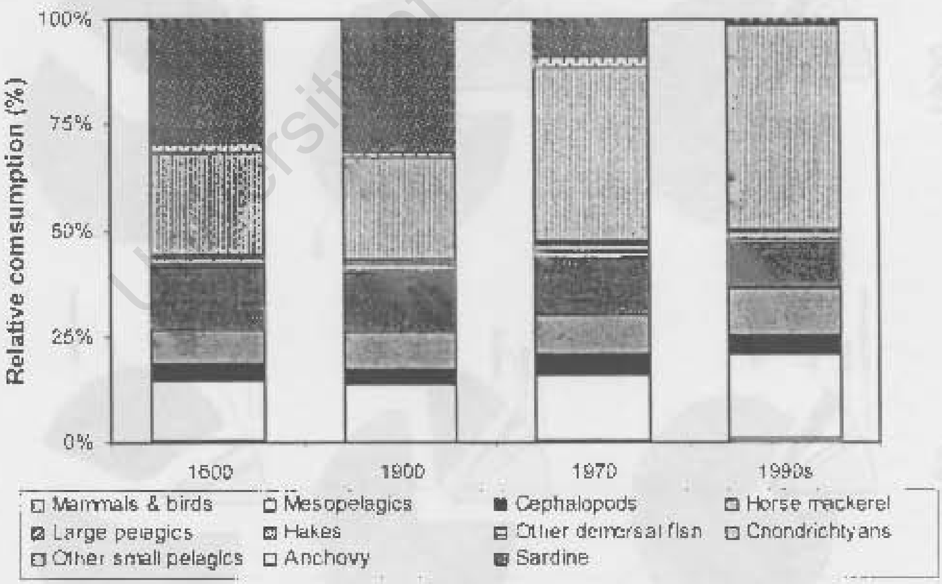


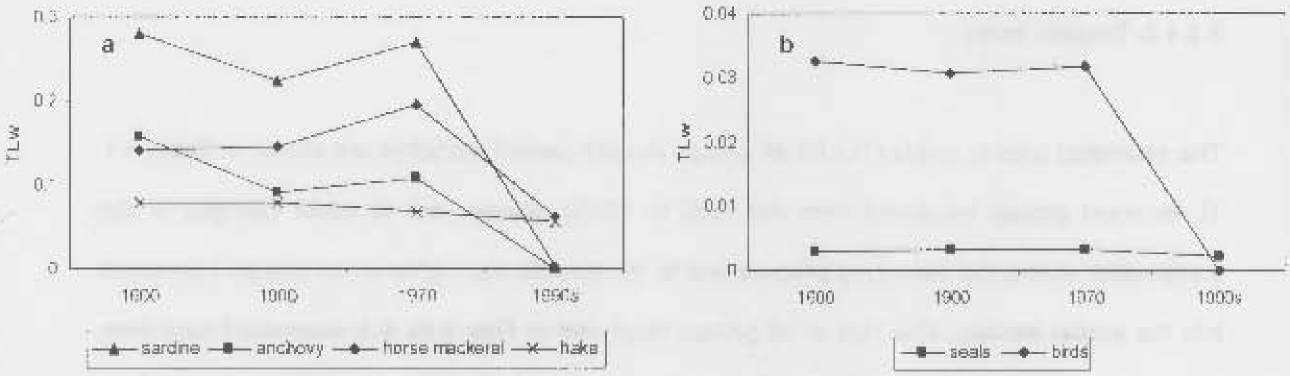
Figure 3.4: The relative consumption by key groups in the northern Benguela in each of the periods modeled. Consumption by chondrichthyan and hake groups was aggregated, as was that of seals, cetacean and seabirds.

3.3.1.3. Trophic level:

The estimated trophic levels (TL) for all groups in each period modelled are shown in Table 3.1. TL for most groups increased from the 1600 to 1990s models, due to minor changes in diet composition during the balancing process and to incorporate the higher small pelagic biomasses into the earlier models. The TLw of all groups displayed in Figs 3.5a & b decreased over time, although that of seals did increase substantially from 1900 to the 1990s, following the drop in TLw that occurred between 1600 and 1900. The mean TL of the community as a whole (excluding plankton) and piscivores (Fig. 3.6) increased over time.

Table 3.1: Estimated trophic level of groups in the northern Benguela for each period modelled.

Group	1600	1900	1970	1990s
Phytoplankton	1	1	1	1
Microzooplankton	2.04	2.06	2.06	2.06
Mesozooplankton	2.47	2.53	2.53	2.53
Macrozooplankton	2.53	2.61	2.61	2.61
Gelatinous zooplankton	3.18	3.23	3.23	3.23
Sardine	2.62	2.65	2.65	2.65
Anchovy	2.99	3.03	3.03	3.03
Pelagic goby	3.06	3.08	3.09	3.1
Mesopelagics	3.5	3.58	3.58	3.58
Cephalopods	3.81	3.88	3.97	3.96
Other small pelagics	3.46	3.52	3.52	3.52
Juvenile horse mackerel	3.34	3.39	3.39	3.39
Adult horse mackerel	3.52	3.6	3.6	3.6
Large pelagics	4.42	4.49	4.52	4.54
Small *M. capensis*	3.81	3.88	3.91	3.97
Large *M. capensis*	4.22	4.22	4.35	4.45
Large *M. paradoxus*	3.83	4.02	3.83	4.11
Benthic-feeding demersals	3.79	3.85	3.91	3.98
Pelagic-feeding demersals	3.79	3.86	3.95	3.95
Chondrichthyans	3.72	3.73	3.75	3.77
Seabirds	4.21	4.25	4.26	4.29
Seals	4.35	4.52	4.55	4.58
Cetaceans	4.15	4.16	4.25	4.26
Meiobenthos	2	2	2	2
Macrobenthos	3	2.96	2.96	3.02



Figures 3.5a & b: The weighted trophic level of selected groups in the northern Benguela for each of the periods modelled.

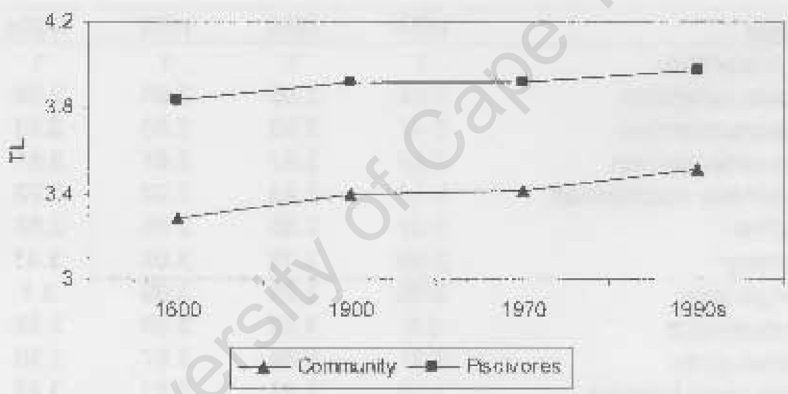


Figure 3.6: TL of the community (excluding detritus and plankton), and of piscivores as a group in the northern Benguela for each period modelled.

3.3.1.4. Fishing:

Although penguin eggs and seals were harvested in 1900, the biomass removed does not compare to that removed by fisheries in 1970 and the 1990s (Fig. 3.7). Landings declined and catch composition was substantially altered from 1970 to the 1990s. Horse mackerel became by far the most important contributor to landings by the 1990s, as opposed to the small pelagics and hake that constituted the vast majority of landings in 1970. The mean TL of the catch was highest in 1900 (4.5) before the advent of most fisheries, declining as the contribution of small pelagics overtook other species by 1970, and increasing slightly again by the 1990s after the collapse of small pelagic stocks forced fishing effort toward the higher TL horse mackerel.

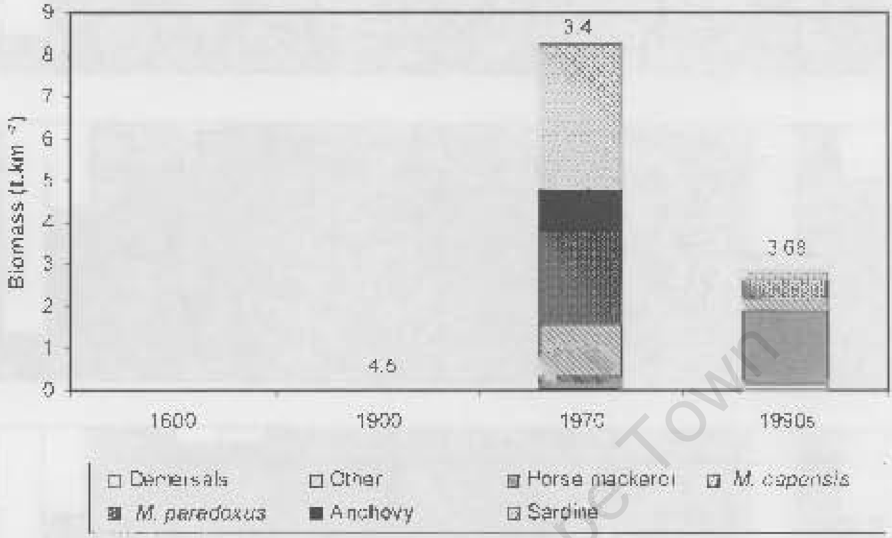


Figure 3.7: Total removals and catch composition by group for each of the periods modeled. The mean TL of the catch is indicated above the column depicting total catch for that model. 'Other' includes the following groups: other small pelagics; pelagic goby; macrobenthos; seabirds, seals, large pelagics and cephalopods.

3.3.1.5. Mortality:

The majority of mortality was attributed to predation (Fig. 3.8), with fishing mortality becoming important in the mid-trophic level groups in 1970 and 1990. Other mortality contributed a fairly large proportion in low and high TL groups of which a low percentage of production is consumed by predators, such as plankton and apex-predator groups. Seals showed the highest proportion of mortality due to fishing, which in 1900 made up 41% of total mortality Z, the highest for any group. Sardine and anchovy were subjected to higher fishing mortality in the 1970 model than the 1990s model, when horse mackerel and large pelagics showed a

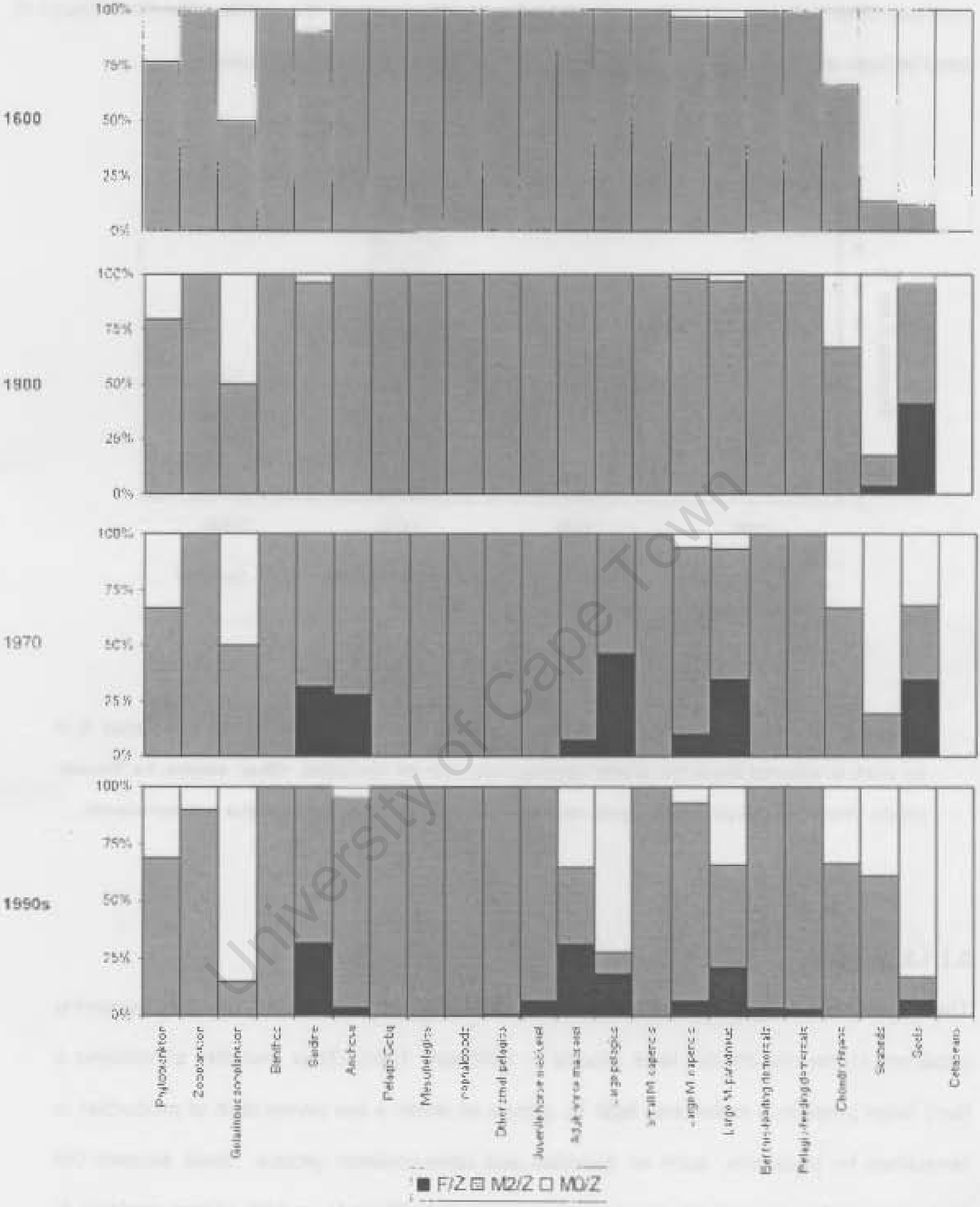


Figure 3.8: Coefficients of mortality by group in the northern Benguela for each period modelled. Zooplankton groups and benthos have been aggregated. F/Z is the proportion of mortality resulting from fishing, M2/Z is the proportion as a result of predation, and M0/Z is other mortality.

higher percentage loss to fishing. Hake, particularly large *M. capensis*, also had a lower proportion of fishing mortality in the 1990s than in the 1970 model.

3.3.2. System indices:

Summary statistics from the periods modelled are shown in Table 3.2. Consumption, throughput, production, and respiration all decreased between the 1600 to the 1990s model, while biomass, exports and flows to detritus increased. The greatest increase for all three indices occurred between the 1900 and 1970 models, as was the case for the largest decrease in consumption. Primary production was relatively constant, apart from a slight peak in the 1970 model.

Table 3.2. Summary statistics for each period modelled in the northern Benguela. All statistics are in $t.km^{-2}.y^{-1}$, except for biomass, which is in $t.km^{-2}$.

	1600	1900	1970	1990s
Total biomass (excluding detritus)	531	477	482	621
Sum of all consumption	14263	14170	12930	12731
Sum of all exports	232	277	1150	820
Sum of all flows into detritus	5157	4933	5639	5534
Total system throughput	26816	26500	26219	25536
Sum of all production	11014	11012	10973	10574
Sum of all respiratory flows	7165	7121	6500	6451
Calculated total net primary production	7397	7397	7650	7271

Finn's mean path length (Fig. 3.9) decreased from a maximum in 1600 to minimum in 1900, followed by an increase and then decrease in 1970 and the 1990s respectively, while Finn's cycling index displayed the opposite pattern (although peaking in the 1990s model). Shannon's and Simpson's diversity indices both decreased over time, with the greatest decrease being observed from the 1970s to the 1990s model (Fig. 3.10). When comparing the overall trends in selected indices to the trends predicted for stressed ecosystems, as suggested by Odum (1985) (Fig. 3.11), R/B, flows to detritus, Finn's mean path length and the diversity indices all conformed to the pattern expected in a stressed system. Respiration (R), P/R P/B, Finn's cycling index and B/P displayed the opposite trend from that of a stressed system. R and the diversity indices displayed the same trends between all models. Six of the ten indices examined in Fig. 3.11 suggested that the ecosystem was stressed from 1600 to 1900, compared with four out of ten over the period from 1900 to 1970, and three between 1970 to the 1990s model.

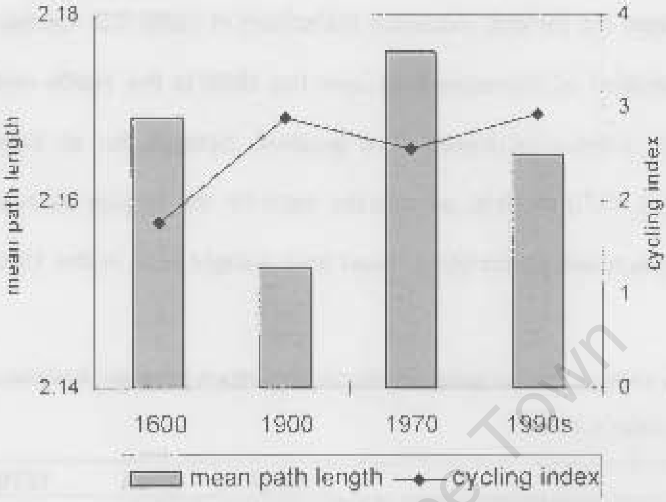


Figure 3.9: Finn's mean path length and cycling index for each period in the northern Benguela.

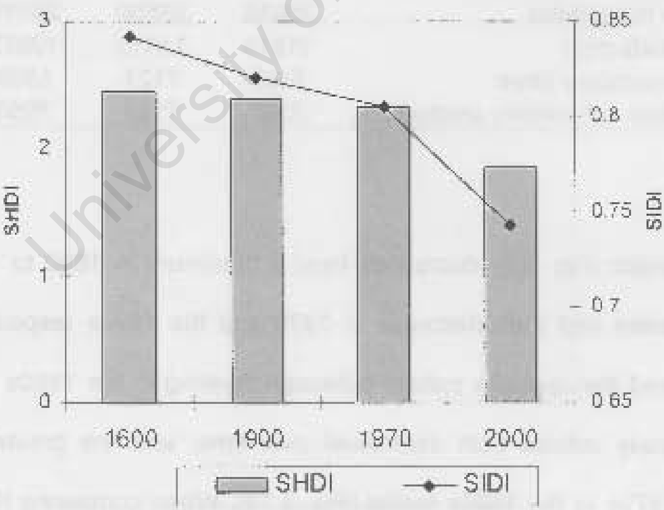


Figure 3.10: Diversity indices for each period in the southern Benguela. SIDI is Shannon's diversity index, SIDI is Simpson's diversity index.

System indices (Odum, 1985)	Expected trend (stressed ecosystems)	1900	1970	1990s	Overall trend (1900-1990s)
Community respiration (*R*)	↗	↘	↘	↘	↘
Production/ respiration (*P/R*)	<1 or >1	>1	>1	>1	>1 (↓)
Maintenance:biomass structure (*P/B*)	↗	↗	↘	↘	↘
(*R/B*)	↗	↗	↘	↘	↘
Unused PP & nutrient loss (*Sum of all flows to detritus*)	↗	↘	↗	↘	↗
Vertical cycling of nutrients (*Finn's cycling index*)	↘	↗	↘	↗	↗
Proportion of r strategists: Size & lifespan of organisms (*B/P*)	↘	↘	↗	↗	↗
Length of food chain (*Finn's mean path length*)	↘	↘	↗	↘	↘
Species diversity (*SIDI*)	↘	↘	↘	↘	↘
(*SHDI*)	↘	↘	↘	↘	↘

Figure 3.11: Trends in selected indices as from Odum (1985) indicating ecosystem stress. For indices of species diversity, *SIDI* is Simpson's diversity index and *SHDI* is Shannon's diversity index.

3.3.3. Sensitivity analyses:

The mixed trophic impact assessments (Appendix B., Figs B.1-4) showed that in all models the plankton groups had relatively significant and widespread impacts, for the most part positive. The hake groups also impacted most fish groups significantly, mostly negatively, although large *M. paradoxus* did have positive impacts on a number of groups, particularly adult horse mackerel. Detritus also positively influenced a number of groups in all models, predominantly the plankton and benthos groups. The impacts of gelatinous zooplankton, sardine, horse mackerel and large *M. capensis* changed the most over time. Sardine had a far greater impact on other groups, particularly seals and predatory fish in the < 1600 model than in the more recent periods. The proliferation of gelatinous zooplankton in the 1990s caused its increased impacts, largely on itself. Horse mackerel had relatively bigger impacts on its consumers and prey in the more recent models, while *M. capensis* had relatively smaller impacts. Results from the sensitivity analysis (Appendix B., Tables B.8-11) were considered significant where a change in an input parameter caused a 40% or more change in the affected estimated parameter. All groups were sensitive to their own input parameters. In the majority of instances, changes in estimated parameters only became significant after the input parameter had been altered by 30% or more. The two exceptions were in the 1600 model, where meiobenthos B was altered by almost 90% after a 20% change in macrobenthos P/B, and in the 1990 model, where the B of pelagic goby was altered by more than 100% after a 20% change in small *M. capensis* P/B. Input parameters that caused significant changes in other parameters and the groups affected are listed in Table 3.3. For full results of the sensitivity analysis including the affecting and affected parameters, see Appendix B., Tables 8-11.

3.4. Discussion:

3.4.1. Internal indices:

The biomasses of the individual groups involved (Fig. 3.1) appear to reflect man's influence upon the system. in the case of seals, the collapse and subsequent recovery of the population can be directly attributed to the commencement of intense and unrestricted harvesting from the 1700s to the early 1900s. After regulation of the seal harvest and ultimately the introduction of TACs, the Namibian seal population recovered to something like its original size (Griffiths *et al.*, 2004). This may also reflect the increased terrestrial breeding space available to seals, after guano and egg harvests disturbed and depleted many bird colonies. The original seal colonies were also restricted to islands, whereas currently the largest colonies are found on the mainland, which has become a viable breeding locality due to the decline in large terrestrial predators. Whether directly or indirectly, human involvement has had a considerable impact on seal biomass. Other species, such as hake and sardine, reflect the well documented exploitation and collapses of these stocks (Boyer & Hampton, 2001; Griffiths *et al.*, 2004; Roux & Shannon, 2004). The decline in seabird stocks has resulted both from the harvesting of eggs and the severe alteration of the terrestrial breeding habitat that was associated with guano harvesting (Crawford *et al.*, 1995; Crawford & Jahncke, 1999), as well as the bycatch of seabirds associated with modern trawling practices (Crawford *et al.*, 1995; Shannon *et al.*, 2005). The collapse of the sardine stocks in the 1970s also negatively impacted a number of seabird species, especially African penguins and Cape gannets, by reducing prey availability (Crawford *et al.*, 1995; Crawford *et al.*, 1999). While the platforms constructed off the Namibian coastline to facilitate guano collection from the 1930s have provided alternative breeding sites for some species (Cooper *et al.*, 1982; Griffiths *et al.*, 2004), the above factors, combined with the encroachment of seals into areas previously inhabited by bird colonies, have prevented seabird populations in the northern Benguela from recovering, or even stabilizing.

Other groups, such as cephalopods and demersal fish, experienced declines without having been directly targeted by fishing to any large extent off Namibia, although demersal fish are likely to have been impacted as bycatch species in hake trawls (Crawford *et al.*, 1987). This is at odds with the southern Benguela situation, where a lucrative chokka squid fishery operates and demersal fish are targeted on the Agulhas Bank (Crawford *et al.*, 1987). This could be a result of the lower B of fished groups like hakes and small pelagics, and therefore scarcity of prey. The most noticeable change from 1970 to the 1990s is the unprecedented proliferation of jellyfish, strengthening the speculation that system-level changes have taken place. The increased gelatinous zooplankton abundance has implications for the transfer of production through the system, as the low consumption of this group within the system means that while they are consumers, the majority of their production flow back to detritus (Heymans *et al.*, 2004). The increased proportions of hakes, small pelagics groups and horse mackerel, for example, consumed by groups such as cephalopods, predatory fish and seals, is a result of the declining overall biomass of the groups consumed as well as of other predators, rather than of an increased consumption on the part of those predatory groups. The recovery of seals in recent years has simply exaggerated this effect though, as has the increasing abundance of horse mackerel relative to other prey groups over the last few decades (Heymans *et al.*, 2004). The declining TLw of selected groups in Fig. 3.5 supports this, resulting from both the decreases in B experienced by most of these groups and their reduced B relative to the rest of the system. The current higher mean TL of the community (excluding plankton) and the piscivore community (Fig. 3.6) is indicative of the scarcity of low trophic level small pelagic fish, such as sardine and anchovy that normally would contribute a relatively high proportion of the community, while higher TL groups have declined to a lesser extent or been replaced to some degree by other relatively higher TL groups (Cury *et al.*, 2005b).

The catch within the system in 1900 was comprised entirely of seals and seabirds, both high TL groups, so the decrease in mean TL of the catch from 1900 to 1970 is to be expected, especially with the large contribution of small pelagics landed by the purse-seine fishery from the 1950s. Although hake landings had decreased considerably by the 1990s, so had the total tonnage landed, resulting in an increased mean TL as higher TL species constituted the bulk of the catch. Replacement of declining hake groups by horse mackerel has also occurred in a limited manner in the northern Benguela, mitigating the trophic effects of the decrease in hakes somewhat (Cury *et al.*, 2005b). Similarly, increased proportions of fishing mortality are not necessarily symptomatic of increased effort (although this is the case for some groups e.g. horse mackerel), cycling in a mature and stressed ecosystem. While an ecosystem out of balance is likely to tend towards smaller, shorter-lived species, especially when affected by fishing, the increasing prevalence of larger, longer-lived species behind the increasing B/P for this ecosystem could superficially appear to be a positive shift. When the biomass of the system as a whole and by group is considered, however, the decline of many groups and the collapse of small pelagic stocks seems the more likely explanation – the loss of small pelagics is merely more extreme than that of other species, thus tipping the balance towards the larger, longer-lived species.

3.4.3. Sensitivity analysis:

The increased impact of horse mackerel on its consumers and prey, particularly in the 1990s model compared to 1600 and 1900, is consistent with the increased importance of this group after the decline in hake stocks in the 1970s (Cury *et al.*, 2005b). Horse mackerel has also been shown to have had larger impacts in the 1980s compared to the 1970s and 1990s, corresponding to its maximal abundance over that period (Cury *et al.*, 2005b). The decreasing role played by hakes in the ecosystem over the periods modelled, as biomass of hakes declined, can be linked to the decreasing impact of the hake groups on their prey species particularly in more recent models. The sensitivity analyses confirm what is already known – that more information on lesser known groups would be extremely valuable as these groups often have significant impacts on other model output parameter estimates. As in the southern Benguela models, while some data are available for economically important groups such as sardine and hake, others such as pelagic goby, planktonic groups, cephalopods, demersal fish and cetaceans are less well documented. The figures produced by these models are attempts at best-estimates, but are still estimates.

3.4.4. Conclusions:

It would appear that since the arrival of man in the northern Benguela some large-scale changes in the structure and functioning of the system have taken place. The biomass of the majority of groups has decreased, in the cases of sardine, hakes and seabirds, fairly dramatically. The high biomass of a few small pelagic fish species typically found in upwelling systems is now absent, replaced to some extent by a wider range of species (Heymans *et al.*, 2004), and in recent decades there has been a not previously recorded rise in the biomass of jellyfish. Catches have decreased along with target-species biomass, and although the mean TL of the catch in the periods modelled here did not display evidence of fishing down the foodweb, as is the case in many overexploited systems (Pauly & Palomares, 2005), over a shorter timescale, the 1980s and 1990s, evidence of fishing down the foodweb has in fact been detected in the Northern Benguela (Heymans *et al.*, 2004). The increased TL of the catch observed over the periods examined and the stable TL of catches observed by Cury *et al.* (2005) in the northern Benguela from 1972 - 2000 is indicative of the depletion of sardine and anchovy stocks and the increase in horse mackerel biomass as hakes declined, rather than of a healthy system (Cury *et al.* (2005). The expected succession of one small pelagic by another as dominant in upwelling systems did not occur in the northern Benguela after the collapse of the sardine stock, when instead of anchovy biomass increasing, other species such as pelagic goby and horse mackerel filled the niche left by sardine (Boyer & Hampton 2001). Evidence of these changes in the structure of the ecosystem was also found in the diet of top predators, such as seabirds and seals, which in many case changed from a sardine-dominated diet to one based on pelagic goby (Crawford *et al.*, 1995; Cury & Shannon, 2004).

Man's influence in the northern Benguela began in the form of harvesting of seals and seabirds. The effects of this initially unrestrained harvesting, and the indirect effects of later fishing practices, are evident in the changes in biomass of these groups, as well as from the numerous accounts telling of vast colonies of seabirds, for one, that subsequently shrank to insignificant levels (Best *et al.*, 1997; Berruti, 1989). The biomass fluctuations in groups such as the hakes and sardine, however, are less easily attributed entirely to the effects of fishing. Changes to the physical environment in the early 1990s, including a low oxygen event in 1994 and a Benguela Niño in 1995, have likely played a considerable role in the failure of management strategies implemented in the early 1990s to salvage already reduced fish stocks and prevent further decline of a number of species (Heymans *et al.*, 2004, Roux & Shannon, 2004, Cury & Shannon, 2004). These events caused upheaval in the system, drastically reducing the stocks, either through migration (e.g. hake) or, where this was not possible, mortality (Gammelsrød *et al.*, 1998; Boyer *et al.*, 2001). There is evidence of declines in the hakes, horse mackerel, sardine, and anchovy as directly affected groups (Boyer *et al.*, 2001; Boyer & Hampton, 2001). The knock-on effects were even more far-reaching, affecting seabird and seal populations to the extent that Roux (1998) estimates that a third of the Namibian seal population was lost over this period as a result of scarcity of prey (Cury & Shannon, 2004). Thus, while the impact of fishing is certainly visible in the system, prompting the decline and collapse of hake and sardine stocks respectively in the 1970s and 1980s, it may be more accurate to credit the additive effects of fishing *and* environmental anomalies and changes with the lack of recovery and further decline in many stocks (Cury & Shannon, 2004; van der Lingen *et al.*, 2006b). Shannon *et al.* (in press) suggest that the type of trophic control operating within the system could be altered as a result of the collapse of small pelagic fish stocks. While upwelling systems are in general hypothesised to operate under wasp-waisted control by the small pelagic species, the removal of these species may allow for bottom-up control by environmental forcing. Alternatively, as has been the case in the northern Benguela, small pelagics may be replaced by opportunistic species such as jellyfish and mesopelagic fish which utilize the production previously consumed by the small pelagic fish, but due to dietary or habitat restrictions, do not pass this production along to their predators (Shannon *et al.*, submitted). Changes of this nature in the functioning of the ecosystem could mean that, in line with Odum (1985), as a system becomes increasingly stressed, fluctuations in biological interactions are more likely to be initiated and regulated by environmental and physical forcing, increasing the vulnerability of northern Benguela stocks to any future environmental anomalies.

Chapter 4:

Comparing the pristine northern and southern Benguela & investigating the effects of fishing

4.1. Introduction:

The EwE software and modelling approach has provided an effective means of describing and quantifying the flows and interactions within a given system, as well as investigating possible trophic impacts or alterations in the pattern of energy flow resulting from fishing. It has been used to describe changes in ecosystem structure over time in a large number of systems, (e.g. Shannon *et al.*, 2003; Heymans *et al.*, 2004, Neira *et al.*, 2004), but also allows for comparison between systems (Moloney *et al.*, 2005; Coll *et al.*, 2006). In the first part of this chapter, models generated in Chapters 2 and 3 for the 'pre-contact' (before man's intervention) northern and southern Benguela will be compared in terms of ecosystem structure and functioning. The modern states of these two systems have been compared previously in a number of studies (Jarre-Teichmann *et al.*, 1998; Shannon & Jarre-Teichmann, 1999; Shannon, 2001; Cury & Shannon, 2004; Coll *et al.*, 2006), and have been found to differ fairly extensively, with regard to both structure and functioning. In the 1980s, higher total biomass and catches in the northern Benguela did not equate to increased trophic flows, which were larger in the southern Benguela. Top predators played a more important role in the southern than in the northern Benguela over this period (Shannon, 2001). Although the species composition of the two ecosystems is similar, dominant species, environmental effects and management histories of the fisheries in the two regions differ considerably (Cury & Shannon, 2004), and these factors contributed to the quite disparate systems found in the modern era. Whether this has always been the case is not certain. Due to the trophic basis of the *Ecopath* modelling process, the possible pristine-state models generated here have not taken into account the effects of environmental events. However, it is hoped that by comparing these models, the fundamental similarities or differences between the two systems would become evident, unobscured by changes wrought by long-term fishing pressures. .

In the second part of this chapter, the impact of fishing on the pristine systems is investigated. While *Ecopath* mass-balancing software can be used to generate a steady-state model of the possible 'pristine' state of the ecosystem, does the application of the levels of fishing pressure representative of the industrial era (1910 – 1980) to the pristine model result in a community structure similar to that which exists today? This would require the assumptions that i) fishing has had a significant impact on the structure and functioning of the Benguela ecosystem, and ii) the pristine models generated for both the northern and southern Benguela in Chapters 2 and 3 are representative of the unfished states of the systems. Simulations based on the southern Benguela models are not necessarily expected to produce a steady-state model similar to that which was constructed to represent the current period in that system, as simulation modelling (Shannon *et al.*, 2004c) and fitting of a southern Benguela model to time series data for the modern era (Shannon *et al.*, 2004b) have shown that fishing has played a relatively minor role in driving major ecosystem changes in the system. Although fishing pressure has been heavier in the northern Benguela, the latter has experienced a number of physical and climatic events in the last few decades that have likely impacted fish stocks and hence ecosystem structure (see Chapter 3). It therefore seems likely that the model produced by the simulation for the northern Benguela will deviate more from the 1990s model than will that for the southern Benguela, which does not seem to have been subjected to environmental fluctuations on the same scale as those registered in the northern Benguela.

4.2. Methods:

4.2.1. Comparison of the northern and southern Benguela pristine models:

The construction and balancing of the models compared here is described in Chapters 2 and 3 of this dissertation, as is the generation of any indices used in this chapter.

4.2.2. Investigating the effects of fishing:

The impacts of fishing effort in the industrial era on the pristine (<1600) models of the southern and northern Benguela were investigated by way of the *Ecosim* dynamic simulation routine (Walters *et al.*, 1997, see Chapter 1). The pristine model of each system was used as a basis for the simulations, which were allowed to run undisturbed for five years, after which the fishing pressure in the industrial era models of each system (see Chapters 2 and 3) was applied to the relevant system. Fs by group were calculated according to F = catch/ biomass and are shown in Table 4.1. Wasp-waisted control, the trophic flow control characteristic of several upwelling systems (Cury *et al.*, 2000) was assumed for the simulations. Although model groups assumed to exert wasp-waisted control (small pelagic groups, juvenile horse mackerel and small *M. capensis*) were obtained from previous models (Shannon *et al.*, 2004), the *Ecosim* default vulnerability settings of 1.2 for interactions with predators and 5 for interactions with prey of these groups, were used because the vulnerabilities previously published (e.g. Shannon *et al.*, 2004b) pertained to models fitted to data for a different starting period and were thus not necessarily directly applicable here. Trophic ontogeny was incorporated, linking the juvenile and adult groups of horse mackerel and hake. Growth parameters used are shown in Table 4.2. Models were run for 50 years in total. The *Ecopath* model generated for each system at the end of the 50-year simulation was then compared to the current model for that system. For the southern Benguela, the model generated by the simulation was compared with that of the 1990s, rather than that of the 2000s, in order to avoid confusion of fishing effects with those of the high small pelagic biomass represented in the model of the early 2000s. An updated version of the 1990s model described in Shannon *et al.* (2003) was used for the southern Benguela comparison. The 1990s model of the northern Benguela, as described by Roux & Shannon (2004), was used. Calculation of any indices was as explained in Chapter 2.

Table 4.1: F y^{-1} values used for the simulations, based on catches in the 1960 and 1970 models for the southern and northern Benguela respectively.

Group	Southern	Northern
Sardine	0.1975	0.4271
Anchovy		0.5042
Redeye	0.0001	
Chub mackerel	0.3539	
Adult horse mackerel	0.1431	0.0617
Snoek	0.3120	
Large pelagics	0.2247	0.2319
Cephalopods	0.0004	
Large *M. capensis*	0.1791	0.1241
Large *M. paradoxus*	0.3806	0.3922
Benthic-feeding demersals	0.0074	0.0020
Pelagic-feeding chondrichthyans	0.0029	
Benthic-feeding chondrichthyans	0.0095	
Seals	0.0250	0.1007

Table 4.2: Parameters used to model the graduation of juvenile/small horse mackerel and hakes into adults. For original sources see Shannon *et al.* (2004).

Parameter	Horse mackerel	*M. capensis*	*M. paradoxus*
Age at transition from juvenile/small to adult/large group	2 years	3 years	3 years
Ave. adult weight as a proportion of ave. weight at transition	3.5	3	3
K (von Bertalanffy growth coefficient)	0.183 y^{-1}	0.046 y^{-1}	0.046 y^{-1}

4.3. Results:

4.3.1. Comparing southern and northern Benguela pristine states:

4.3.1.1. Summary statistics and biomass:

Total biomass, consumption and respiration were higher in the northern Benguela, though production and throughput were larger in the southern Benguela model (Fig. 4.1). Finn's mean path length in both systems was relatively short, although longer in the northern Benguela (2.17) than in the southern Benguela (2.05).

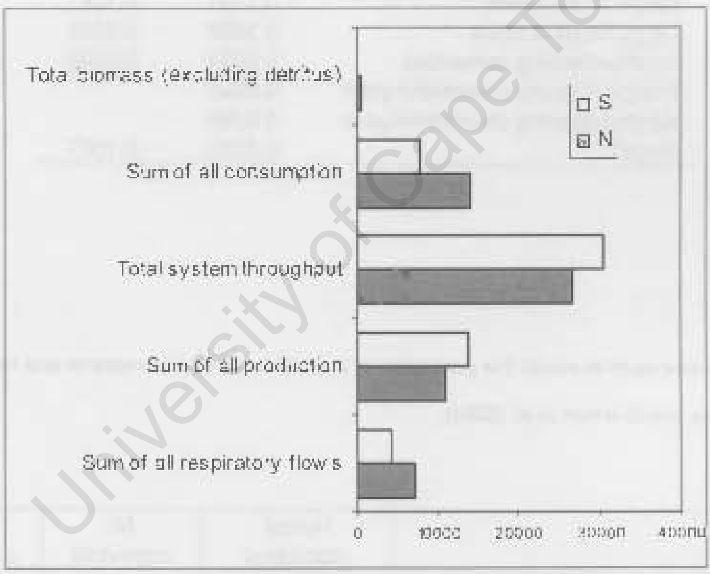


Figure 4.1: Summary statistics for the southern and northern Benguela pristine models. All statistics are in $t.km^{-2}.y^{-1}$, except for biomass, which is in $t.km^{-2}$.

The biomass of non-planktonic consumers in the northern Benguela was far higher than in the southern (Fig. 4.2), particularly with regard to small pelagic groups and hake. The ratio of planktivores: piscivores in the pristine systems was, however, higher in the southern Benguela (Fig. 4.3).

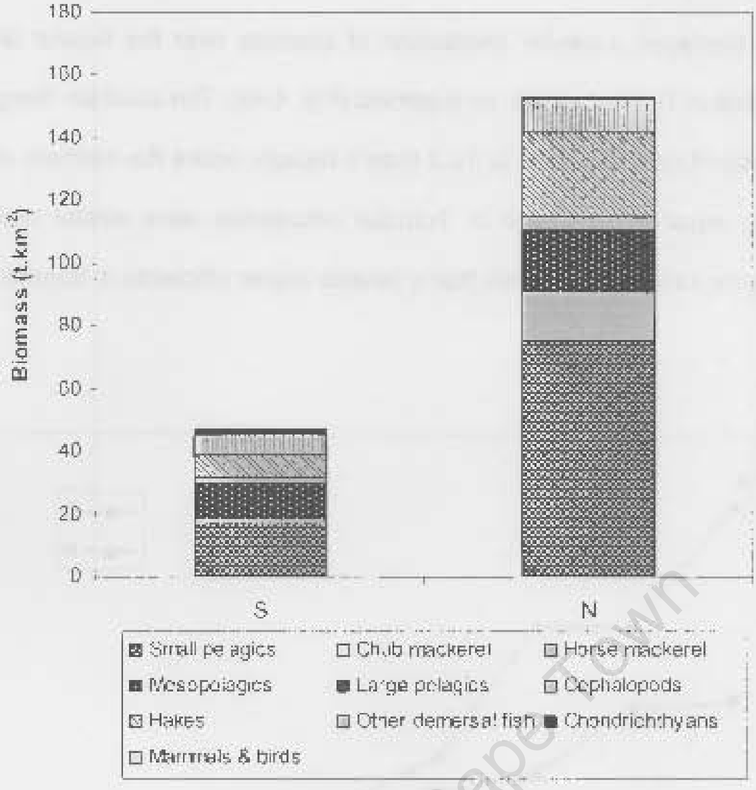


Figure 4.2: Biomass of non-planktonic consumers in southern and northern Benguela pristine models. Small pelagics include sardine, anchovy, pelagic goby and other small pelagics, mammals and birds includes seals, cetaceans and seabirds, and hake and horse mackerel groups were aggregated.

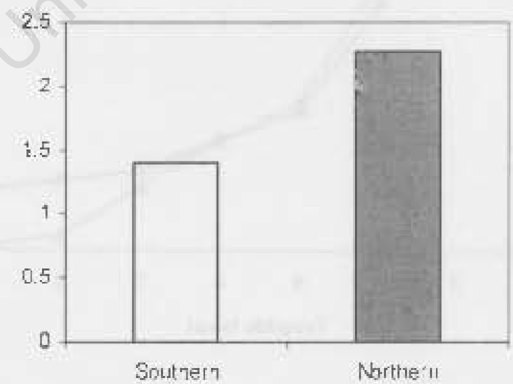
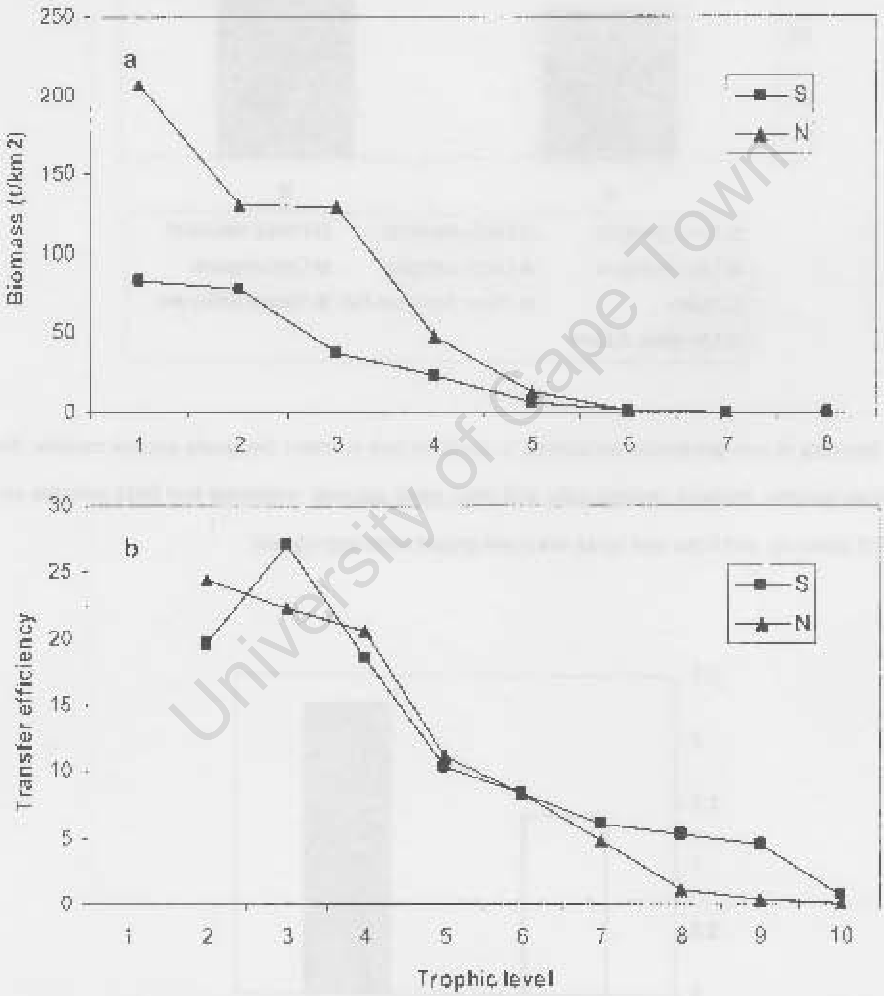


Figure 4.3: Biomass ratio of planktivores: piscivores in the pristine systems for the southern and northern Benguela.

4.3.1.2. Trophic aggregation:

Both subsystems displayed a similar distribution of biomass over the trophic levels, with the majority concentrated in TLs 1, 2 and 3, as expected (Fig. 4.4a). The southern Benguela did have a slightly higher proportion of biomass at TL 2 than 3 though, unlike the northern where biomass was approximately equal in TL 2 and 3. Transfer efficiencies were similar between the two systems, although the southern Benguela had a notable higher efficiency in transfers from TL 2 to TL 3 (Fig. 4.4b).



Figures 4.4: Biomass (a) and transfer efficiency (b) aggregated by trophic level for the southern and northern Benguela pristine models

4.3.1.3. Consumption:

In both subsystems zooplankton were the main consumers, responsible for 73% and 82% of total consumption in the northern and southern systems respectively. Small pelagics consumed a higher proportion of production in the northern Benguela, while mesopelagics were relatively more important consumers in the southern Benguela (Fig. 4.5). Although hakes were responsible for approximately 14% of the consumption by non-planktonic consumers in both systems, they consumed a greater proportion of both small pelagic and hake production in the northern Benguela, as compared with the southern Benguela (Fig. 4.6). Marine mammals and seabirds both played a greater role in consumption of the two abovementioned groups in the southern Benguela, while horse mackerel was more important in the northern Benguela.

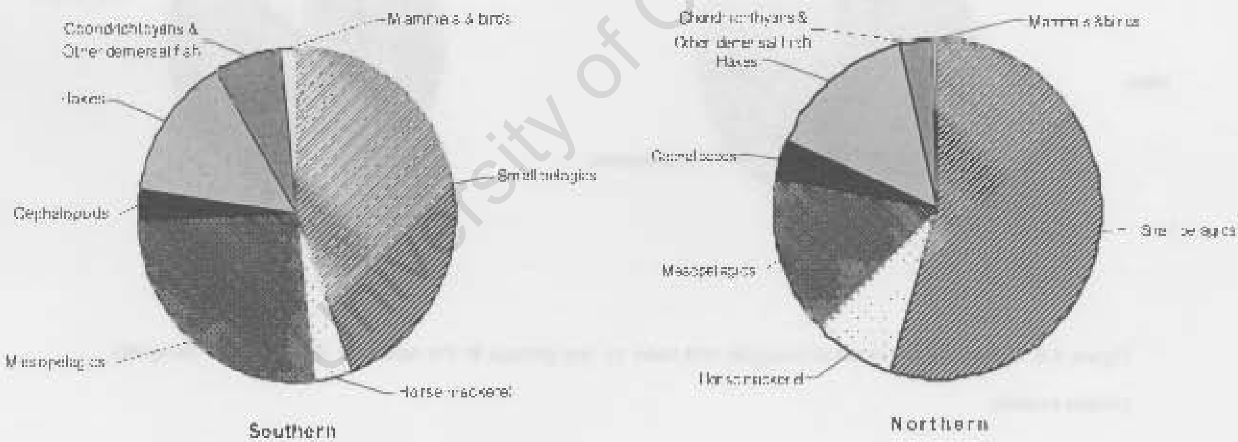


Figure 4.5: Consumption by key groups in the southern and northern Benguela pristine models (excl. zooplankton groups).

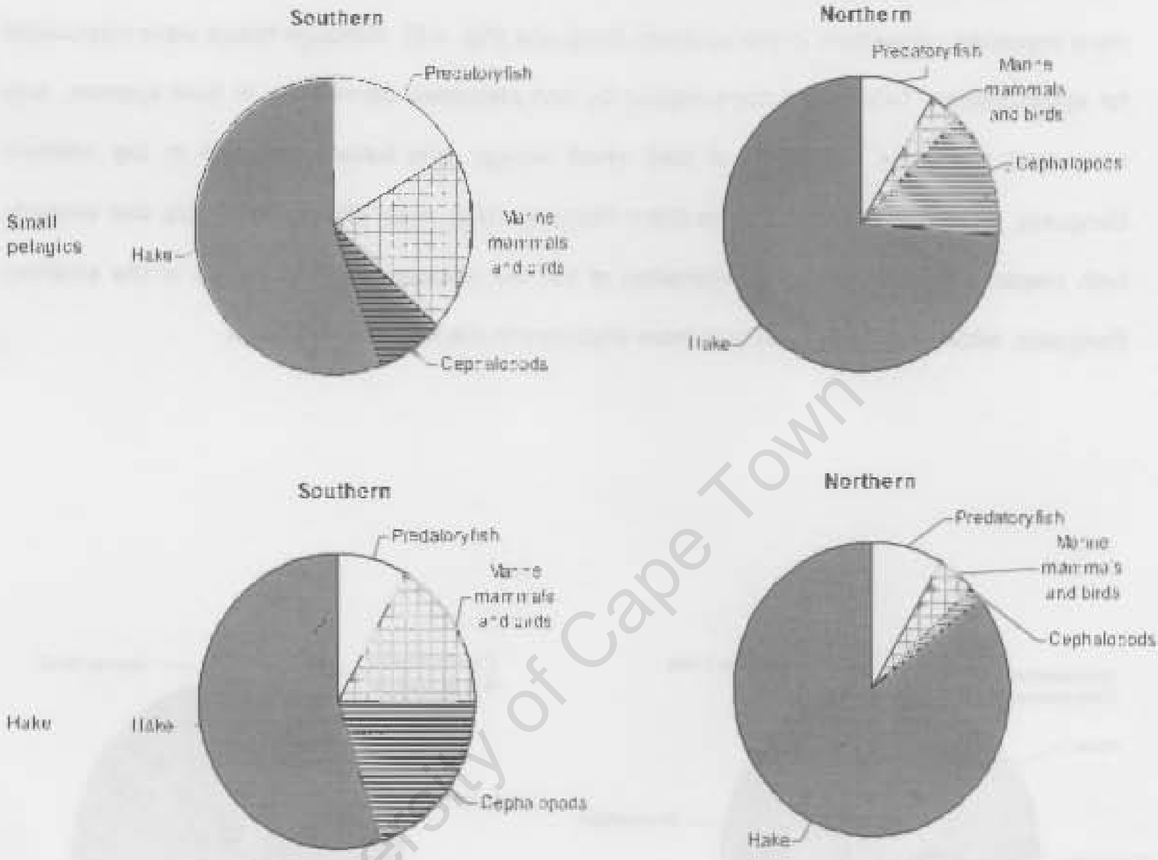


Figure 4.6: Consumption of small pelagics and hake by key groups in the southern and northern Benguela pristine models.

4.3.2. Investigating the impacts of fishing via simulations:

4.3.2.1. Biomass:

For the majority of groups in the southern Benguela models, the differences in biomass between the 1990s model and the model generated by *Ecosim* (Fig. 4.7) were less than 30%.

Mesozooplankton, sardine, chub mackerel and large pelagics showed large discrepancies for the southern Benguela. Biomasses in the northern Benguela models displayed larger alterations from the 1990s value, although the majority were within a range of 60% difference. Gelatinous zooplankton and large pelagics had the highest degree of dissimilarity.

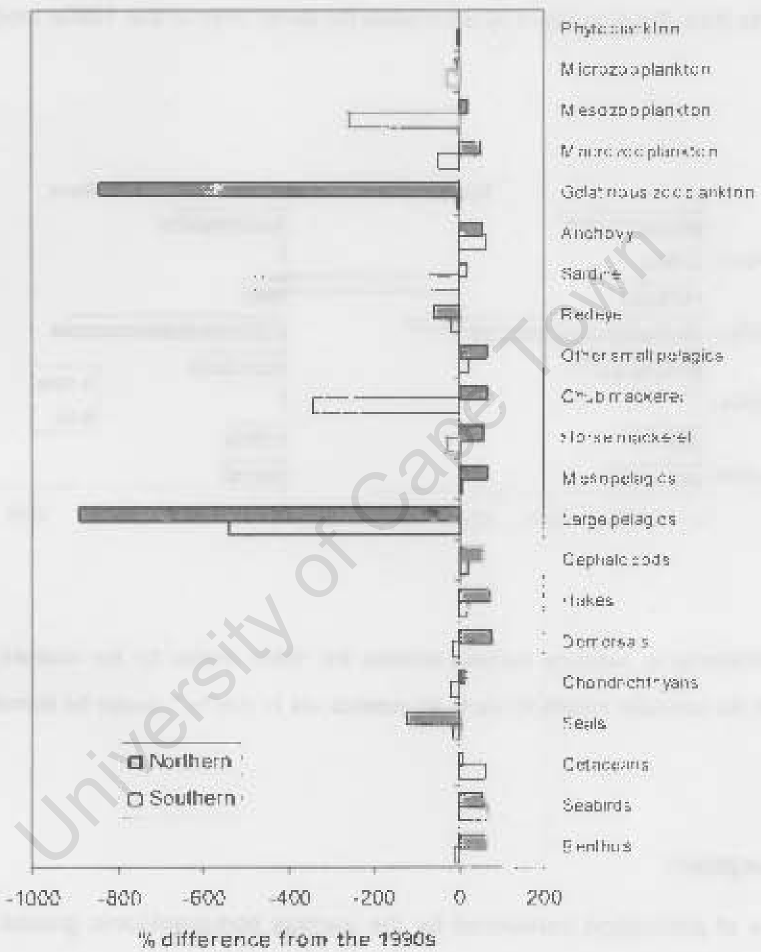


Figure 4.7: The difference between the current (1990s) models for the northern (Roux & Shannon, 2004) and southern Benguela (Shannon *et al.*, 2003) and their respective models resulting from the simulation of industrial fishing pressure on the pristine systems over a period of 50 years.

4.3.2.2. Summary statistics:

In both the northern and southern Benguela cases the summary statistics (Fig. 4.8) were similar in the 1990s and simulation-generated models. For the southern Benguela consumption, throughput, production and respiration were all higher in the 1990s model, whereas exports and flows to detritus were greater in the simulated system. For the northern Benguela all displayed parameters were greater in the simulated system, except for exports, flows to detritus and total biomass. Exports from the simulated system were far lower than in the 1990s model.

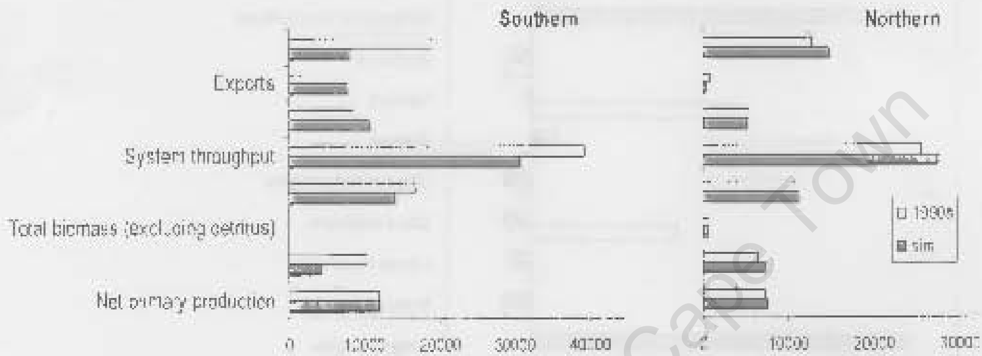


Figure 4.8: Difference in summary statistics between the 1990s models for the southern and northern Benguela and the simulated models for each. All statistics are in t.km^{-2}.y^{-1}, except for biomass, which is in t.km^{-2}.

4.3.2.3. Consumption:

The proportions of production consumed by the various non-planktonic groups in the southern Benguela were similar in the two models (Fig. 4.9), although small pelagics and hake in the simulated system consumed a slightly higher proportion of production relative to other groups, such as horse mackerel, mesopelagics and demersals. In the northern Benguela models, larger differences were evident, with a much higher proportion of production consumed by small pelagics in the 1990s model, versus by hake, demersal, mesopelagic and horse mackerel groups in the simulated system. The simulation-based models for both ecosystems estimated a higher biomass of fish than in the 1990s models, so that, for example, the smaller relative proportion of the consumption attributed to small pelagic species in the northern Benguela simulation-based model is in fact a greater absolute amount than consumed by these groups in the 1990s model.

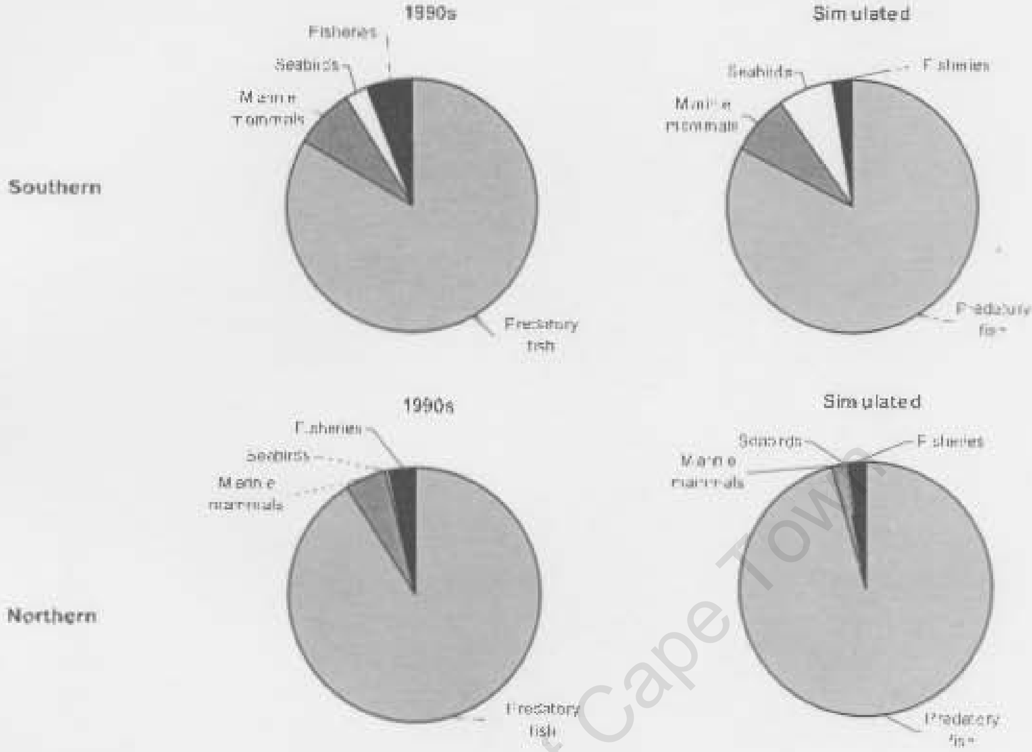


Figure 4.9: Consumption by aggregated non-planktonic groups in the 1990s compared to in the simulated models for the northern and southern Benguela.

4.3.2.4. Trophic level:

The biomass, transfer efficiency and total throughput by trophic level for the 1990s and simulated models, as well as the percentage change in each parameter between the 1990s and the simulated system, are shown in Table 4.3. Fairly large differences in the biomass at a specific TL occurred, especially at TL 3 and 4, where a much higher biomass was concentrated in the simulated modern model of the southern Benguela, and in the 1990s model for the northern Benguela models. This did not, however, translate into greatly altered proportions of total biomass at each TL. In the southern Benguela, a marginally lower proportion of total biomass was found at TL 1 and 2 and a slightly higher proportion at 3 and 4 in the simulated model compared to the 1990s system. The northern Benguela simulated model displayed the opposite trend, with

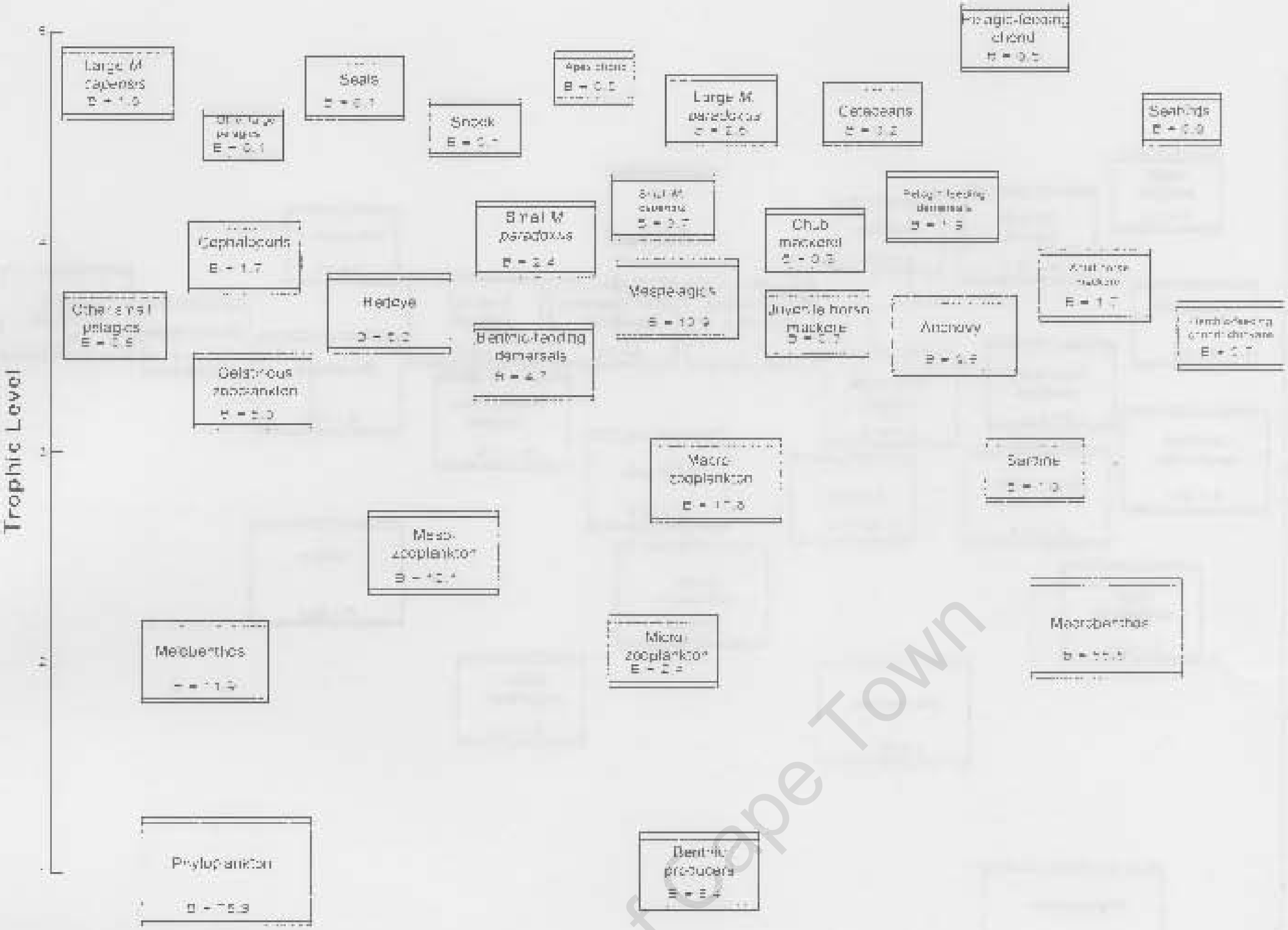


Figure 4.5a: Groups and biomasses (B) in t.km^{-2} of groups in the southern Benguela pristine model (1600), arranged vertically according to trophic level. The area of each block is proportional to its B

higher proportion of biomass at TLs 1 and 2 and a lower proportion at 3 and 4 relative to the 1990s model. While the greatest changes in biomass occurred at the intermediate TLs, transfer efficiency and throughput varied most at both extremes of the trophic chain, at both low and high TLs. Transfer efficiencies in both models derived from simulations followed the pattern expected of an upwelling system: higher at low TLs, lower at high TLs where exports and flows to detritus are relatively high. The proportion of primary production transferred was higher in both simulated systems, relative to their respective 1990s models. Throughput differed fairly significantly between the 1990s and simulated systems in both the northern and southern ecosystems, although to opposite effect in each – lower in the southern simulated

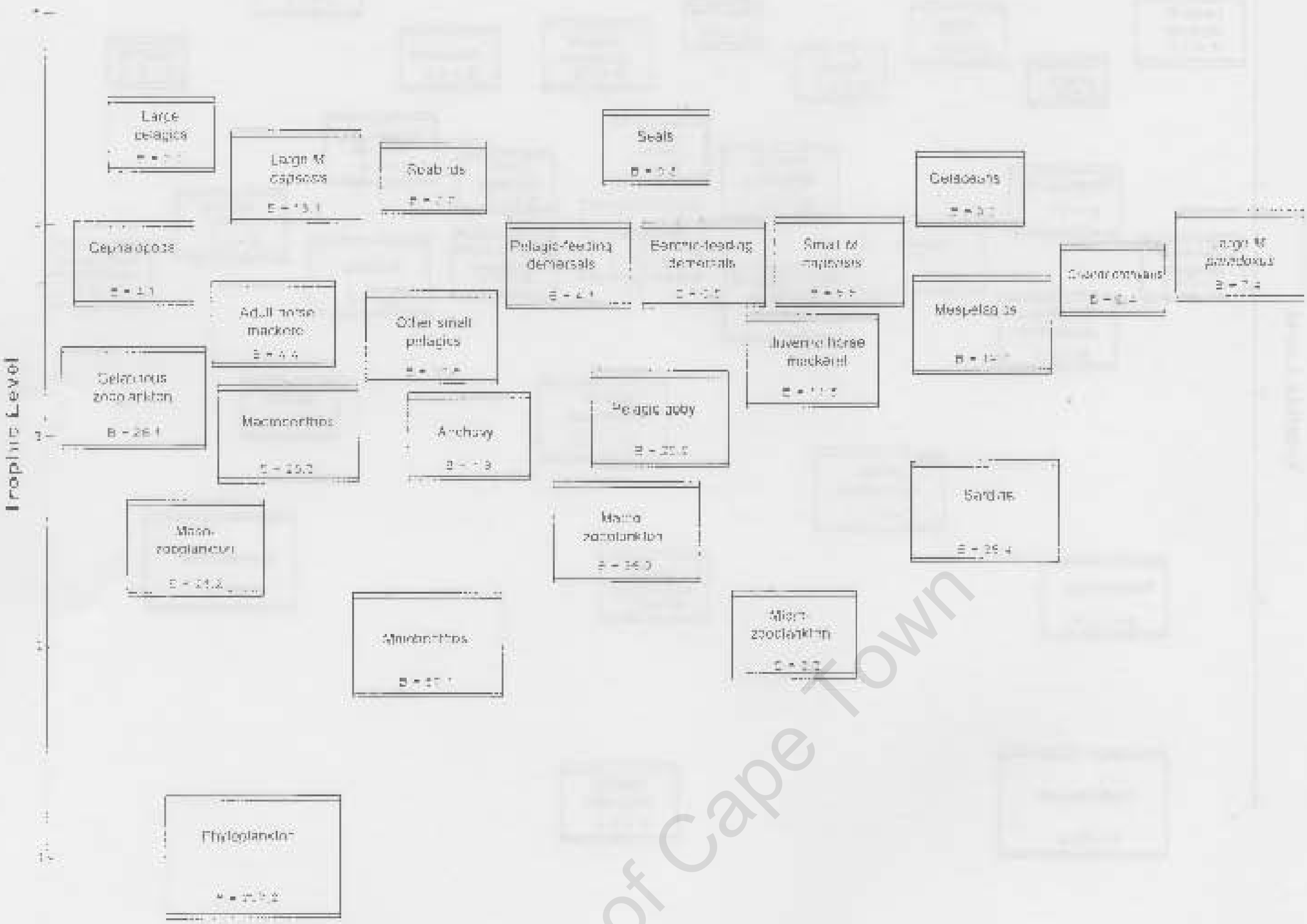


Figure 4.5b: Groups and biomasses (B) in t.km⁻² of groups in the northern Benguela pristine model (1600), arranged vertically according to trophic level. The area of each block is proportional to its B

system and higher in the northern versus in their 1990s models. Groups in the southern Benguela were generally operating at higher TLs than in the northern Benguela (Figs 4.5a&b), although the fact that some high TL groups found in the northern Benguela, such as chondrichthyans and large pelagics, are divided into two or more component groups in the southern model must be taken into account when examining Figs 4.5a&b. In particular, anchovy, large *M. capensis* and large *M. paradoxus*, found at TLs of 2.62, 4.22 and 3.83 respectively in the northern Benguela, were operating at TLs of 3.54, 4.75 and 4.62 in the southern Benguela.

4.4. Discussion:

4.4.1. Comparing southern and northern Benguela pristine states:

Coll *et al.* (2006) state that the many differences between upwelling ecosystems result largely from differences in primary production, and this appears to be a factor when considering the northern and southern Benguela. Lower production and the higher transfer efficiency from producers to TL 2 in the northern Benguela suggest that this system is slightly more food-limited than the southern Benguela. This may simply be due to the far higher consumer biomass in the northern Benguela (Fig. 4.2), also accounting for the higher consumption and respiration in this system. During the 1980s, the total biomass excluding detritus was also lower in the southern Benguela than in the northern, although the pristine biomass estimate here for the southern Benguela (230 t.km^{-2}), was lower even than the 1980s value (297 t.km^{-2}) (Shannon, 2001). In the 1980s all major flows were higher in the southern Benguela, the more productive system at the time, whereas in the pristine models respiration and consumption were higher in the northern Benguela. This could be due to the much higher total biomass in the pristine northern Benguela model compared to that of the 1980s (Shannon, 2001). The abundance of pelagic goby in the northern system could also account for the more even distribution of biomass between TLs 2 and 3 in this system, compared with the lower biomass at TL 3 in the southern Benguela. The higher transfer efficiency for TL 3 in the pristine southern Benguela translated into the more even allotment of biomass in TL 3 and 4 in this system, compared with the northern Benguela, where there was a substantial reduction in biomass from TL 3 to 4 (Figs 4.4a &b). The pattern of groups observed functioning at higher TLs in the southern Benguela than in the northern fits that found during the 1980s (Shannon, 2001).

Both small pelagics and hake play a larger role in terms of biomass and consumption in the northern Benguela, although they are important consumers in both systems. As in the 1980s (Shannon, 2001), demersal fish were expected to, and did, contribute more to consumption in the southern Benguela, due largely to the inclusion of the Agulhas Bank into the extent of that ecosystem (Shannon & Jarre-Teichmann, 1999). The higher consumption by horse mackerel in the northern Benguela also repeated the pattern observed in the 1980s, although the increased abundance of this group that occurred after the decline of hake stocks in the northern Benguela from the 1970s, was not depicted in the pristine model. Thus while consumption by this group was higher in the northern pristine system, the difference in contribution to consumption in the northern versus southern system was not as marked as has been observed in these systems during the 1980s (Shannon, 2001).

4.4.2. Investigating the effects of fishing:

The models produced by the simulation scenario investigated here differ to a certain extent from the models that have been developed based on the 1990s ecosystem structure, although summary statistics/indicators (ecosystem scale) and biomass per model group are fairly similar. The larger discrepancies come into play when indices are compared per trophic level, and here there seems to be a larger gap between the simulation-based model and the 1990s model for the northern Benguela, than for the southern. In both systems, those groups that differed the most with regard to biomass were either those known to have been atypically high in the 1990s, such as the northern Benguela gelatinous zooplankton, groups that are not consumed to a great extent within the system and therefore likely to be underestimated, e.g. large pelagics, or groups having low biomass thus resulting in fairly insignificant changes appearing large relative to the original value. A similar pattern was seen when comparing relative consumption within the systems, with simulated consumption by groups in the southern Benguela resembling that of the 1990s far more closely than was the case in the northern Benguela. The increased transfer efficiency between producers and TL 2 in the simulation-based southern Benguela model signifies an increased dependence on phytoplankton, and hence herbivory, in this model.

Total system throughput is calculated as the sum of the flows within a system, and is positively linked to the quantity of matter passing through a system (Ulanowicz, 1986). Thus in the northern Benguela throughput was higher in the simulated model, which had the higher biomass when compared with the 1990s, and in the southern Benguela where the simulated biomass was the lower, throughput was higher in the 1990s. The higher biomass at TL 3 and

4 in the simulated model of the southern Benguela and in the 1990s model for the northern Benguela likely resulted from the discrepancies in fishing effort applied to the simulations and the actual effort in each system since exploitation began. Although the level of fishing pressure from the 1960 model was used for simulation purposes, removals from the region had increased by the 1980s, and in fact peak catches of both sardine and hake occurred in the interim (Crawford *et al.*, 1987; Rademeyer & Butterworth, 2001).

Although slightly less biomass was removed from the southern Benguela system in the 1990s than in the 1980s (Shannon *et al.*, 2003), the overall trend in removals since 1960 has been positive. The northern Benguela has experienced a different scenario. The relatively constant total catch over the 1970s and 1980s declined by almost 50% in the 1990s (Heymans *et al.*, 2004), thus fishing has diminished over time. It seems reasonable then that the southern Benguela simulation, with an applied fishing effort lower than what has occurred in reality over the past half-century, would result in a model with higher biomasses at mid-trophic levels than those observed in the 1990s (Fig. 4.3a). Conversely, where a higher than average fishing pressure experienced was applied, as in the northern Benguela, the simulated model presented lower than current biomasses at trophic levels 2, 3 and 4 (Fig. 4.3b). Although applying a varied and more accurate level of fishing to the simulations might have resulted in a more representative simulation, the aim here was not to investigate the effects of changing effort, but rather to ascertain the broader impacts of fishing on a pristine system. By comparing the simulated models to those for the 1990s in each system, it was hoped that inconsistency or similarity between the two eras would either disqualify or support fishing pressure as an agent of the changes that have occurred in the ecosystems since man's intervention, rather than that a replica system had been created. The modern situation was unlikely to have been recreated by the simulation scenario explored above, for a number of reasons. As explained above, accurate levels and variation in fishing were not applied, but rather the level at the time of the industrial model constructed as part of this dissertation were assumed. The assumption was also made that trophic controls in the pristine ecosystems were equivalent to those operating today. This was not necessarily the case, but for lack of any evidence to the contrary, groups found to exert strong controls in more recent periods were assumed to have also done so in the pristine state, and the default wasp-waist vulnerabilities described above (methods, this chapter) were adopted. Finally, any impacts caused by changes in the environment have not been taken into account. Given the altered physical conditions in the northern Benguela during the early 1990s, as a result of a Benguela Niño event (Gammelsrød *et al.*, 1998), amongst others, and previous simulation results for the southern Benguela (Shannon *et al.*, 2004c), it is unlikely that fishing pressure alone could have shaped biomass levels, and the fairly large discrepancies between the simulated model and the 1990s model do not oppose this assumption.

Although the models produced after the simulations are not structured in exactly the same way as the ecosystems are currently believed to be, they do represent a substantial shift towards that structure when compared with the 'pristine' state models. This would suggest that fishing has had a role in the reshaping of the ecosystems. On the whole, however, more similar patterns and flows were observed between the southern Benguela simulation and 1990s models than for the northern Benguela.

4.4.3. Conclusions:

The possible 'pristine' models constructed for the northern and southern Benguela differ from one another with regard to structure and functioning, but to a lesser extent than in comparisons of more recent models (Jarre-Teichmann *et al.*, 1998; Shannon & Jarre-Teichmann, 1999; Shannon, 2001). They showed that in the past, the northern Benguela may have supported far greater stocks than were found in the southern Benguela. Both the northern and southern Benguela ecosystems have experienced changes in structure and functioning over the periods examined in Chapters 2 and 3 and also over shorter timescales in the modern era, as examined elsewhere (Shannon *et al.*, 2003; Heymans *et al.*, 2004; Shannon *et al.*, 2004). That fishing is largely responsible for these changes, however, is unlikely. While trophic interactions have been investigated in this study, environmental effects have not. In the northern Benguela, the negative impact of environmental events in the 1990s has been exhibited by many species (Gammelsrød *et al.*, 1998; Roux, 1998; Crawford *et al.*, 1999. Boyer & Hampton, 2001; Cury & Shannon, 2004; Roux & Shannon, 2004) whether

4 in the simulated model of the southern Benguela and in the 1990s model for the northern Benguela likely resulted from the discrepancies in fishing effort applied to the simulations and the actual effort in each system since exploitation began. Although the level of fishing pressure from the 1960 model was used for simulation purposes, removals from the region had increased by the 1980s, and in fact peak catches of both sardine and hake occurred in the interim (Crawford *et al.*, 1987; Rademeyer & Butterworth, 2001).

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Assumptions made in the simulation scenarios, such as constant Fs and the application of modern era flow controls to the pristine system, may well have affected the outcomes described above. It is hoped though that the aim of gaining an understanding of the impacts of fishing in a broader sense on the pristine systems, rather than for specific scenarios, has nonetheless been fulfilled. However, these assumptions must be taken into account when considering the results in detail.

Understanding of the ecological processes that shape ecosystem structure and function is essential to an EAF and informed decision-making in the future with regard to fisheries policy (Cury, 2004; Cochrane *et al.*, 2004). Data on long-term trends in ecosystems are required if any attempts to rebuild ecosystems to their former states are to be incorporated into management strategies (Pitcher & Pauly, 1998; Parr *et al.*, 2003). Unfortunately these data are often unavailable, especially in systems where exploitation has been occurring for many centuries. The reconstruction of past ecosystem states (Pauly *et al.*, 1998; Heymans & Pitcher, 2002) can provide valuable insight into what may have been, based on what knowledge we do have.

There are a variety of modelling approaches available to ecologists today and any conclusions or decisions drawn from these models can only be strengthened by weighing against those obtained using alternative techniques, whilst maintaining an awareness of the limitations of each method. A mass-balanced trophic model such *Ecopath* with *Ecosim* is a very useful tool in that it provides a quantitative snap-shot view of the system as well as potential for investigating causal factors and time-dynamics using *Ecosim*. However, when examining results from models such as these it is important to keep in mind that even a best estimate is still an estimate. While additional input data would be valuable, a more realistic pursuit would be to gain a better understanding of the life-histories of the species involved. While some shadow of doubt may always be cast upon suggestions of what might have been, a clearer idea of what could not have been may be the only certainty within our grasp.

Chapter 5:

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Appendix A

Diet matrices, balanced model parameters and sensitivity analyses for the southern Benguela ecosystem models

Table A.1 contains the unbalanced diet composition used in each model for the southern Benguela, obtained from the 1978 model of the system (Shannon *et al.*, 2004b). Tables A. 2-4 contain the balanced diet compositions for the 1600, 1900 and 1960 models respectively. Tables A. 5-7 contain the balanced model parameters for the 1600, 1900 and 1960 models respectively. Tables A. 8-11 show the results from sensitivity anlysis performed on each model. Only strong effects, taken as those resulting in a ± 40% in the altered parameter, are displayed.

Table A.1: Unaltered diet composition used in southern Benguela models, balanced for the 1978 model of the southern Benguela referred to in Shannon *et al.* (2004b).

	Prey\Predator	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
1	Phytoplankton	0.4	0.5	0.333		0.05	0.32												
2	Benthic producers																		
3	Microzooplankton	0.05	0.5	0.333		0.04	0.32												
4	Mesozooplankton			0.334	0.64	0.57	0.29	0.6	0.81	0.01	0.75	0.39	0.4						
5	Macrozooplankton				0.12	0.34	0.07	0.4	0.16	0.8	0.25	0.52	0.6	0.17	0.083	0.27	0.616	0.046	0.769
6	Gelatinous zooplankton				0.04				0.03										
7	Anchovy									0.02		0.024		0.477	0.25	0.05	0.18	0.299	0.084
8	Sardine									0.01		0.01		0.03	0.15	0.001	0.01	0.001	0.005
9	Redeye									0.01		0.056		0.06	0.03	0.05	0.031	0.087	0.05
10	Other small pelagics													0.001	0.033			0.01	0.001
11	Chub mackerel													0.001	0.031			0.02	
12	Juvenile horse mackerel													0.01	0.051			0.03	
13	Adult horse mackerel													0.001				0.158	
14	Mesopelagics									0.15				0.05	0.02	0.1	0.088	0.05	0.081
15	Snoek													*				0.002	
16	Other large pelagics														0.001				
17	Cephalopods													0.01	0.141	0.05	0.052	0.03	0.01
18	Small *M. capensis*													0.02	0.01	0.022		0.095	
19	Large *M. capensis*																	0.02	
20	Small *M. paradoxus*													0.06	0.034	0.078	0.021	0.15	
21	Large *M. paradoxus*																		
22	Pelagic-feeding demersals													0.11	0.086		0.001	0.001	*
23	Benthic-feeding demersals																0.001	0.001	*
24	Pelagic-feeding chondrichthyans																		
25	Benthic-feeding chondrichthyans																		
26	Apex chondrichthyans																		
27	Seals																		
28	Cetaceans																		
29	Seabirds																		
30	Meiobenthos																		
31	Macrobenthos														0.03	0.379			
32	Detritus	0.55			0.2														
33	Import														0.05				

Table A.1 continued.

	Prey\Predator	21	22	23	24	25	26	27	28	29	30	31
1	Phytoplankton											
2	Benthic producers										0.05	0.05
3	Microzooplankton											
4	Mesozooplankton		0.01	0.01					0.03	0.009		
5	Macrozooplankton	0.21	0.648	0.05					0.04	0.1		
6	Gelatinous zooplankton											
7	Anchovy	0.002	0.002	0.005	0.02			0.25	0.3	0.4		
8	Sardine	*	*		0.01			0.03	0.07	0.05		
9	Redeye	0.028	0.11	0.025	0.049			0.003	0.03	0.02		
10	Other small pelagics	0.002			0.02			0.003	0.02	0.06		
11	Chub mackerel				0.01			0.013		0.003		
12	Juvenile horse mackerel							0.01		0.01		
13	Adult horse mackerel				0.09	0.01	0.025	0.022	0.27			
14	Mesopelagics	0.364	0.15	0.05	0.25	0.01		0.01	0.04	0.103		
15	Snoek	0.001			0.001		0.01			0.002		
16	Other large pelagics				0.01		0.005	0.001				
17	Cephalopods	0.104	0.02	0.02	0.2	0.03		0.231	0.154	0.07		
18	Small *M. capensis*		0.004	0.001				0.1	0.01	0.04		
19	Large *M. capensis*			0.002	0.04	0.01		0.022	0.01			
20	Small *M. paradoxus*	0.145	0.016	0.008				0.1	0.017	0.13		
21	Large *M. paradoxus*	0.02		0.002	0.05			0.018	0.009			
22	Pelagic-feeding demersals	0.03	0.03	0.02	0.05	0.005	0.01	0.049		0.001		
23	Benthic-feeding demersals	0.094	0.01	0.02	0.1	0.15	0.01	0.084				
24	Pelagic-feeding chondrichthyans				0.1		0.1					
25	Benthic-feeding chondrichthyans			0.005		0.06	0.77					
26	Apex chondrichthyans											
27	Seals						0.03			0.002		
28	Cetaceans						0.04					
29	Seabirds									*		
30	Meiobenthos											0.08
31	Macrobenthos			0.782		0.725		0.054				0.07
32	Detritus										0.95	0.8
33	Import											

Table A.2: Balanced diet matrix for the 1600 model of the southern Benguela.

	Prey\Predator	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
1	**Phytoplankton**	0.4	0.5	0.333		0.05	0.32												
2	**Benthic producers**																		
3	**Microzooplankton**	0.05	0.5	0.333		0.04	0.32												
4	**Mesozooplankton**			0.334	0.64	0.57	0.29	0.6	0.81	0.01	0.75	0.39	0.4						
5	**Macrozooplankton**				0.12	0.34	0.07	0.4	0.16	0.8	0.25	0.52	0.6	0.17	0.083	0.27	0.616	0.046	0.799
6	**Gelatinous zooplankton**				0.04				0.03										
7	**Anchovy**									0.02		0.024		0.477	0.25	0.05	0.18	0.299	0.084
8	**Sardine**									0.01		0.01		0.03	0.15	0.001	0.01	0.001	0.005
9	**Redeye**									0.01		0.056		0.06	0.03	0.05	0.031	0.087	0.05
10	**Other small pelagics**													0.001	0.033			0.01	0.001
11	**Chub mackerel**													0.001	0.031			0.02	
12	**Juvenile horse mackerel**													0.01	0.051			0.03	
13	**Adult horse mackerel**													0.001				0.158	
14	**Mesopelagics**									0.15				0.05	0.02	0.1	0.088	0.05	0.051
15	**Snoek**													*				0.002	
16	**Other large pelagics**														0.001				
17	**Cephalopods**													0.01	0.141	0.05	0.052	0.03	0.01
18	**Small *M. capensis***													0.02	0.01	0.022		0.095	
19	**Large *M. capensis***																	0.02	
20	**Small *M. paradoxus***													0.06	0.034	0.078	0.021	0.15	
21	**Large *M. paradoxus***																		
22	**Pelagic-feeding demersals**													0.11	0.086		0.001	0.001	*
23	**Benthic-feeding demersals**																0.001	0.001	*
24	**Pelagic-feeding chondrichthyans**																		
25	**Benthic-feeding chondrichthyans**																		
26	**Apex chondrichthyans**																		
27	**Seals**																		
28	**Cetaceans**																		
29	**Seabirds**																		
30	**Meiobenthos**																		
31	**Macrobenthos**														0.03	0.379			
32	**Detritus**	0.55			0.2														
33	**Import**														0.05				
	* indicates < 0.1% of diet																		

Table A.2 continued.

	Prey\Predator	21	22	23	24	25	26	27	28	29	30	31
1	Phytoplankton											
2	Benthic producers										0.05	0.05
3	Microzooplankton											
4	Mesozooplankton		0.01	0.01					0.01	0.009		
5	Macrozooplankton	0.21	0.648	0.05					0.013	0.1		
6	Gelatinous zooplankton											
7	Anchovy	0.002	0.002	0.005	0.02			0.25	0.412	0.4		
8	Sardine	*	*		0.01			0.03	0.084	0.05		
9	Redeye	0.028	0.11	0.025	0.049			0.003	0.01	0.02		
10	Other small pelagics	0.002			0.02			0.003	0.007	0.06		
11	Chub mackerel				0.01			0.013		0.003		
12	Juvenile horse mackerel							0.01		0.01		
13	Adult horse mackerel				0.09	0.01	0.025	0.022	0.383			
14	Mesopelagics	0.35	0.15	0.03	0.25	0.01		0.01	0.013	0.103		
15	Snoek	0.001			0.001		0.01			0.002		
16	Other large pelagics				0.01		0.005	0.001				
17	Cephalopods	0.104	0.02	0.02	0.2	0.03		0.231	0.052	0.07		
18	Small *M. capensis*		0.004	0.001				0.1	0.003	0.04		
19	Large *M. capensis*			0.002	0.045	0.01		0.022	0.003			
20	Small *M. paradoxus*	0.145	0.016	0.008				0.1	0.006	0.13		
21	Large *M. paradoxus*	0.034		0.002	0.05			0.018	0.003			
22	Pelagic-feeding demersals	0.03	0.03	0.02	0.05	0.005	0.01	0.049		0.001		
23	Benthic-feeding demersals	0.094	0.01	0.02	0.1	0.15	0.01	0.084				
24	Pelagic-feeding chondrichthyans				0.095		0.1					
25	Benthic-feeding chondrichthyans			0.005		0.06	0.77					
26	Apex chondrichthyans											
27	Seals						0.03			0.002		
28	Cetaceans						0.04					
29	Seabirds									*		
30	Meiobenthos											0.08
31	Macrobenthos			0.802		0.725		0.054				0.07
32	Detritus										0.95	0.8
33	Import											
	* indicates < 0.1% of diet											

Table A.3: Balanced diet matrix for the 1900 model of the southern Benguela.

	Prey\Predator	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
1	Phytoplankton	0.4	0.5	0.333		0.05	0.32												
2	Benthic producers																		
3	Microzooplankton	0.05	0.5	0.333		0.04	0.32												
4	Mesozooplankton			0.334	0.64	0.57	0.29	0.6	0.81	0.01	0.75	0.39	0.4						
5	Macrozooplankton				0.12	0.34	0.07	0.4	0.16	0.8	0.25	0.52	0.6	0.17	0.083	0.27	0.616	0.046	0.779
6	Gelatinous zooplankton				0.04				0.03										
7	Anchovy									0.02		0.024		0.477	0.25	0.05	0.18	0.299	0.084
8	Sardine									0.01		0.01		0.03	0.15	0.001	0.01	0.001	0.005
9	Redeye									0.01		0.056		0.06	0.03	0.05	0.031	0.087	0.05
10	Other small pelagics													0.001	0.033			0.01	0.001
11	Chub mackerel													0.001	0.031			0.02	
12	Juvenile horse mackerel													0.01	0.051			0.03	
13	Adult horse mackerel													0.001				0.158	
14	Mesopelagics									0.15				0.05	0.02	0.1	0.088	0.05	0.071
15	Snoek													*				0.002	
16	Other large pelagics														0.001				
17	Cephalopods													0.01	0.141	0.05	0.052	0.03	0.01
18	Small *M. capensis*													0.02	0.01	0.022		0.095	
19	Large *M. capensis*																	0.02	
20	Small *M. paradoxus*													0.06	0.034	0.078	0.021	0.15	
21	Large *M. paradoxus*																		
22	Pelagic-feeding demersals													0.11	0.086		0.001	0.001	*
23	Benthic-feeding demersals																0.001	0.001	*
24	Pelagic-feeding chondrichthyans																		
25	Benthic-feeding chondrichthyans																		
26	Apex chondrichthyans																		
27	Seals																		
28	Cetaceans																		
29	Seabirds																		
30	Meiobenthos																		
31	Macrobenthos														0.03	0.379			
32	Detritus	0.55			0.2														
33	Import														0.05				
	* indicates < 0.1% of diet																		

Table A.3 continued

	Prey\Predator	21	22	23	24	25	26	27	28	29	30	31
1	Phytoplankton											
2	Benthic producers										0.05	0.05
3	Microzooplankton											
4	Mesozooplankton		0.01	0.01					0.01	0.009		
5	Macrozooplankton	0.24	0.648	0.05					0.013	0.1		
6	Gelatinous zooplankton											
7	Anchovy	0.002	0.002	0.005	0.02			0.25	0.412	0.4		
8	Sardine	*	*		0.01			0.03	0.084	0.05		
9	Redeye	0.028	0.11	0.025	0.049			0.003	0.01	0.02		
10	Other small pelagics	0.002			0.02			0.003	0.007	0.06		
11	Chub mackerel				0.01			0.013		0.003		
12	Juvenile horse mackerel							0.01		0.01		
13	Adult horse mackerel				0.09	0.01	0.043	0.022	0.383			
14	Mesopelagics	0.327	0.15	0.05	0.25	0.01		0.01	0.013	0.103		
15	Snoek	0.004			0.001		0.01			0.002		
16	Other large pelagics				0.01		0.005	0.001				
17	Cephalopods	0.104	0.02	0.02	0.2	0.03		0.231	0.052	0.07		
18	Small *M. capensis*		0.004	0.001				0.1	0.003	0.04		
19	Large *M. capensis*			0.002	0.045	0.01		0.022	0.003			
20	Small *M. paradoxus*	0.145	0.016	0.008				0.1	0.006	0.132		
21	Large *M. paradoxus*	0.034		0.002	0.05			0.018	0.003			
22	Pelagic-feeding demersals	0.03	0.03	0.02	0.05	0.005	0.01	0.049		0.001		
23	Benthic-feeding demersals	0.084	0.01	0.02	0.1	0.15	0.01	0.084				
24	Pelagic-feeding chondrichthyans				0.095		0.1					
25	Benthic-feeding chondrichthyans			0.005		0.06	0.78					
26	Apex chondrichthyans											
27	Seals						*			*		
28	Cetaceans						0.041					
29	Seabirds									*		
30	Meiobenthos											0.08
31	Macrobenthos			0.782		0.725		0.054				0.07
32	Detritus										0.95	0.8
33	Import											
	* indicates < 0.1% of diet											

Table A.4: Balanced diet matrix for the 1960 southern Benguela model.

	Prey\Predator	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
1	Phytoplankton	0.4	0.5	0.333		0.05	0.32												
2	Benthic producers																		
3	Microzooplankton	0.05	0.5	0.333		0.04	0.32												
4	Mesozooplankton			0.334	0.64	0.57	0.29	0.6	0.81	0.01	0.75	0.39	0.4						
5	Macrozooplankton				0.12	0.34	0.07	0.4	0.16	0.8	0.25	0.52	0.6	0.17	0.083	0.27	0.616	0.046	0.773
6	Gelatinous zooplankton				0.04				0.03										
7	Anchovy									0.01		0.01		0.03	0.15	0.001	0.01	0.001	0.005
8	Sardine									0.02		0.024		0.477	0.25	0.05	0.18	0.28	0.08
9	Redeye									0.01		0.056		0.06	0.03	0.05	0.031	0.087	0.05
10	Other small pelagics													0.001	0.033			0.01	0.001
11	Chub mackerel													0.001	0.031			0.02	
12	Juvenile horse mackerel													0.01	0.051			0.03	
13	Adult horse mackerel													0.001				0.177	
14	Mesopelagics									0.15				0.05	0.02	0.1	0.088	0.05	0.081
15	Snoek													*				0.002	
16	Other large pelagics														0.001				
17	Cephalopods													0.01	0.141	0.05	0.052	0.03	0.01
18	Small *M. capensis*													0.02	0.01	0.022		0.095	
19	Large *M. capensis*																	0.02	
20	Small *M. paradoxus*													0.06	0.034	0.078	0.021	0.15	
21	Large *M. paradoxus*																		
22	Pelagic-feeding demersals													0.11	0.086		0.001	0.001	*
23	Benthic-feeding demersals																0.001	0.001	*
24	Pelagic-feeding chondrichthyans																		
25	Benthic-feeding chondrichthyans																		
26	Apex chondrichthyans																		
27	Seals																		
28	Cetaceans																		
29	Seabirds																		
30	Meiobenthos																		
31	Macrobenthos														0.03	0.379			
32	Detritus	0.55			0.2														
33	Import														0.05				

* indicates < 0.1% of diet

Table A 4 continued

	Prey\Predator	21	22	23	24	25	26	27	28	29	30	31
1	Phytoplankton											
2	Benthic producers										0.05	0.05
3	Microzooplankton											
4	Mesozooplankton		0.01	0.01					0.018	0.009		
5	Macrozooplankton	0.21	0.648	0.05					0.024	0.1		
6	Gelatinous zooplankton											
7	Anchovy	*	*	0.005	0.01			0.03	0.369	0.05		
8	Sardine	0.002	0.002		0.015			0.25	0.079	0.4		
9	Redeye	0.028	0.11	0.025	0.049			0.003	0.016	0.02		
10	Other small pelagics	0.002			0.02			0.003	0.012	0.06		
11	Chub mackerel				0.01			0.013		0.003		
12	Juvenile horse mackerel							0.01		0.01		
13	Adult horse mackerel				0.1	0.01	0.03	0.022	0.34			
14	Mesopelagics	0.364	0.15	0.05	0.25	0.01		0.01	0.024	0.103		
15	Snoek	0.001			0.001		0.01			0.002		
16	Other large pelagics				0.01		0.005	0.001				
17	Cephalopods	0.104	0.02	0.02	0.2	0.03		0.231	0.091	0.07		
18	Small *M. capensis*		0.004	0.001				0.1	0.006	0.04		
19	Large *M. capensis*			0.002	0.04	0.01		0.022	0.006			
20	Small *M. paradoxus*	0.145	0.016	0.008				0.1	0.01	0.13		
21	Large *M. paradoxus*	0.02		0.002	0.05			0.018	0.005			
22	Pelagic-feeding demersals	0.03	0.03	0.02	0.05	0.005	0.01	0.049		0.001		
23	Benthic-feeding demersals	0.094	0.01	0.02	0.1	0.15	0.01	0.084				
24	Pelagic-feeding chondrichthyans				0.095		0.1					
25	Benthic-feeding chondrichthyans			0.005		0.06	0.77					
26	Apex chondrichthyans											
27	Seals						0.025			0.002		
28	Cetaceans						0.04					
29	Seabirds											
30	Meiobenthos											0.08
31	Macrobenthos			0.782		0.725		0.054				0.07
32	Detritus										0.95	0.8
33	Import											

* indicates < 0.1% of diet

Table A.5 Balanced model parameters for the 1600 southern Benguela model. Inputs are marked in bold. Other parameters were estimated by the model

Group	TL	B	P/B	Q/B	EE	P/Q	Catch
Phytoplankton	1	76.938	154.4	-	0.261	-	-
Benthic producers	1	6.381	15	-	0.5	-	-
Microzooplankton	2.05	2.406	482	1928	0.95	0.25	-
Mesozooplankton	2.53	10.093	40	133.333	0.95	0.3	-
Macrozooplankton	2.86	17.763	13	31.707	0.95	0.41	-
Gelatinous zooplankton	3.29	5	0.584	1.669	0.166	0.35	-
Anchovy	3.54	9.616	1.4	14.4	0.95	0.097	-
Sardine	2.91	0.959	1.2	12.371	0.95	0.097	-
Redeye	3.66	5.349	1.3	13	0.95	0.1	-
Other small pelagics	3.6	0.508	1	10	0.95	0.1	-
Chub mackerel	4.01	0.317	0.8	8	0.95	0.1	-
Juvenile horse mackerel	3.61	0.289	1.2	12	0.95	0.1	-
Adult horse mackerel	3.79	1.731	1.5	10	0.95	0.15	-
Mesopelagics	3.73	10.877	1.2	12	0.95	0.1	-
Snoek	4.54	0.0874	0.5	5	0.95	0.1	-
Other large pelagics	4.51	0.059	0.493	4.93	0.95	0.1	-
Cephalopods	3.93	1.663	3.5	10	0.95	0.35	-
Small *M. capensis*	4.17	0.684	2.5	16.666	0.95	0.15	-
Large *M. capensis*	4.75	1.834	0.8	4.4	0.298	0.182	-
Small *M. paradoxus*	4.01	2.363	2.5	16.666	0.95	0.15	-
Large *M. paradoxus*	4.62	2.585	0.8	4.7	0.298	0.17	-
Pelagic-feeding demersals	4.17	1.92	0.7	3.5	0.95	0.2	-
Benthic-feeding demersals	3.43	4.672	0.7	3.5	0.95	0.2	-
Pelagic-feeding chondrichthyans	4.97	0.521	0.5	4.545	0.95	0.11	-
Benthic-feeding chondrichthyans	3.56	0.729	1	10	0.95	0.1	-
Apex chondrichthyans	4.8	0.045	0.5	5	0	0.1	-
Seals	4.73	0.133	0.25	19.306	0.462	0.013	-
Cetaceans	4.6	0.22	0.15	10	0.273	0.015	-
Seabirds	4.58	0.035	0.123	123	0.1	0.001	-
Meiobenthos	2	11.889	4	33	0.95	0.121	-
Macrobenthos	2.16	56.475	1.2	10	0.95	0.12	-
Detritus	1	-	-	-	0.315	-	-

Table A.6: Balanced model parameters for the 1900 southern Benguela model. Inputs are marked in bold, other parameters estimated by the model.

Group	TL	B	P/B	Q/B	EE	P/Q	Catch
Phytoplankton	1	**76.938**	**154.4**	-	0.248	-	-
Benthic producers	1	5.53	**15**	-	**0.5**	-	-
Microzooplankton	2.05	2.271	**482**	**1928**	**0.95**	0.25	-
Mesozooplankton	2.53	9.53	**40**	**133.333**	**0.95**	0.3	-
Macrozooplankton	2.86	16.755	**13**	**31.707**	**0.95**	0.41	-
Gelatinous zooplankton	3.29	**5**	**0.584**	**1.669**	0.167	0.35	-
Anchovy	3.54	8.774	**1.4**	**14.4**	**0.95**	0.097	-
Sardine	2.91	0.892	**1.2**	12.371	**0.95**	0.097	-
Redeye	3.66	4.958	**1.3**	**13**	**0.95**	0.1	-
Other small pelagics	3.6	0.511	**1**	**10**	**0.95**	0.1	-
Chub mackerel	4.01	0.283	**0.8**	**8**	**0.95**	0.1	-
Juvenile horse mackerel	3.61	0.28	**1.2**	**12**	**0.95**	0.1	-
Adult horse mackerel	3.79	1.694	**1.5**	**10**	**0.95**	0.15	-
Mesopelagics	3.73	10.812	**1.2**	**12**	**0.95**	0.1	-
Snoek	4.54	0.167	**0.5**	**5**	**0.95**	0.1	**0.001**
Other large pelagics	4.51	0.0909	**0.493**	**4.93**	**0.95**	0.1	**0.017**
Cephalopods	3.93	1.406	**3.5**	**10**	**0.95**	0.35	-
Small *M. capensis*	4.17	0.562	**2.5**	**15.666**	**0.95**	0.15	-
Large *M. capensis*	4.75	**1.834**	**0.8**	**4.4**	0.257	0.182	-
Small *M. paradoxus*	4.03	2.169	**2.5**	**15.666**	**0.95**	0.15	-
Large *M. paradoxus*	4.61	**2.585**	**0.8**	**4.7**	0.275	0.17	-
Pelagic-feeding demersals	4.17	1.726	**0.7**	**3.5**	**0.95**	0.2	-
Benthic-feeding demersals	3.46	4.048	**0.7**	**3.5**	**0.95**	0.2	-
Pelagic-feeding chondrichthyans	4.97	0.521	**0.5**	**4.545**	**0.95**	0.11	-
Benthic-feeding chondrichthyans	3.56	0.704	**1**	**10**	**0.95**	0.1	-
Apex chondrichthyans	4.77	**0.045**	**0.5**	**5**	0	0.1	-
Seals	4.74	**0.0075**	**0.25**	19.306	0.995	0.013	**0.001**
Cetaceans	4.6	**0.22**	**0.15**	**10**	0.279	0.015	-
Seabirds	4.58	**0.036**	**0.123**	**123**	0.162	0.001	-
Meiobenthos	2	10.303	**4**	**33**	**0.95**	0.121	-
Macrobenthos	2.16	48.941	**1.2**	**10**	**0.95**	0.12	-
Detritus	1	-	-	-	0.291	-	-

Table A7. Balanced model parameters for the 1960 southern Benguela model. Inputs are marked in bold, other parameters estimated by the model.

Group	TL	B	P/B	Q/B	EE	P/Q	Catch
Phytoplankton	1	**76.938**	**154.4**	-	0.176	-	-
Benthic producers	1	4.797	**15**	-	0.5	-	-
Microzooplankton	2.05	1.519	**482**	**1928**	0.95	0.25	-
Mesozooplankton	2.53	6.101	**40**	**133.333**	0.95	0.3	-
Macrozooplankton	2.86	10.693	**13**	**31.707**	0.95	0.41	-
Gelatinous zooplankton	3.29	**5**	**0.584**	**1.669**	0.146	0.35	-
Anchovy	3.54	**0.9**	1.4	**14.4**	0.96	0.097	-
Sardine	2.91	**7.34**	1.2	**12.371**	0.958	0.097	**1.45**
Redeye	3.66	3.809	**1.3**	**13**	0.95	0.1	-
Other small pelagics	3.6	0.309	**1**	**10**	0.95	0.1	-
Chub mackerel	4	0.373	**0.8**	**8**	0.95	0.1	**0.132**
Juvenile horse mackerel	3.61	0.176	**1.2**	**12**	0.95	0.1	-
Adult horse mackerel	3.78	**2.012**	**1.5**	**10**	0.614	0.15	**0.288**
Mesopelagics	3.73	7.845	**1.2**	**12**	0.95	0.1	-
Snoek	4.25	0.15	**0.5**	**5**	0.95	0.1	**0.047**
Other large pelagics	4.43	0.114	**0.493**	**4.93**	0.95	0.1	**0.026**
Cephalopods	3.89	1.062	**3.5**	**10**	0.95	0.35	-
Small *M. capensis*	4.06	0.378	**2.5**	**16.666**	0.95	0.15	-
Large *M. capensis*	4.56	**1.016**	**0.8**	**4.4**	0.606	0.182	**0.182**
Small *M. paradoxus*	3.99	1.369	**2.5**	**16.666**	0.95	0.15	**0**
Large *M. paradoxus*	4.6	**1.432**	**0.8**	**4.7**	0.745	0.17	**0.545**
Pelagic-feeding demersals	4.16	1.43	**0.7**	**3.5**	0.95	0.2	-
Benthic-feeding demersals	3.46	3.506	**0.7**	**3.5**	0.95	0.2	**0.026**
Pelagic-feeding chondrichthyans	4.94	0.558	**0.5**	**4.545**	0.95	0.11	**0.002**
Benthic-feeding chondrichthyans	3.56	0.689	**1**	**10**	0.95	0.1	**0.007**
Apex chondrichthyans	4.79	**0.045**	**0.5**	**5**	0	0.1	-
Seals	4.57	**0.046**	**0.25**	**19.306**	0.952	0.013	**0.001**
Cetaceans	4.6	**0.125**	**0.15**	**10**	0.461	0.015	-
Seabirds	4.35	**0.017**	**0.123**	**123**	0.1	0.001	-
Meiobenthos	2	8.939	**4**	**33**	0.95	0.121	-
Macrobenthos	2.16	42.459	**1.2**	**10**	0.95	0.12	-
Detritus	1	-	-	-	0.203	-	-

Table A.8: Sensitivity analysis for 1500 southern Benguela model. The group and input parameter causing sensitivity are shown in the first two columns, followed by the group and parameter affected. The percentage change in input parameter at which the estimated parameter became altered by 40% or more is noted as the percentage change in input.

Group	Input parameter	Sensitive Group	Estimated parameter	% change in input
3	P/B	1	Q/B	-40%
	Q/B	1	Q/B	-20%
	EE	1	Q/B	-40%
4	P/B	1	Q/B	-40%
	P/B	3	B	-40%
	EE	1	Q/B	-40%
	EE	3	B	-40%
5	P/B	1	Q/B	-50%
	P/B	3	B	-50%
	P/B	4	B	-50%
	EE	1	Q/B	-50%
	EE	3	B	-50%
	EE	4	B	-50%
17	P/B	30	B	-50%
	P/B	31	B	-50%
	EE	30	B	-50%
	EE	31	B	-50%
23	P/B	22	B	-50%
	P/B	25	B	-50%
	P/B	30	B	-40%
	P/B	31	B	-40%
	Q/B	30	B	50%
	Q/B	31	B	50%
	EE	22	B	-50%
	EE	25	B	-50%
	EE	30	B	-40%
	EE	31	B	-40%
24	P/B	16	B	10%
	Q/B	1	Q/B	10%
	Q/B	3	B	10%
	Q/B	4	B	10%
	Q/B	5	B	10%
	Q/B	6	EE	10%
	Q/B	7	B	10%
	Q/B	8	B	10%
	Q/B	9	B	10%
	Q/B	10	B	10%
	Q/B	11	B	10%
	Q/B	12	B	10%
	Q/B	13	B	10%
	Q/B	14	B	10%
	Q/B	15	B	10%
	Q/B	16	B	± 10%
	Q/B	17	B	10%
	Q/B	18	B	10%
	Q/B	19	EE	10%
	Q/B	20	B	10%
	Q/B	21	EE	10%
	Q/B	22	B	10%
	Q/B	23	B	10%
	Q/B	25	B	10%
	Q/B	30	B	10%
	Q/B	31	B	10%
	EE	16	B	10%
25	P/B	1	Q/B	-30%
	P/B	3	B	-30%
	P/B	4	B	-30%
	P/B	5	B	-30%
	P/B	9	B	-30%
	P/B	13	B	-30%
	P/B	14	B	-30%
	P/B	17	B	-30%
	P/B	19	EE	-30%
	P/B	20	B	-30%
	P/B	22	B	-30%
	P/B	23	B	-20%
	P/B	30	B	-20%
	P/B	31	B	-20%
	Q/B	7	B	50%
	Q/B	8	B	50%
	Q/B	9	B	40%
	Q/B	13	B	50%
	Q/B	14	B	40%
	Q/B	17	B	40%
	Q/B	18	B	50%
	Q/B	19	EE	30%
	Q/B	20	B	50%
	Q/B	22	B	40%
	Q/B	23	B	20%
	Q/B	30	B	20%
	Q/B	31	B	20%
	EE	1	Q/B	-30%
	EE	3	B	-30%
	EE	4	B	-30%
	EE	5	B	-30%
	EE	9	B	-30%
	EE	13	B	-30%
	EE	14	B	-30%
	EE	17	B	-30%
	EE	19	EE	-30%
	EE	20	B	-30%
	EE	22	B	-30%
	EE	23	B	-20%
	EE	25	B	-10%
	EE	30	B	-20%
	EE	31	B	-20%
26	B	16	B	± 50%
	B	24	B	± 40%
	B	25	B	± 50%
	B	28	EE	± 40%
	Q/B	16	B	± 50%
	Q/B	24	B	± 40%
	Q/B	25	B	± 50%
	Q/B	28	EE	± 40%
30	P/B	30	B	-10%
31	P/B	30	B	-20%
	Q/B	30	B	-30%
	EE	30	B	-20%

Table A.9: Results of sensitivity analysis showing strongly influenced groups for the 1900 southern Benguela model.

Group	Input parameter	Sensitive Group	Estimated parameter	% change in input
3	Q/B	1	Q/B	50%
	EE	1	Q/B	-40%
4	P/B	1	Q/B	-40%
	P/B	3	B	-40%
	EE	1	Q/B	-40%
	EE	3	B	-40%
5	P/B	3	B	-50%
	P/B	4	B	-50%
	EE	3	B	-50%
	EE	4	B	-50%
17	P/B	30	B	-50%
	P/B	31	B	-50%
	EE	30	B	-50%
	EE	31	B	-50%
23	P/B	22	B	-50%
	P/B	25	B	-50%
	P/B	30	B	-40%
	P/B	31	B	-40%
	Q/B	30	B	50%
	Q/B	31	B	50%
	EE	22	B	-40%
	EE	25	B	-40%
	EE	30	B	-40%
	EE	31	B	-40%
24	P/B	16	B	30%
	Q/B	1	Q/B	10%
	Q/B	3	B	10%
	Q/B	4	B	10%
	Q/B	5	B	10%
	Q/B	6	EE	10%
	Q/B	7	B	10%
	Q/B	8	B	10%
	Q/B	9	B	10%
	Q/B	10	B	10%
	Q/B	11	B	10%
	Q/B	12	B	10%
	Q/B	13	B	10%
	Q/B	14	B	10%
	Q/B	15	B	10%
	Q/B	16	B	-20%
	Q/B	17	B	10%
	Q/B	18	B	10%
	Q/B	19	EE	10%
	Q/B	20	B	10%
	Q/B	21	EE	10%
	Q/B	22	B	10%
	Q/B	23	B	10%
	Q/B	25	B	10%
	Q/B	30	B	10%
	Q/B	31	B	10%
25	P/B	1	Q/B	-30%
	P/B	3	B	-30%
25	P/B	4	B	-30%
	P/B	5	B	-30%
	P/B	9	B	-30%
	P/B	13	B	-30%
	P/B	14	B	-30%
	P/B	17	B	-30%
	P/B	18	B	-30%
	P/B	19	EE	-30%
	P/B	20	B	-30%
	P/B	22	B	-30%
	P/B	23	B	-20%
	P/B	30	B	-20%
	P/B	31	B	-20%
	Q/B	5	B	40%
	Q/B	7	B	50%
	Q/B	8	B	50%
	Q/B	9	B	40%
	Q/B	13	B	50%
	Q/B	14	B	40%
	Q/B	17	B	40%
	Q/B	18	B	50%
	Q/B	19	EE	30%
	Q/B	20	B	50%
	Q/B	22	B	30%
	Q/B	23	B	20%
	Q/B	30	B	20%
	Q/B	31	B	20%
	EE	1	Q/B	-30%
	EE	3	B	-30%
	EE	4	B	-30%
	EE	5	B	-30%
	EE	9	B	-30%
	EE	13	B	-30%
	EE	14	B	-30%
	EE	17	B	-30%
	EE	18	B	-30%
	EE	19	EE	-30%
	EE	20	B	-30%
	EE	22	B	-30%
	EE	23	B	-20%
	EE	30	B	-20%
	EE	31	B	-20%
26	B	24	B	±40%
	B	25	B	50%
	B	28	EE	±40%
	Q/B	24	B	±40%
	Q/B	25	B	-50%
	Q/B	28	EE	±40%
31	P/B	30	B	30%
	Q/B	30	B	-30%
	EE	30	B	30%

Table A.9: Results of sensitivity analysis showing strongly influenced groups for the 1900 southern Benguela model

Group	Input parameter	Sensitive Group	Estimated parameter	% change in input
3	Q/B	1	Q/B	50%
	EE	1	Q/H	-40%
4	P/H	1	Q/B	-40%
	P/B	3	B	-40%
	EE	1	Q/B	-40%
	EE	3	B	-40%
5	P/B	3	B	-50%
	P/B	4	H	-50%
	EE	3	B	-50%
	EE	4	B	-50%
17	P/B	30	B	-50%
	P/B	31	H	50%
	EE	30	B	-50%
	EE	31	B	-50%
23	P/B	22	B	-50%
	P/B	25	H	-50%
	P/B	30	B	-40%
	P/B	31	H	-40%
	Q/B	30	B	50%
	Q/B	31	B	50%
	EE	22	H	-40%
	EE	25	B	-40%
	EE	30	B	-40%
	EE	31	H	-40%
24	P/H	16	B	30%
	Q/H	1	Q/B	10%
	Q/B	3	H	10%
	Q/B	4	H	10%
	Q/B	5	B	10%
	Q/B	6	EE	10%
	Q/B	7	B	10%
	Q/B	8	B	10%
	Q/B	9	H	10%
	Q/B	10	B	10%
	Q/B	11	B	10%
	Q/B	12	B	10%
	Q/B	13	H	10%
	Q/B	14	B	10%
	Q/B	15	B	10%
	Q/B	16	H	-20%
	Q/H	17	B	10%
	Q/B	18	H	10%
	Q/B	19	EE	10%
	Q/B	20	B	10%
	Q/B	21	EE	10%
	Q/B	22	H	10%
	Q/B	23	H	10%
	Q/H	25	B	10%
	Q/B	30	B	10%
	Q/B	31	B	10%
25	P/B	1	Q/B	-30%
	P/B	3	B	-30%
25	P/B	4	B	-30%
	P/B	5	H	-30%
	P/B	9	B	-30%
	P/B	13	B	-30%
	P/B	14	H	-30%
	P/B	17	B	-30%
	P/B	18	B	-30%
	P/B	19	EE	-30%
	P/B	20	B	-30%
	P/B	22	B	-30%
	P/B	23	B	-20%
	P/B	30	H	-20%
	P/B	31	B	-20%
	Q/B	5	B	40%
	Q/B	7	H	50%
	Q/B	8	H	50%
	Q/B	9	B	40%
	Q/B	13	H	50%
	Q/B	14	B	40%
	Q/B	17	B	40%
	Q/B	18	B	50%
	Q/B	19	EE	30%
	Q/B	20	B	50%
	Q/B	22	H	30%
	Q/B	23	B	20%
	Q/B	30	B	20%
	Q/B	31	H	20%
	EE	1	Q/B	-30%
	EE	3	B	-30%
	EE	4	B	-30%
	EE	5	B	-30%
	EE	9	H	-30%
	EE	13	B	-30%
	EE	14	B	-30%
	EE	17	H	-30%
	EE	18	B	30%
	EE	19	EE	-30%
	EE	20	B	-30%
	EE	22	B	-30%
	EE	23	B	-20%
	EE	30	H	-20%
	EE	31	B	-20%
26	H	24	B	±40%
	B	25	B	50%
	B	28	EE	±40%
	Q/B	24	B	±40%
	Q/B	25	H	-50%
	Q/B	28	EE	±40%
31	P/B	30	B	30%
	Q/B	30	H	-30%
	EE	30	B	30%

Table A.10: Results of sensitivity analysis showing strongly influenced groups for the 1960 southern Benguela model.

Group	Input parameter	Sensitive Group	Estimated parameter	% change in input
3	P/B	1	Q/B	-50%
	Q/B	1	Q/B	50%
	EE	1	Q/B	-50%
4	P/B	1	Q/B	-50%
	P/B	3	B	-50%
	EE	1	Q/B	-50%
	EE	3	B	-50%
5	P/B	1	Q/B	-50%
	P/B	3	B	-50%
	P/B	4	B	-50%
	EE	1	Q/B	-50%
	EE	3	B	-50%
	EE	4	B	-50%
	EE	5	B	-30%
17	P/B	18	B	-50%
	P/B	20	B	-50%
	EE	18	B	-50%
	EE	20	B	-50%
23	P/B	22	B	-50%
	P/B	25	B	-50%
	P/B	30	B	-50%
	P/B	31	B	-40%
	Q/B	30	B	40%
	Q/B	31	B	40%
	EE	22	B	-50%
	EE	25	B	-50%
	EE	30	B	-50%
	EE	31	B	-60%
24	P/B	16	B	40%
	Q/B	1	Q/B	10%
	Q/B	3	B	10%
	Q/B	4	B	10%
	Q/B	5	B	10%
	Q/B	6	EE	10%
	Q/B	7	EE	10%
	Q/B	8	EE	10%
	Q/B	9	B	10%
	Q/B	10	B	10%
	Q/B	11	B	10%
	Q/B	12	B	10%
	Q/B	13	EE	10%
	Q/B	14	B	10%
	Q/B	15	B	10%
	Q/B	16	B	10%
	Q/B	17	B	10%
	Q/B	18	B	10%
	Q/B	19	EE	10%
	Q/B	20	B	10%
	Q/B	21	EE	10%
	Q/B	22	B	10%
	Q/B	23	B	10%
	Q/B	25	B	10%
	Q/B	30	B	10%
	Q/B	31	B	10%
25	P/B	1	Q/B	-30%
	P/B	3	B	-30%
	P/B	4	B	-30%
	P/B	5	B	-30%
	P/B	7	EE	-30%
	P/B	9	B	-30%
	P/B	13	EE	-30%
	P/B	14	B	-30%
	P/B	17	B	-30%
	P/B	18	B	-30%
	P/B	19	EE	-30%
	P/B	20	B	-30%
	P/B	22	B	-30%
	P/B	23	B	-20%
	P/B	30	B	-20%
	P/B	31	B	-20%
	Q/B	3	B	40%
	Q/B	4	B	40%
	Q/B	5	B	40%
	Q/B	9	B	40%
	Q/B	14	B	40%
	Q/B	17	B	40%
	Q/B	19	EE	30%
	Q/B	20	B	40%
	Q/B	22	B	30%
	Q/B	23	B	20%
	Q/B	30	B	20%
	Q/B	31	B	20%
	EE	1	Q/B	-30%
	EE	3	B	-30%
	EE	4	B	-30%
	EE	6	B	-30%
	EE	7	EE	-30%
	EE	9	B	-30%
	EE	13	EE	-30%
	EE	14	B	-30%
	EE	17	B	-30%
	EE	18	B	-30%
	EE	19	EE	-30%
	EE	20	B	-30%
	EE	22	B	-30%
	EE	23	B	-20%
	EE	30	B	-20%
	EE	31	B	-20%
26	B	24	B	±60%
	B	25	B	±50%
	B	28	EE	40%
	Q/B	24	B	±50%
	Q/B	25	B	±60%
	Q/B	28	EE	40%
31	P/B	30	B	-20%
	Q/B	23	B	10%
	Q/B	30	B	10%
	EE	30	B	-20%

Table A.11: Results of sensitivity analysis showing strongly influenced groups for the 2000s southern Benguela model.

Group	Input parameter	Sensitive Group	Estimated parameter	% change in input
3	P/B	1	Q/B	-40%
	EE	1	Q/B	-40%
4	P/B	1	Q/B	-40%
	P/B	3	B	-40%
	EE	1	Q/B	-40%
	EE	3	B	-40%
5	P/B	1	Q/B	-50%
	P/B	3	B	-50%
	EE	1	Q/B	-50%
	EE	3	B	-50%
23	P/B	2	Q/B	-50%
	P/B	30	B	-50%
	P/B	31	B	-50%
	EE	2	Q/B	-50%
	EE	30	B	-50%
	EE	31	B	-50%
26	B	28	EE	±40%
	Q/B	28	EE	±40%
30	P/B	2	Q/B	-50%
	EE	2	Q/B	-50%
31	Q/B	2	Q/B	20%
	Q/B	31	B	-50%

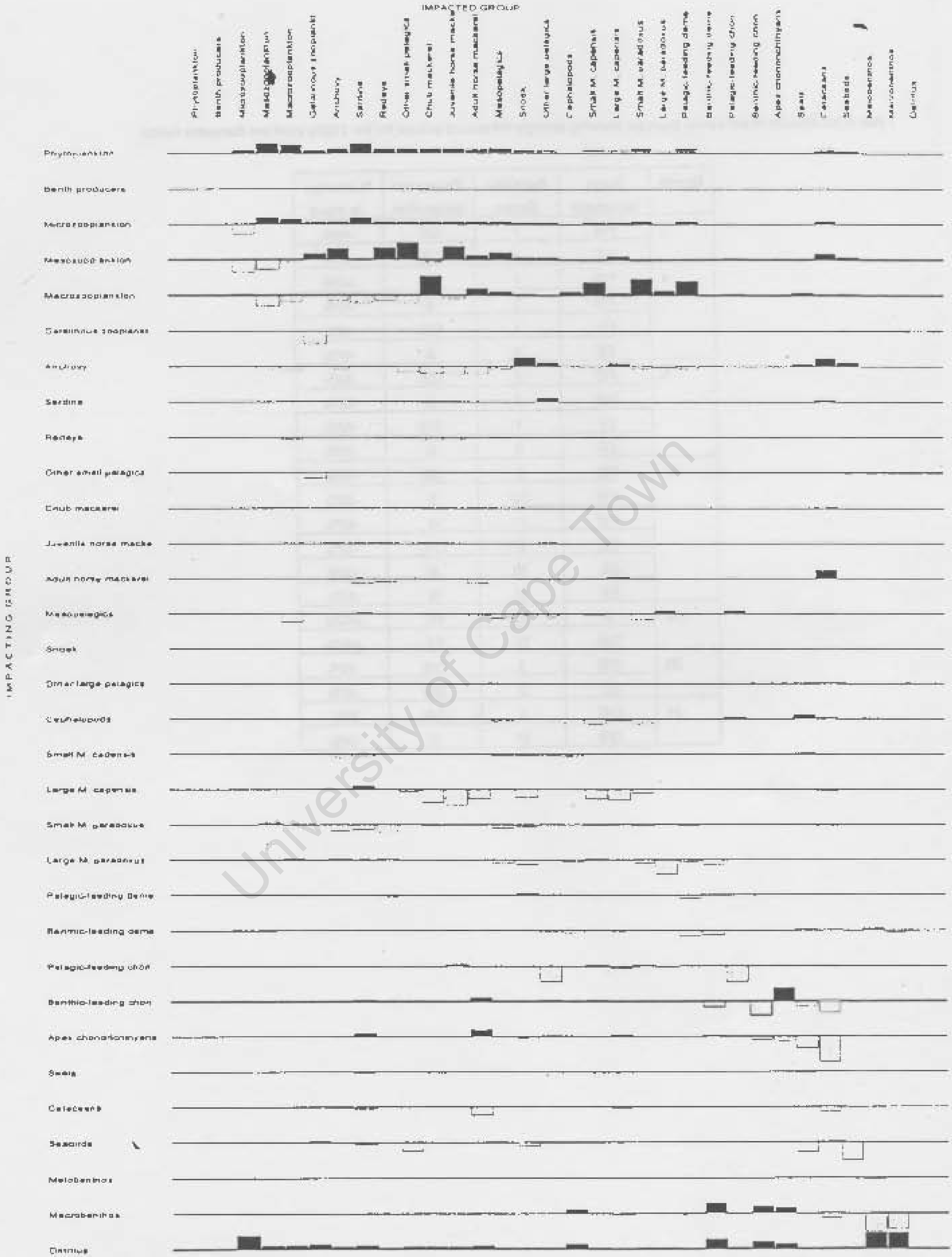

Figure A.7: Mixed trophic impacts in the 1600 southern Benguela model.

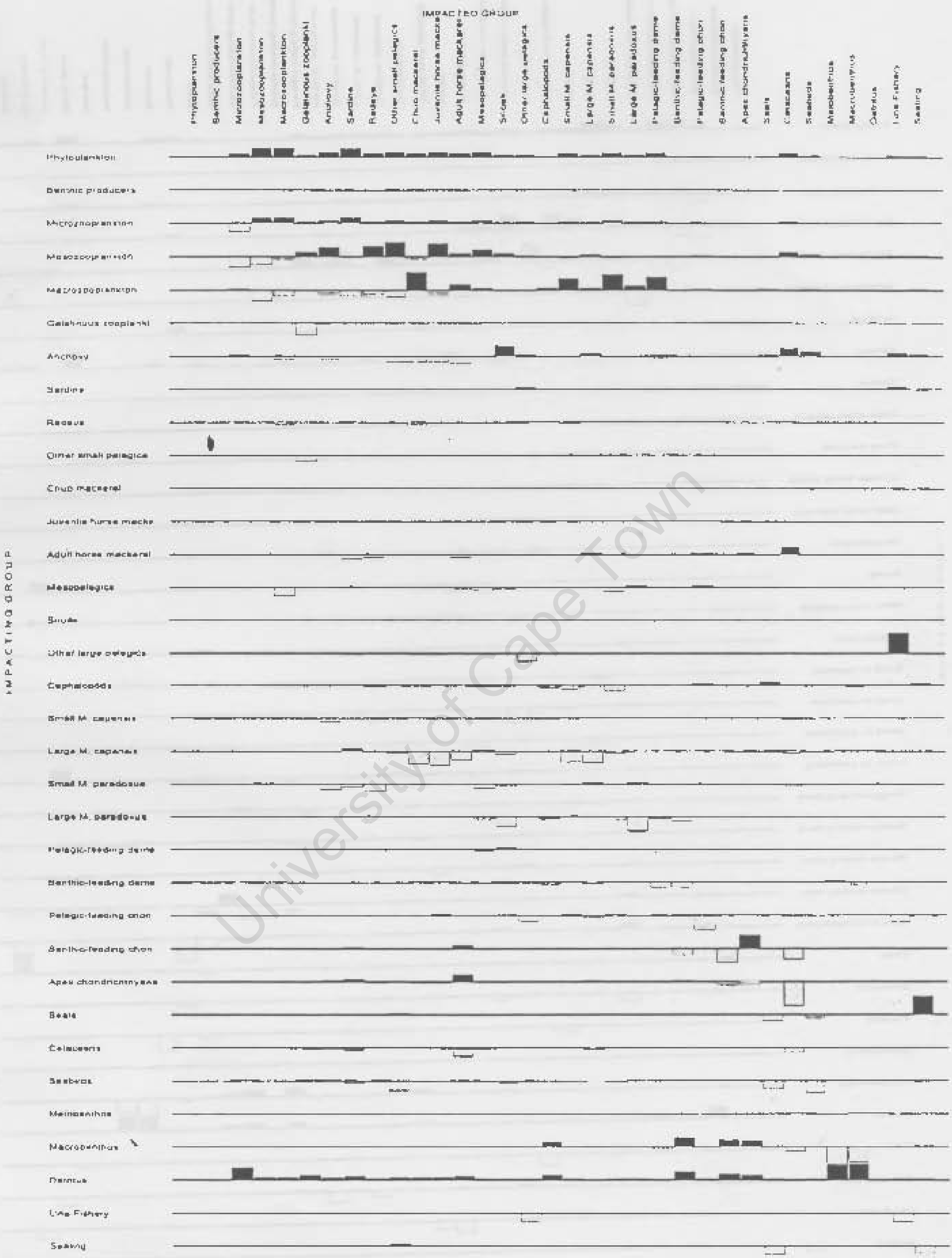

Figure A.2: Mixed trophic impacts in the 1900 southern Benguela model.

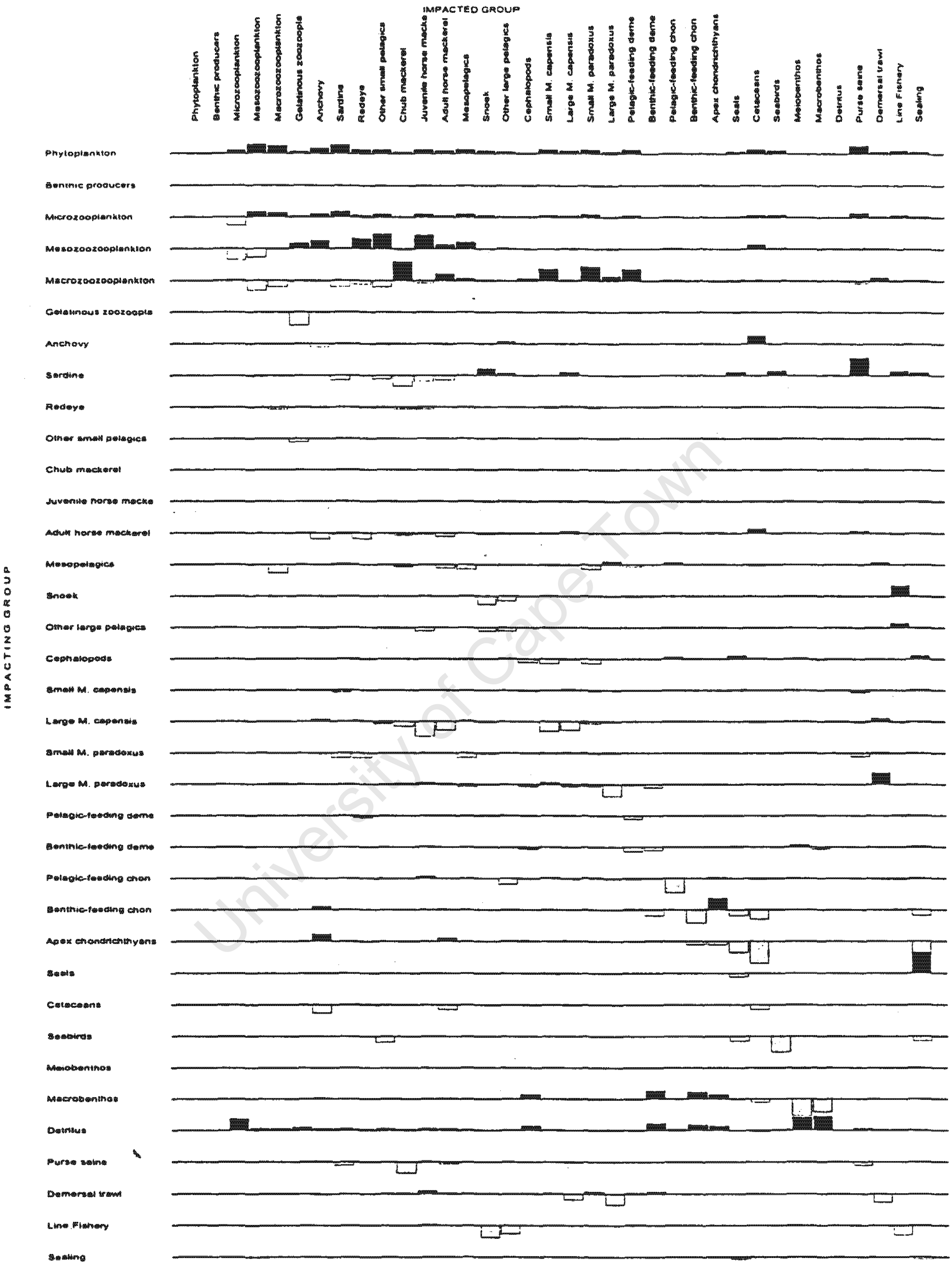

Figure A.3: Mixed trophic impacts in the 1960 southern Benguela model.

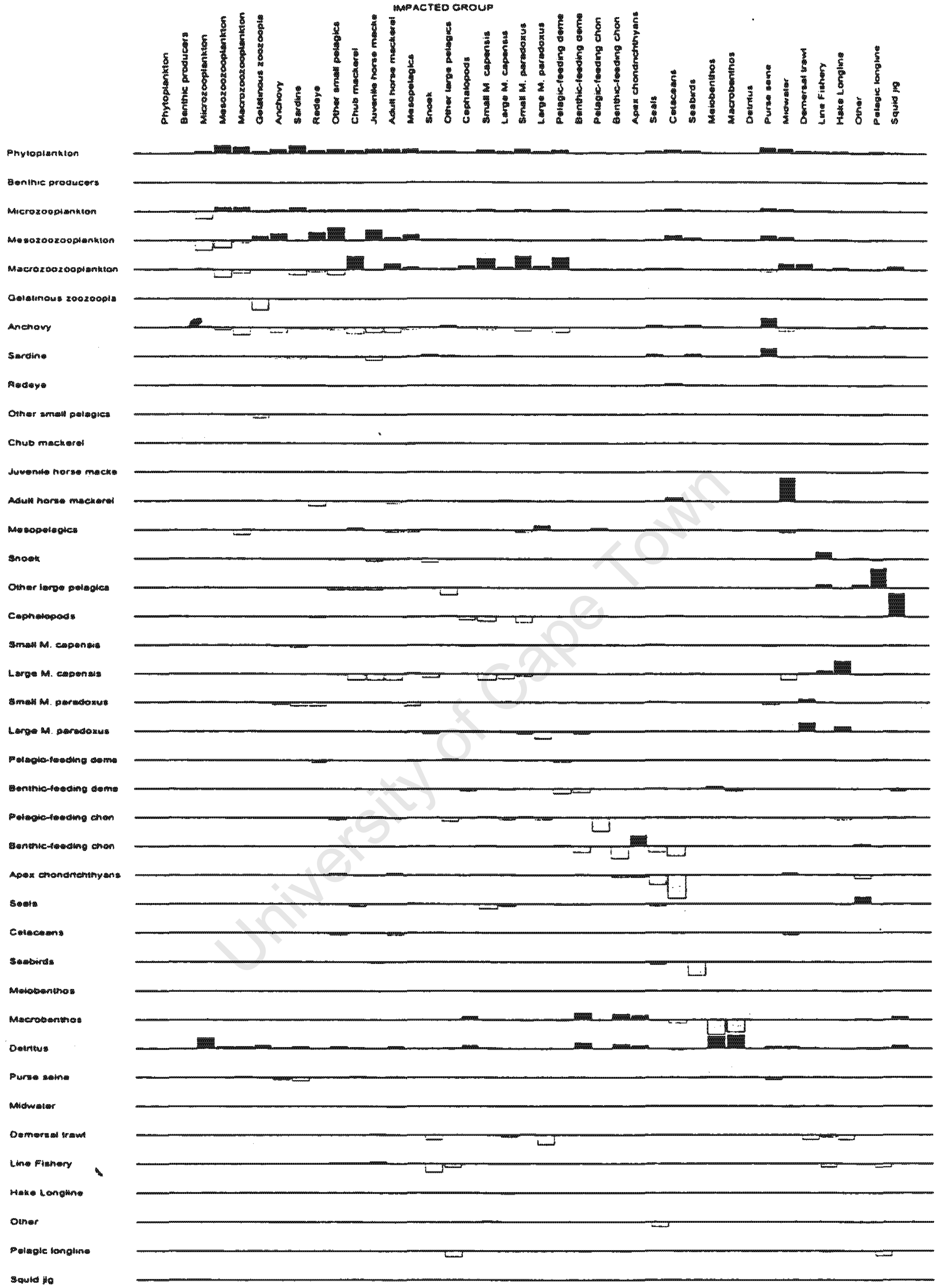

Figure A.4: Mixed trophic impacts in the 2000s southern Benguela model.

Appendix B

Diet matrices, balanced model parameters, sensitivity analyses and mixed trophic impact assessments for the northern Benguela ecosystem models

Table B.1 contains the unbalanced diet composition used in each model for the northern Benguela, obtained from the 1990s model of the system (Roux & Shannon, 2004). Tables B. 2-4 contain the balanced diet compositions for the 1600, 1900 and 1970 models respectively. Tables B. 5-7 contain the balanced model parameters for the 1600, 1900 and 1970 models respectively. Tables B. 8-11 show the results from sensitivity analysis performed on each model. Only strong effects, taken as those resulting in a ± 40% in the altered parameter, are displayed. Results from the mixed trophic impact assessments on the northern Benguela models are shown in Figs B.1-4.

Table B.1: Unaltered diet composition used for each of the northern Benguela models, based on the system in the 1990s (Roux & Shannon, 2004).

	Prey \ Predator	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
1	Phytoplankton	0.47	0.5	0.6	0.02			0.56	0.33				0.007							
2	Microzooplankton	0.06	0.5					0.08	0.04				0.006							
3	Mesozooplankton			0.4	0.62			0.18	0.31	0.06	0.4	0.02	0.774	0.5	0.15		0.06			
4	Macrozooplankton				0.12			0.18	0.32	0.14	0.6	0.54	0.17	0.2	0.65	0.2	0.36	0.095	0.2	0.08
5	Gelatinous zooplankton				0.04								0.026							
6	Meiobenthos						0.86			0.65				0.3	0.1				0.18	0.27
7	Macrobenthos						0.08			0.025									0.05	0.16
8	Sardine											0.005				0.017		0.004		
9	Anchovy											0.001				0.003		0.002		
10	Pelagic Goby									0.02		0.123			0.08	0.05	0.462	0.36	0.07	
11	Mesopelagics									0.005		0.123			0.02	0.133	0.033	0.076	0.26	0.03
12	Cephalopods											0.01				0.295	0.07	0.049	0.065	0.26
13	Other small pelagics									0.01		0.068				0.08	0.015	0.055	0.01	0.025
14	Juvenile horse mackerel											0.1				0.028		0.072		
15	Adult horse mackerel																	0.033		0.015
16	Large pelagics																			
17	Small *M. capensis*															0.023		0.123	0.013	
18	Large *M. capensis*											0.01				0.025		0.068	0.027	0.025
19	Large *M. paradoxus*															0.046		0.017		0.025
20	Benthic-feeding demersals																	0.033	0.075	0.04
21	Pelagic-feeding demersals															0.1		0.013	0.04	0.01
22	Chondrichthyans																			
23	Seabirds																			
24	Seals																			
25	Cetaceans																			
26	Detritus	0.47			0.2	1	0.06			0.09			0.017						0.01	0.06
27	Import																			

Table B.2: Balanced diet matrix for the 1600 model of the northern Benguela.

	Prey \ Predator	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
1	Phytoplankton	0.55	0.64	0.02			0.56	0.33				0.007							
2	Microzooplankton	0.45					0.08	0.04				0.006							
3	Mesozooplankton		0.36	0.62			0.18	0.31	0.06	0.4	0.02	0.774	0.5	0.15		0.112			
4	Macrozooplankton			0.12			0.18	0.32	0.15	0.6	0.54	0.17	0.2	0.67	0.2	0.49	0.095	0.27	0.11
5	Gelatinous zooplankton			0.04								0.026							
6	Meiobenthos					0.86			0.65				0.3	0.1				0.18	0.27
7	Macrobenthos					0.07			0.025									0.05	0.16
8	Sardine										0.143				0.017		0.304		
9	Anchovy										0.011				0.003		0.022		
10	Pelagic Goby								0.005		0.005			0.06	0.05	0.28	0.05	0.04	
11	Mesopelagics								0.005		0.093			0.02	0.133	0.023	0.076	0.085	0.03
12	Cephalopods										0.01				0.295	0.07	0.029	0.035	0.2
13	Other small pelagics								0.01		0.068				0.08	0.025	0.055	0.01	0.025
14	Juvenile horse mackerel										0.1				0.028		0.072		
15	Adult horse mackerel																0.023		0.015
16	Large pelagics																		
17	Small *M. capensis*														0.023		0.113	0.013	
18	Large *M. capensis*										0.01				0.025		0.068	0.112	0.035
19	Large *M. paradoxus*														0.046		0.06		0.045
20	Benthic-feeding demersals																0.02	0.075	0.01
21	Pelagic-feeding demersals														0.1		0.013	0.04	0.01
22	Chondrichthyans																		
23	Seabirds																		
24	Seals																		
25	Cetaceans																		
26	Detritus			0.2	1	0.07			0.095			0.017						0.09	0.09
27	Import																		

Table B.2 continued.

	Prey \ Predator	21	22	23	24	25
1	Phytoplankton					
2	Microzooplankton					
3	Mesozooplankton	0.18		0.003		0.05
4	Macrozooplankton	0.5		0.043		0.416
5	Gelatinous zooplankton					
6	Meiobenthos		0.215			
7	Macrobenthos		0.17			
8	Sardine	0.076	0.012	0.038	0.315	0.009
9	Anchovy	0.001	0.01	0.149	0.016	0.005
10	Pelagic Goby	0.019	0.025	0.465	0.077	0.066
11	Mesopelagics	0.036	0.025	0.05	0.104	
12	Cephalopods	0.104	0.1	0.045	0.035	0.254
13	Other small pelagics	0.034	0.07	0.083	0.023	0.004
14	Juvenile horse mackerel		0.003	0.005	0.05	0.05
15	Adult horse mackerel	0.02	0.02		0.053	0.043
16	Large pelagics		0.004	0.003		0.019
17	Small *M. capensis*			0.002	0.158	
18	Large *M. capensis*		0.002	0.052	0.158	0.024
19	Large *M. paradoxus*	0.02	0.002	0.046		0.024
20	Benthic-feeding demersals		0.05			
21	Pelagic-feeding demersals	0.01	0.02	0.015	0.011	
22	Chondrichthyans		0.1			
23	Seabirds					0.003
24	Seals		0.002	0.001		0.033
25	Cetaceans					
26	Detritus		0.17			
27	Import					

Table B.3: Balanced diet matrix for the 1900 northern Benguela model.

	Prey \ Predator	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	
1	Phytoplankton	0.5	0.6	0.04			0.56	0.33				0.007								
2	Microzooplankton	0.5					0.08	0.04				0.006								
3	Mesozooplankton		0.4	0.62			0.18	0.31	0.08	0.4	0.02	0.774	0.5	0.15		0.08				
4	Macrozooplankton			0.12			0.18	0.32	0.14	0.6	0.54	0.17	0.2	0.65	0.2	0.5	0.095	0.23	0.09	
5	Gelatinous zooplankton			0.02								0.026								
6	Meiobenthos					0.86			0.65				0.3	0.1				0.18	0.28	
7	Macrobenthos					0.05			0.015									0.05	0.13	
8	Sardine										0.141				0.017		0.348			
9	Anchovy										0.011				0.003		0.017			
10	Pelagic Goby								0.005		0.01			0.08	0.05	0.302	0.07	0.07		
11	Mesopelagics								0.005		0.09			0.02	0.133	0.033	0.03	0.15	0.005	
12	Cephalopods										0.01				0.295	0.07	0.034	0.065	0.2	
13	Other small pelagics								0.01		0.068				0.08	0.015	0.055	0.01	0.025	
14	Juvenile horse mackerel										0.1				0.028		0.072			
15	Adult horse mackerel																0.033		0.015	
16	Large pelagics																			
17	Small *M. capensis*														0.023		0.08	0.013		
18	Large *M. capensis*										0.01				0.025		0.068	0.102	0.085	
19	Large *M. paradoxus*														0.046		0.058		0.055	
20	Benthic-feeding demersals																0.027	0.06	0.005	
21	Pelagic-feeding demersals														0.1		0.013	0.03	0.01	
22	Chondrichthyans																			
23	Seabirds																			
24	Seals																			
25	Cetaceans																			
26	Detritus			0.2	1	0.09			0.095			0.017						0.04	0.1	
27	Import																			

Table B.3. continued.

	Prey \ Predator	21	22	23	24	25
1	Phytoplankton					
2	Microzooplankton					
3	Mesozooplankton	0.18		0.003		0.05
4	Macrozooplankton	0.5		0.043		0.446
5	Gelatinous zooplankton					
6	Meiobenthos		0.215			
7	Macrobenthos		0.17			
8	Sardine	0.091	0.013	0.039	0.015	0.012
9	Anchovy	0.001	0.01	0.149	0.016	0.005
10	Pelagic Goby	0.004	0.025	0.465	0.377	0.066
11	Mesopelagics	0.036	0.025	0.05	0.104	
12	Cephalopods	0.104	0.1	0.045	0.035	0.254
13	Other small pelagics	0.034	0.07	0.083	0.023	0.004
14	Juvenile horse mackerel		0.003	0.005	0.05	0.05
15	Adult horse mackerel	0.02	0.02		0.053	0.043
16	Large pelagics		0.004	0.003		0.019
17	Small *M. capensis*			0.002	0.158	
18	Large *M. capensis*		0.002	0.052	0.158	0.024
19	Large *M. paradoxus*	0.02	0.002	0.046		0.024
20	Benthic-feeding demersals		0.05			
21	Pelagic-feeding demersals	0.01	0.02	0.015	0.011	
22	Chondrichthyans		0.1			
23	Seabirds					0.003
24	Seals		*	*		*
25	Cetaceans					
26	Detritus		0.17			
27	Import					

* signifies a contribution of < 0.01%.

Table B.4: Balanced diet matrix for the 1970 model of the northern Benguela.

	Prey \ Predator	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
1	**Phytoplankton**	0.5	0.6	0.02			0.56	0.33				0.007							
2	**Microzooplankton**	0.5					0.08	0.04				0.006							
3	**Mesozooplankton**		0.4	0.62			0.18	0.31	0.068	0.4	0.02	0.774	0.5	0.15		0.15			
4	**Macrozooplankton**			0.12			0.18	0.32	0.143	0.6	0.56	0.17	0.2	0.65	0.2	0.432	0.142	0.27	0.095
5	**Gelatinous zooplankton**			0.04								0.026							
6	**Meiobenthos**					0.86			0.65				0.3	0.1				0.182	0.27
7	**Macrobenthos**					0.05			0.025									0.05	0.07
8	**Sardine**										0.005				0.017		0.088		
9	**Anchovy**										0.001				0.003		0.026		
10	**Pelagic Goby**								0.009		0.103			0.08	0.05	0.25	0.218	0.07	
11	**Mesopelagics**								0.005		0.103			0.02	0.133	0.033	0.056	0.1	0.03
12	**Cephalopods**										0.01				0.295	0.07	0.049	0.075	0.27
13	**Other small pelagics**								0.01		0.068				0.08	0.065	0.106	0.01	0.025
14	**Juvenile horse mackerel**										0.1				0.028		0.054		
15	**Adult horse mackerel**																0.033		0.015
16	**Large pelagics**																		
17	**Small *M. capensis***														0.023		0.083	0.023	
18	**Large *M. capensis***										0.03				0.025		0.08	0.025	0.025
19	**Large *M. paradoxus***														0.046		0.019		0.065
20	**Benthic-feeding demersals**																0.033	0.055	0.025
21	**Pelagic-feeding demersals**														0.1		0.013	0.05	0.01
22	**Chondrichthyans**																		
23	**Seabirds**																		
24	**Seals**																		
25	**Cetaceans**																		
26	**Detritus**			0.2	1	0.09			0.09			0.017						0.09	0.1
27	**Import**																		

Table B.4. continued.

	Prey \ Predator	21	22	23	24	25
1	**Phytoplankton**					
2	**Microzooplankton**					
3	**Mesozooplankton**	0.18		0.003		0.05
4	**Macrozooplankton**	0.5		0.043		0.416
5	**Gelatinous zooplankton**					
6	**Meiobenthos**		0.215			
7	**Macrobenthos**		0.17			
8	**Sardine**	0.006	0.012	0.038	0.015	0.009
9	**Anchovy**	0.001	0.01	0.149	0.016	0.005
10	**Pelagic Goby**	0.039	0.025	0.465	0.377	0.066
11	**Mesopelagics**	0.036	0.025	0.05	0.104	
12	**Cephalopods**	0.154	0.1	0.045	0.035	0.254
13	**Other small pelagics**	0.034	0.07	0.083	0.023	0.004
14	**Juvenile horse mackerel**		0.003	0.005	0.05	0.05
15	**Adult horse mackerel**	0.02	0.02		0.053	0.043
16	**Large pelagics**		0.004	0.003		0.019
17	**Small *M. capensis***			0.002	0.158	
18	**Large *M. capensis***		0.002	0.052	0.158	0.024
19	**Large *M. paradoxus***	0.02	0.002	0.046		0.024
20	**Benthic-feeding demersals**		0.05			
21	**Pelagic-feeding demersals**	0.01	0.02	0.015	0.011	
22	**Chondrichthyans**		0.1			
23	**Seabirds**					0.003
24	**Seals**		0.002	0.001		0.033
25	**Cetaceans**					
26	**Detritus**		0.17			
27	**Import**					

Table B.5: Balanced model parameters for the 1600 northern Benguela model. Inputs are marked in bold, other parameters were estimated by the model.

Group	TL	B	P/B	Q/B	EE	P/Q	Catch
Phytoplankton	1	**207.2**	**35.7**	-	0.786	-	-
Microzooplankton	2.04	3.254	**482**	**1928**	**0.999**	0.25	-
Mesozooplankton	2.47	21.235	**40**	**133.333**	**0.999**	0.3	-
Macrozooplankton	2.53	35.964	**13**	**31.707**	**0.999**	0.41	-
Gelatinous zooplankton	3.18	26.073	**0.44**	**1.467**	**0.5**	0.3	-
Meiobenthos	2	57.138	**8**	**33**	**0.999**	0.242	-
Macrobenthos	3	28.308	**1.2**	**10**	**0.999**	0.12	-
Sardine	2.62	**35.369**	**1.35**	**14**	0.904	0.096	-
Anchovy	2.99	1.87	**1.8**	**18**	**0.999**	0.1	-
Pelagic Goby	3.06	20.203	**1.8**	**12**	**0.999**	0.15	-
Mesopelagics	3.5	19.651	**1.23**	**12.3**	**0.999**	0.1	-
cephalopods	3.81	4.129	**5**	**15**	**0.999**	0.333	-
Other small pelagics	3.46	17.629	**0.958**	**9.349**	**0.999**	0.102	-
Juvenile horse mackerel	3.34	11.54	**1.2**	**10**	**0.999**	0.12	-
Adult horse mackerel	3.52	4.419	**0.8**	**5.333**	**0.999**	0.15	-
Large pelagics	4.42	0.0277	**0.5**	**5**	**0.999**	0.1	-
Small *M. capensis*	3.81	6.518	**2**	**13.333**	**0.999**	0.15	-
Large *M. capensis*	4.22	**13.107**	**1.228**	**7.824**	0.968	0.157	-
Large *M. paradoxus*	3.83	**7.373**	**1.14**	**7.278**	0.967	0.157	-
Benthic-feeding demersals	3.79	6.465	**1**	**5**	**0.999**	0.2	-
Pelagic-feeding demersals	3.79	4.134	**1**	**5**	**0.999**	0.2	-
Chondrichtians	3.72	**0.36**	**0.5**	**3.333**	0.667	0.15	-
Seabirds	4.21	**0.0177**	**0.156**	**120.3**	0.137	0.001	-
Seals	4.35	**0.253**	**0.29**	**18.25**	0.125	0.016	-
Cetaceans	4.15	**0.019**	**0.15**	**7.418**	0	0.02	-
Detritus	1	-	-	-	0.981	-	-

Table B.6: Balanced model parameters for the 1900 northern Benguela model. Inputs are marked in bold, other parameters were estimated by the model.

Group	TL	B	P/B	Q/B	EE	P/Q	Catch
Phytoplankton	1	**207.2**	**35.7**	-	0.807	-	-
Microzooplankton	2.06	3.832	**482**	**1928**	**0.999**	0.25	-
Mesozooplankton	2.53	20.406	**40**	**133.333**	**0.999**	0.3	-
Macrozooplankton	2.61	32.548	**13**	**31.707**	**0.999**	0.41	-
Gelatinous zooplankton	3.19	20.108	**0.44**	**1.467**	0.5	0.3	-
Meiobenthos	2	41.332	**8**	**33**	**0.999**	0.242	-
Macrobenthos	2.96	14.795	**1.2**	**10**	**0.999**	0.12	-
Sardine	2.65	**35.369**	**1.35**	**14**	0.961	0.096	-
Anchovy	3.03	1.533	**1.8**	**18**	**0.999**	0.1	-
Pelagic Goby	3.08	18.974	**1.8**	**12**	**0.999**	0.15	-
Mesopelagics	3.58	17.239	**1.23**	**12.3**	**0.999**	0.1	-
cephalopods	3.88	4.02	**5**	**15**	**0.999**	0.333	-
Other small pelagics	3.52	15.771	**0.958**	**9.349**	**0.999**	0.102	-
Juvenile horse mackerel	3.39	11.218	**1.2**	**10**	**0.999**	0.12	-
Adult horse mackerel	3.6	5.305	**0.8**	**5.333**	**0.999**	0.15	-
Large pelagics	4.49	0.0277	**0.5**	**5**	**0.999**	0.1	-
Small *M. capensis*	3.88	4.473	**2**	**13.333**	**0.999**	0.15	-
Large *M. capensis*	4.22	**13.107**	**1.228**	**7.824**	0.984	0.157	-
Large *M. paradoxus*	4.02	**7.373**	**1.14**	**7.278**	0.966	0.157	-
Benthic-feeding demersals	3.85	6.21	**1**	**5**	**0.999**	0.2	-
Pelagic-feeding demersals	3.86	3.504	**1**	**5**	**0.999**	0.2	-
Chondrichtians	3.73	**0.36**	**0.5**	**3.333**	0.667	0.15	-
Seabirds	4.25	**0.0177**	**0.156**	**120.3**	0.375	0.001	**0.001**
Seals	4.52	**0.00922**	**0.29**	**18.25**	0.796	0.016	**0.001**
Cetaceans	4.16	**0.019**	**0.15**	**7.418**	0	0.02	-
Detritus	1	-	-	-	0.998	-	-

Table B.7: Balanced model parameters for the 1970 northern Benguela model. Inputs are marked in bold, other parameters were estimated by the model.

Group	TL	B	P/B	Q/B	EE	P/Q	Catch
Phytoplankton	1	**214.286**	**35.7**	-	0.692	-	-
Microzooplankton	2.06	3.497	**482**	**1928**	**0.999**	0.25	-
Mesozooplankton	2.53	19.012	**40**	**133.333**	**0.999**	0.3	-
Macrozooplankton	2.61	28.869	**13**	**31.707**	**0.999**	0.41	-
Gelatinous zooplankton	3.23	33.928	**0.44**	**1.467**	**0.5**	0.3	-
Meiobenthos	2	50.101	**8**	**33**	**0.999**	0.242	-
Macrobenthos	2.96	17.404	**1.2**	**10**	**0.999**	0.12	-
Sardine	2.65	**8.184**	**1.35**	**14**	0.999	0.096	**3.495**
Anchovy	3.03	1.887	**1.8**	**18**	**0.999**	0.1	**0.95**
Pelagic Goby	3.09	26.274	**1.8**	**12**	**0.999**	0.15	-
Mesopelagics	3.58	17.202	**1.23**	**12.3**	**0.999**	0.1	-
cephalopods	3.97	4.45	**5**	**15**	**0.999**	0.333	-
Other small pelagics	3.52	22.516	**0.958**	**9.349**	**0.999**	0.102	-
Juvenile horse mackerel	3.39	9.242	**1.2**	**10**	**0.999**	0.12	-
Adult horse mackerel	3.6	4.786	**0.8**	**5.333**	**0.999**	0.15	**0.287**
Large pelagics	4.52	0.047	**0.5**	**5**	**0.999**	0.1	**0.011**
Small *M. capensis*	3.91	3.919	**2**	**13.333**	**0.999**	0.15	-
Large *M. capensis*	4.35	**10.165**	**1.228**	**7.824**	0.94	0.157	**1.261**
Large *M. paradoxus*	3.83	**5.718**	**1.14**	**7.278**	0.931	0.157	**2.243**
Benthic-feeding demersals	3.91	5.7	**1**	**5**	**0.999**	0.2	**0.009**
Pelagic-feeding demersals	3.95	3.678	**1**	**5**	**0.999**	0.2	-
Chondrichtians	3.75	**0.36**	**0.5**	**3.333**	0.667	0.15	-
Seabirds	4.26	**0.014**	**0.156**	**120.3**	0.194	0.001	-
Seals	4.55	**0.0908**	**0.29**	**18.25**	0.678	0.016	**0.009**
Cetaceans	4.25	**0.019**	**0.15**	**7.418**	0	0.02	-
Detritus	1	-	-	-	0.875	-	-

Table B.8: Results of sensitivity analysis of the 1600 northern Benguela model, showing inputs that had a strong influence and the parameters affected.

Group	Input parameter	Sensitive Group	Estimated parameter	% change in input
1	Biom	1	Cons/biom	-30%
2	EE	1	Cons/biom	-40%
3	Prod/biom	1	Cons/biom	-40%
	Prod/biom	2	Biom	-30%
	Cons/biom	2	Biom	-50%
	EE	1	Cons/biom	-40%
	EE	2	Biom	-30%
4	Prod/biom	1	Cons/biom	-50%
	Prod/biom	2	Biom	-50%
	Prod/biom	3	Biom	-50%
	EE	1	Cons/biom	-50%
	EE	2	Biom	-50%
	EE	3	Biom	-50%
7	Prod/biom	6	Biom	-20%
	Cons/biom	6	Biom	-50%
	EE	6	Biom	-20%
10	Prod/biom	6	Biom	-50%
	Prod/biom	7	Biom	-50%
	EE	6	Biom	-50%
	EE	7	Biom	-50%
12	Prod/biom	14	Biom	-50%
	EE	14	Biom	-50%
13	Prod/biom	5	Biom	-30%
	Cons/biom	5	Biom	-40%
	EE	5	Biom	-30%
17	Prod/biom	10	Biom	-40%
	EE	10	Biom	-40%
18	Biom	8	EE	-50%
	Biom	10	Biom	-50%
	Biom	17	Biom	-50%
	Biom	19	EE	-50%
	Cons/biom	8	EE	-50%
	Cons/biom	10	Biom	-50%
	Cons/biom	17	Biom	-50%
	Cons/biom	19	EE	-50%
20	Prod/biom	7	Biom	-50%
	EE	7	Biom	-50%
25	Biom	23	EE	-50%
25	Cons/biom	23	EE	-50%

Table B.9: Results of sensitivity analysis of the 1900 northern Benguela model, showing inputs that had a strong influence and the parameters affected.

Group	Input parameter	Sensitive Group	Estimated parameter	% change in input
2	P/B	1	Q/B	-40%
	Q/B	1	Q/B	50%
	EE	1	Q/B	-40%
3	P/B	1	Q/B	-40%
	P/B	2	B	-30%
	Q/B	2	B	-50%
	EE	1	Q/B	-40%
	EE	2	B	-30%
4	P/B	1	Q/B	-50%
	P/B	2	B	-50%
	P/B	3	B	-50%
	EE	1	Q/B	-50%
	EE	2	B	-50%
	EE	3	B	-50%
7	P/B	6	B	-30%
	Q/B	6	B	50%
	EE	6	B	-30%
10	P/B	6	B	-50%
	EE	6	B	-50%
12	P/B	14	B	-50%
	EE	14	B	-50%
13	P/B	5	B	-30%
	Q/B	5	B	-50%
	EE	5	B	-30%
17	P/B	10	B	-50%
	EE	10	B	-50%
18	B	8	EE	±50%
	B	14	B	±50%
	B	15	B	±50%
	B	17	B	±50%
	B	19	EE	±50%
	Q/B	8	EE	±50%
	Q/B	14	B	±50%
	Q/B	15	B	±50%
	Q/B	17	B	±50%
	Q/B	19	EE	±50%
20	P/B	7	B	±50%
	EE	7	B	±50%

Table B.10: Results of sensitivity analysis of the 1970 northern Benguela model, showing inputs that had a strong influence and the parameters affected.

Group	Input parameter	Sensitive Group	Estimated parameter	% change in input
2	P/B	1	Q/B	-40%
	Q/B	1	Q/B	50%
	EE	1	Q/B	-40%
3	P/B	1	Q/B	-40%
	P/B	2	B	-30%
	Q/B	1	Q/B	±50%
	Q/B	2	B	±50%
	EE	1	Q/B	-40%
	EE	2	B	-30%
4	P/B	1	Q/B	-50%
	P/B	2	B	-50%
	P/B	3	B	-50%
	EE	1	Q/B	-50%
	EE	2	B	-50%
	EE	3	B	-50%
7	P/B	6	B	-40%
	Q/B	6	B	50%
	EE	6	B	-40%
10	P/B	6	B	-40%
	P/B	7	B	-40%
	Q/B	6	B	50%
	EE	6	B	-40%
	EE	7	B	-40%
12	P/B	14	B	-40%
	EE	14	B	-40%
13	P/B	5	B	-30%
	Q/B	5	B	±40%
	EE	5	B	±40%
18	B	17	B	±50%
	Q/B	17	B	±50%
20	P/B	12	B	-50%
	EE	12	B	-50%
25	B	23	EE	±40%
	Q/B	23	EE	±40%

Table B.11: Results of sensitivity analysis of the 1990 northern Benguela model, showing inputs that had a strong influence and the parameters affected.

Group	Input parameter	Sensitive Group	Estimated parameter	% change in input
2	P/B	1	Q/B	-30%
	Q/B	1	Q/B	40%
	EE	1	Q/B	-30%
3	P/B	1	Q/B	-40%
	P/B	2	B	-30%
	Q/B	1	Q/B	±50%
	Q/B	2	B	-40%
	EE	1	Q/B	-40%
	EE	2	B	-30%
4	P/B	1	Q/B	-50%
	P/B	3	B	-50%
	EE	1	Q/B	-50%
	EE	3	B	-50%
10	P/B	6	B	-30%
	P/B	7	B	-40%
	P/B	13	B	-50%
	Q/B	6	B	±50%
	Q/B	7	B	50%
	EE	6	B	-30%
	EE	7	B	-40%
	EE	13	B	-50%
12	P/B	14	B	-50%
	EE	14	B	-50%
17	P/B	10	B	-50%
	EE	10	B	-20%
20	P/B	12	B	-50%
	EE	7	B	-50%
	EE	12	B	-50%
25	B	23	EE	±40%
	Q/B	23	EE	±40%

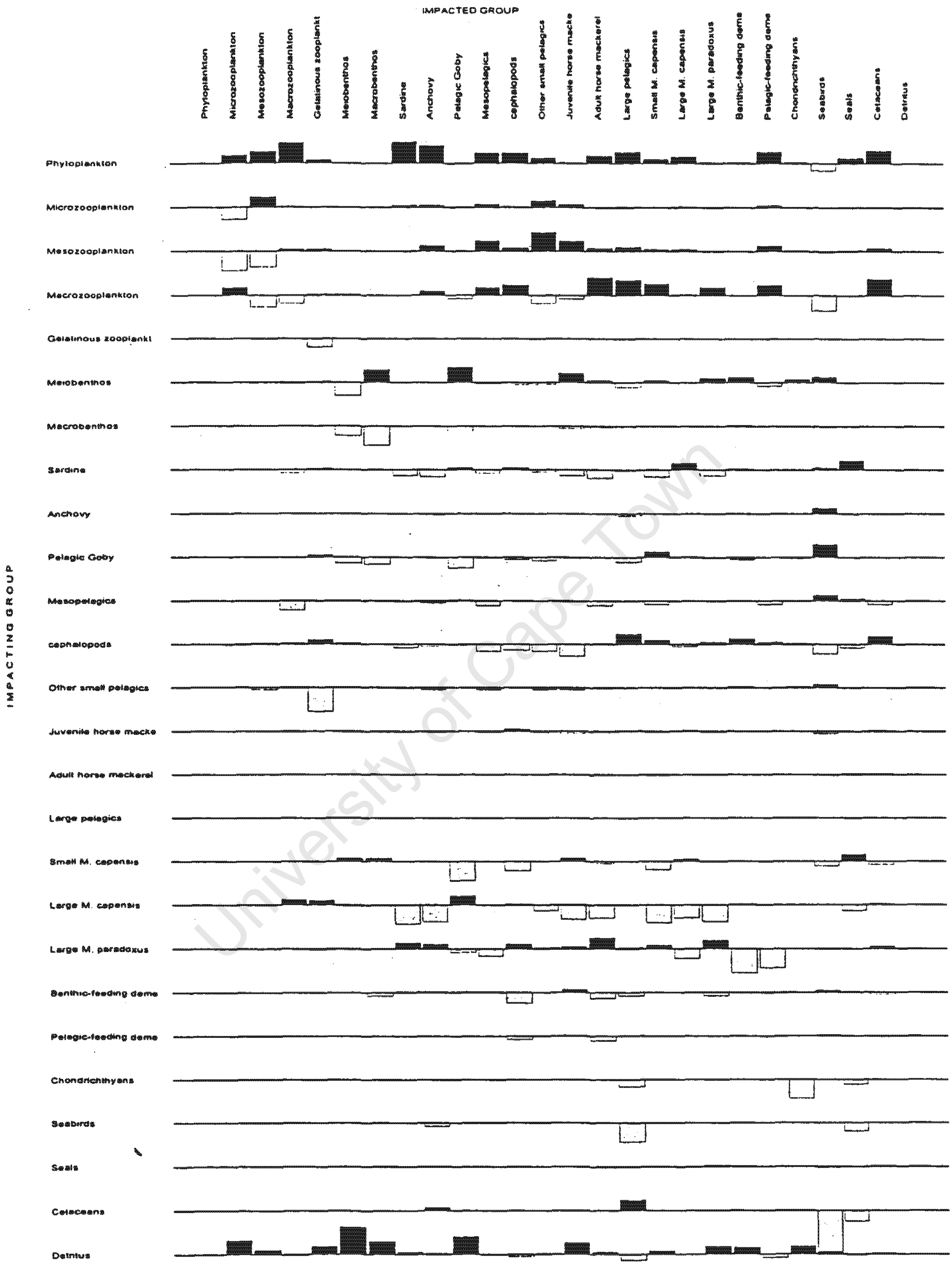

Figure B.1: Mixed trophic impacts in the 1600 northern Benguela model.

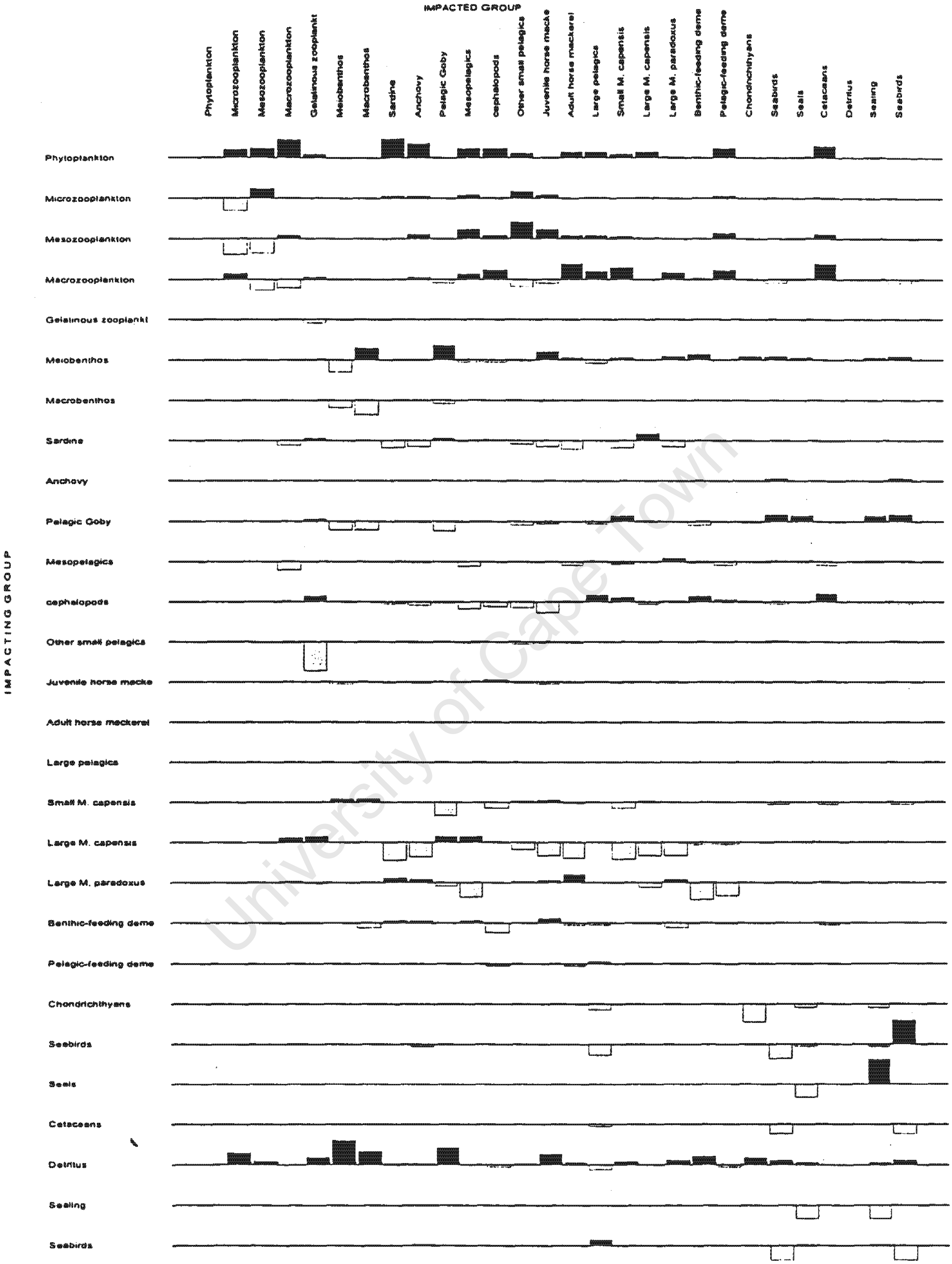

Figure B.2: Mixed trophic impacts in the 1900 northern Benguela model.

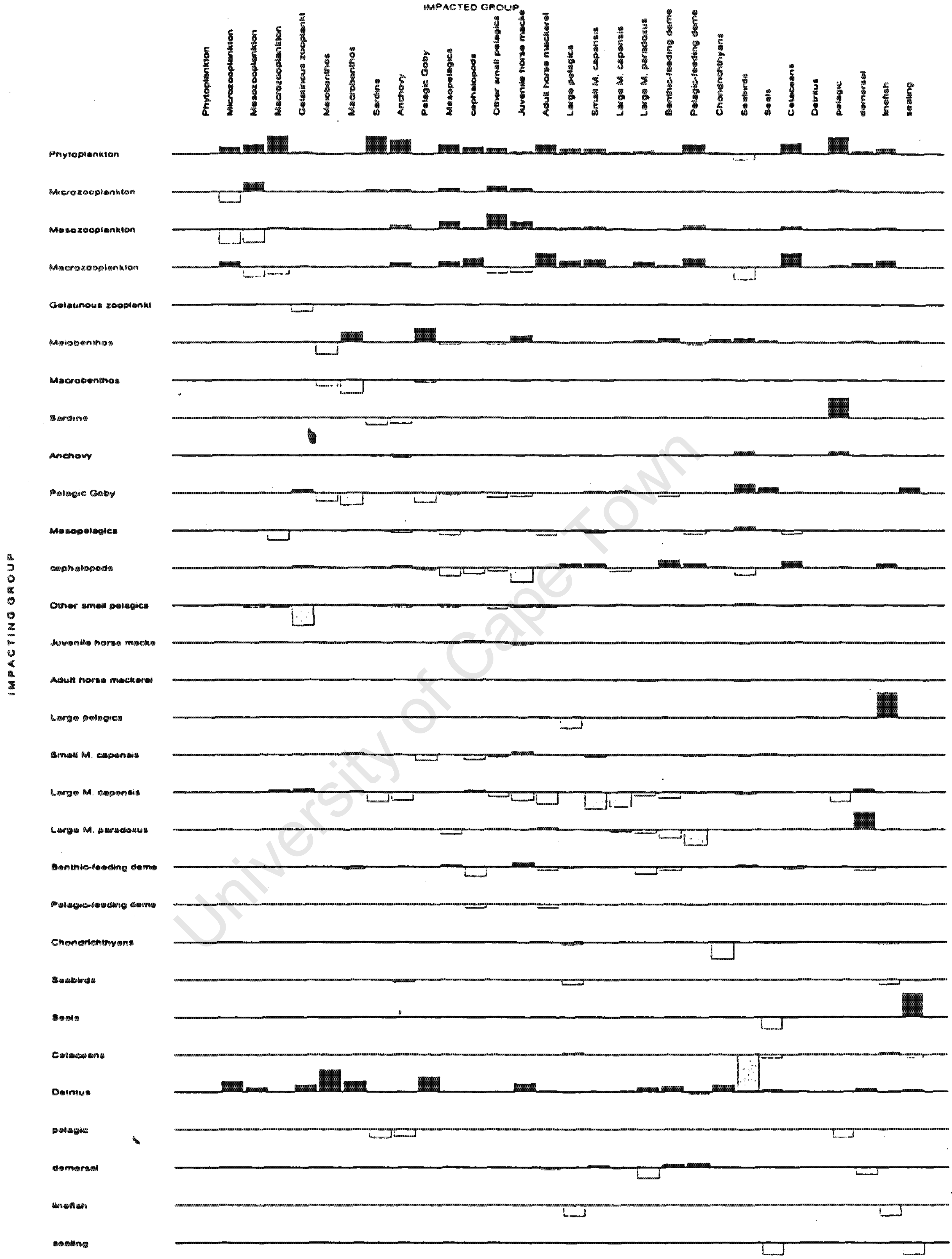

Figure B.3: Mixed trophic impacts in the 1970 northern Benguela model.

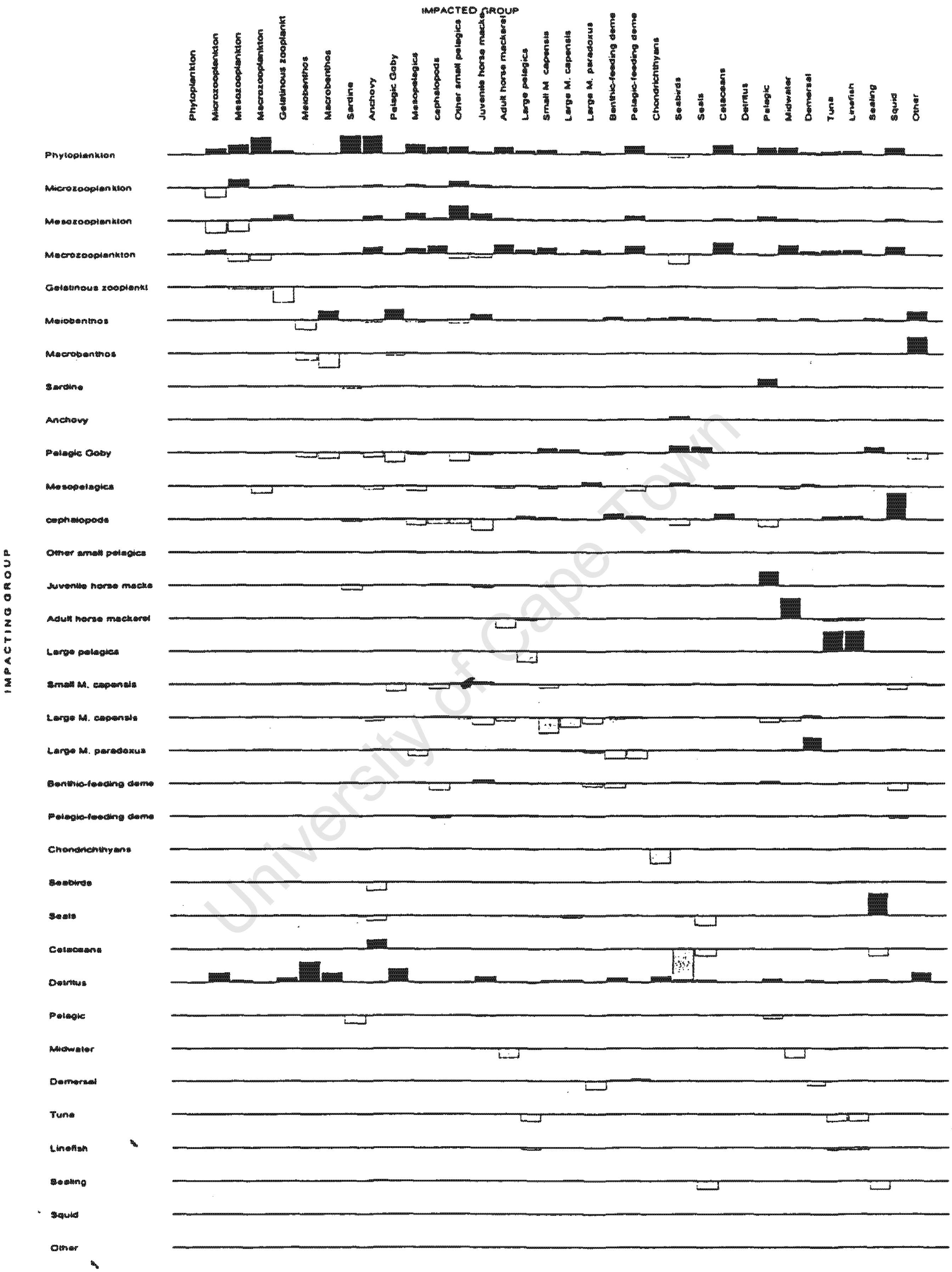

Figure B.4: Mixed trophic impacts in the 1990s model of the northern Benguela.

Appendix C

Tabulated sources of input data for a) southern and b) northern Benguela models

Table C1: Input parameters and sources for southern Benguela models

Group	Parameter	Value	Source
Phytoplankton	B	76.396	Shannon *et al.*, 2004b
	P/B	154.4	Shannon *et al.* (2003); Brown et al. (1991)
Benthic producers	P/B	15	Jarre-Teichmann *et al.*, 1998).
Microzooplankton	P/B	482	Jarre-Teichmann *et al.*, 1998).
	Q/B	1928	Jarre-Teichmann *et al.*, 1998).
Mesozooplankton	P/B	40	Shannon *et al.* (2003)
	Q/B	133.33	Shannon *et al.* (2003)
Macrozooplankton	P/B	13	Jarre-Teichmann *et al.*, 1998).
	Q/B	31.707	Jarre-Teichmann *et al.*, 1998).
Gelatinous	B	5	Shannon et al., 2004b
zooplankton	P/B	0.584	Shannon *et al.* (2003)
	Q/B	1.669	Shannon *et al.* (2003)
Anchovy	P/B	1.4	Armstrong *et al.* (1991)
	Q/B	14.4	Hewitson & Cruikshank (1993)
Sardine	B 1960	7.340909	Schwartzlose *et al.*, 1999
	P/B	1.2	Shannon *et al.*, 2004b
	Q/B	12.371	Shannon *et al.*, 2004b
	Catch 1960	1.445455	Schwartzlose *et al.*, 1999
Redeye	P/B	1.3	Shannon *et al.*, 2004b
	Q/B	13	Shannon *et al.*, 2004b
	Catch 1960	0.000455	Crawford *et al.*, 1987
Other small pelagics	P/B	1	Jarre-Teichmann *et al.*, 1998).
	Q/B	10	Jarre-Teichmann *et al.*, 1998).
Chub mackerel	P/B	0.8	Shannon *et al.*, 2004b
	Q/B	8	Shannon *et al.*, 2004b
	Catch 1960	0.132273	www.fao.org
Juvenile horse mackerel	P/B	1.2	Shannon *et al.*, 2004b
	Q/B	12	Shannon *et al.*, 2004b
Adult horse mackerel	B 1960	1.045455	Crawford, 1989
	P/B	1.5	Shannon *et al.*, 2004b
	Q/B	10	Shannon *et al.*, 2004b
	Catch 1960	0.287859	Johnston & Butterworth, 2001
Mesopelagics	P/B	1.2	Jarre-Teichmann *et al.*, 1998).
	Q/B	12	Jarre-Teichmann *et al.*, 1998).
Snoek	P/B	0.5	Jarre-Teichmann *et al.*, 1998).
	Q/B	5	Jarre-Teichmann *et al.*, 1998).
	Catch 1960	0.046818	www.fao.org
Other large pelagics	P/B	0.493	Shannon *et al.*, 2004b
	Q/B	4.93	Shannon *et al.*, 2004b
	Catch 1900	0.017175	Crawford et al., 1987; Griffiths et al., 2004
	Catch 1960	0.025679	Crawford et al., 1987; Griffiths et al., 2005
Cephalopods	P/B	3.5	Shannon *et al.* (2003)
	Q/B	10	Shannon *et al.* (2003)
	Catch 1960	0.000455	www.fao.org
Small M. capensis	P/B	2.5	Shannon *et al.*, 2004b
	Q/B	16.666	Shannon *et al.*, 2004b

Appendix C

Tabulated sources of input data for a) southern and b) northern Benguela models

Table C1: Input parameters and sources for southern Benguela models

Group	Parameter	Value	Source
Phytoplankton	B	76.396	Shannon *et al.*, 2004b
	P/B	154.4	Shannon *et al.* (2003); Brown et al. (1991)
Benthic producers	P/B	15	Jarre-Teichmann *et al.*, 1998).
Microzooplankton	P/B	482	Jarre-Teichmann *et al.*, 1998).
	Q/B	1928	Jarre-Teichmann *et al.*, 1998).
Mesozooplankton	P/B	40	Shannon *et al.* (2003)
	Q/B	133.33	Shannon *et al.* (2003)
Macrozooplankton	P/B	13	Jarre-Teichmann *et al.*, 1998).
	Q/B	31.707	Jarre-Teichmann *et al.*, 1998).
Gelatinous	B	5	Shannon et al., 2004b
zooplankton	P/B	0.584	Shannon *et al.* (2003)
	Q/B	1.669	Shannon *et al.* (2003)
Anchovy	P/B	1.4	Armstrong *et al.* (1991)
	Q/B	14.4	Hewitson & Cruikshank (1993)
Sardine	B 1960	7.340909	Schwartzlose *et al.*, 1999
	P/B	1.2	Shannon *et al.*, 2004b
	Q/B	12.371	Shannon *et al.*, 2004b
	Catch 1960	1.445455	Schwartzlose *et al.*, 1999
Redeye	P/B	1.3	Shannon *et al.*, 2004b
	Q/B	13	Shannon *et al.*, 2004b
	Catch 1960	0.000455	Crawford *et al.*, 1987
Other small pelagics	P/B	1	Jarre-Teichmann *et al.*, 1998).
	Q/B	10	Jarre-Teichmann *et al.*, 1998).
Chub mackerel	P/B	0.8	Shannon *et al.*, 2004b
	Q/B	8	Shannon *et al.*, 2004b
	Catch 1960	0.132273	www.fao.org
Juvenile horse mackerel	P/B	1.2	Shannon *et al.*, 2004b
	Q/B	12	Shannon *et al.*, 2004b
Adult horse mackerel	B 1960	1.045455	Crawford, 1989
	P/B	1.5	Shannon *et al.*, 2004b
	Q/B	10	Shannon *et al.*, 2004b
	Catch 1960	0.287859	Johnston & Butterworth, 2001
Mesopelagics	P/B	1.2	Jarre-Teichmann *et al.*, 1998).
	Q/B	12	Jarre-Teichmann *et al.*, 1998).
Snoek	P/B	0.5	Jarre-Teichmann *et al.*, 1998).
	Q/B	5	Jarre-Teichmann *et al.*, 1998).
	Catch 1960	0.046818	www.fao.org
Other large pelagics	P/B	0.493	Shannon *et al.*, 2004b
	Q/B	4.93	Shannon *et al.*, 2004b
	Catch 1900	0.017175	Crawford et al., 1987; Griffiths et al., 2004
	Catch 1960	0.025679	Crawford et al., 1987; Griffiths et al., 2005
Cephalopods	P/B	3.5	Shannon *et al.* (2003)
	Q/B	10	Shannon *et al.* (2003)
	Catch 1960	0.000455	www.fao.org
Small M. capensis	P/B	2.5	Shannon *et al.*, 2004b
	Q/B	16.666	Shannon *et al.*, 2004b

Large M. capensis	B 1960	1.016	Rademeyer & Butterworth, 2001
	P/B	0.8	Shannon *et al.*, 2004b
	Q/B	4.4	Shannon *et al.*, 2004b
	Catch 1960	0.182	Geromont *et al.*, 2000
Small M. paradoxus	P/B	2.5	Shannon *et al.*, 2004b
	Q/B	16.666	Shannon *et al.*, 2004b
Large M. paradoxus	B 1960	1.432	Rademeyer & Butterworth, 2001
	P/B	0.8	Shannon *et al.*, 2004b
	Q/B	4.7	Shannon *et al.*, 2004b
	Catch 1960	0.545	Geromont *et al.*, 2000
Pelagic-feeding demersals	P/B	0.7	Shannon *et al.*, 2004b
	Q/B	3.5	Shannon *et al.*, 2004b
Benthic-feeding demersals	P/B	0.7	Shannon *et al.*, 2004b
	Q/B	3.5	Shannon *et al.*, 2004b
	Catch 1960	0.026	Crawford *et al.*, 1987; www.fao.org
Pelagic-feeding	P/B	0.5	Shannon *et al.*, 2004b
chondrichthyans	Q/B	4.545	Shannon *et al.*, 2004b
	Catch 1960	0.002	www.fao.org
Benthic-feeding	P/B	1	Shannon *et al.*, 2004b
chondrichthyans	Q/B	10	Shannon *et al.*, 2004b
	Catch 1960	0.007	www.fao.org
Apex chondrichthyans	B	0.045	Shannon *et al.*, 2004b
	P/B	0.5	Shannon *et al.*, 2004b
	Q/B	5	Shannon *et al.*, 2004b
Seals	B 1960	0.133	Best *et al.*, 1997
	B 1960	0.0076	Best *et al.*, 1997
	B 1960	0.046	Best *et al.*, 1997
	P/B	0.25	Shannon *et al.*, 2004b
	Q/B	19.306	Shannon *et al.*, 2004b
Cetaceans	B	0.125	Shannon *et al.*, 2004b
	P/B	0.15	Shannon *et al.*, 2004b
	Q/B	10	Shannon *et al.*, 2004b
Seabirds	B 1600	0.035	Crawford *et al*, 1991, Shannon *et al.*, 2003
	B 1900	0.036	Crawford *et al*, 1991, Shannon *et al.*, 2003
	B 1960	0.017	Crawford *et al*, 1991, Shannon *et al.*, 2003
	P/B	0.123	Shannon *et al.*, 2004b
	Q/B	123	Shannon *et al.*, 2004b
Meiobenthos	P/B	4	Shannon *et al.*, 2004b
	Q/B	33	Shannon *et al.*, 2004b
Macrobenthos	P/B	1.2	Shannon *et al.*, 2004b
	Q/B	10	Shannon *et al.*, 2004b

Table C2: Input parameters and sources for northern Benguela models

Group	Parameter	Value	Source
Phytoplankton	B 1970	214.29	Jarre-Teichmann *et al.*, 1998
	B 1600/1900	207.2	Jarre-Teichmann *et al.*, 1998; Shannon & Jarre-Teichmann,1999;
			Roux & Shannon, 2004
	P/B	35.7	Shannon & Jarre-Teichmann, 1999
Microzooplankton	P/B	482	Shannon, 2001
	Q/B	1928	Roux & Shannon, 2004
Mesozooplankton	P/B	40	Hutchings *et al.*, 1991
	Q/B	133.333	Shannon & Jarre-Teichmann, 1999
Macrozooplankton	P/B	13	Hutchings *et al.*, 1991
	Q/B	31.707	Shannon & Jarre-Teichmann, 1999
Gelatinous zooplankton	P/B	0.44	Shannon, 2001
	Q/B	1.467	Roux & Shannon, 2004
Meiobenthos	P/B	8	Roux & Shannon, 2004
	Q/B	33	Roux & Shannon, 2004
Macrobenthos	P/B	1.2	Roux & Shannon, 2004
	Q/B	10	Roux & Shannon, 2004
Sardine	B 1970	8.184	Boyer & Hampton, 2001
	P/B	1.35	Roux & Shannon, 2004
	Q/B	14	Roux & Shannon, 2004
	Catch 1970	3.324022	Griffiths *et al.*, 2004
Anchovy	P/B	1.8	Roux & Shannon, 2004
	Q/B	18	Roux & Shannon, 2004
	Catch 1970	0.949721	Griffiths *et al.*, 2004
Pelagic Goby	P/B	1.8	Roux & Shannon, 2004
	Q/B	12	Roux & Shannon, 2004
Mesopelagics	P/B	1.23	Roux & Shannon, 2004
	Q/B	12.3	Roux & Shannon, 2004
Cephalopods	P/B	5	Roux & Shannon, 2004
	Q/B	15	Roux & Shannon, 2004
Other small pelagics	P/B	0.958	Roux & Shannon, 2004
	Q/B	9.349	Roux & Shannon, 2004
Juvenile horse mackerel	P/B	1.2	Roux & Shannon, 2004
	Q/B	10	Roux & Shannon, 2004
Adult horse mackerel	P/B	0.8	Roux & Shannon, 2004
	Q/B	5.333	Roux & Shannon, 2004
	Catch 1970	0.287151	Crawford *et al.*, 1987
Large pelagics	P/B	0.5	Roux & Shannon, 2004
	Q/B	5	Roux & Shannon, 2004
	Catch 1970	0.01095	Crawford *et al.*, 1987
Small M. capensis	P/B	2	Roux & Shannon, 2004
	Q/B	13.333	Roux & Shannon, 2004
Large M. capensis	B 1970	10.165	Rademeyer & Butterworth, 2001
	P/B	1.228	Roux & Shannon, 2004
	Q/B	7.824	Roux & Shannon, 2004
	Catch 1970	1.261	Geromont *et al.*, 2000
Large M. paradoxus	B 1970	5.718	Rademeyer & Butterworth, 2001

	P/B	1.14	Roux & Shannon, 2004
	Q/B	7.278	Roux & Shannon, 2004
	Catch 1970	2.243	Geromont *et al.*, 2000
Benthic-feeding demersals	P/B	1	Roux & Shannon, 2004
	Q/B	5	Roux & Shannon, 2004
	Catch 1970	0.009	Crawford *et al.*, 1987
Pelagic-feeding demersals	P/B	1	Roux & Shannon, 2004
	Q/B	5	Roux & Shannon, 2004
Chondrichthyans	B	0.36	Roux & Shannon, 2004
	P/B	0.5	Roux & Shannon, 2004
	Q/B	3.333	Roux & Shannon, 2004
Seabirds	B 1600	0.0177	Berruti, 1989; Crawford *et al.*, 1983; Underhill & Crawford, 2005
	B 1900	0.0177	Berruti, 1989; Crawford *et al.*, 1983; Underhill & Crawford, 2005
	B 1970	0.014	Berruti, 1989; Crawford *et al.*, 1983; Underhill & Crawford, 2005
	P/B	0.156	Roux & Shannon, 2004
	Q/B	120.3	Roux & Shannon, 2004
	Catch 1900	0.001	Best *et al.*, 1997
Seals	B 1600	0.253	Best *et al.*, 1997
	B 1900	0.00922	Best *et al.*, 1997
	B 1970	0.0908	Best *et al.*, 1997
	P/B	0.29	Roux & Shannon, 2004
	Q/B	18.25	Roux & Shannon, 2004
	Catch 1900	0.001	Griffiths *et al.*, 2004
	Catch 1970	0.009	Griffiths *et al.*, 2004
Cetaceans	B	0.019	Roux & Shannon, 2004
	P/B	0.15	Roux & Shannon, 2004
	Q/B	7.418	Roux & Shannon, 2004